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Author

Parsons, John K.

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Using unoccupied aerial vehicles to uncover patterns of density, size structure, and distribution of white sharks (*Carcharodon carcharias*) at a southern California coastal aggregation site

A Thesis submitted in partial satisfaction of the requirements

for the degree of Master of Science

in Ecology, Evolution, and Marine Biology

by

John K. Parsons

Committee in charge:

Professor Douglas McCauley, chair

Professor Deron Burkepile

Dr. Jenn Caselle, Adjunct Professor

Professor Christopher Lowe, California State University Long Beach

December 2022

The thesis of John K. Parsons is approved.

Deron Burkepile

Jenn Caselle

Christopher Lowe

Douglas McCauley, Committee Chair

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ABSTRACT

Using unoccupied aerial vehicles to uncover patterns of density, size structure, and distribution of white sharks (*Carcharodon carcharias*) at a southern California coastal aggregation site

by

John K. Parsons

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 adult white sharks. Unoccupied aerial vehicles (UAVs) are a promising tool for studying coastal shark aggregations, especially in instances where sharks' proximity to human activity has both conservation and public safety implications. In this study, we conducted UAV survey flights over a white shark (*Carcharodon carcharias*) aggregation site in Southern California from 2019 to 2021. We determined the density of observed individuals, their location within the aggregation site, and their body length using photogrammetry. We also determined how temporal and oceanographic factors affect white sharks at different developmental stages. We observed a year-over-year increase in the average density of white sharks. We also noted that the temporal pattern of density within each year was not consistent across years. White shark detections were much higher in the immediate inshore area of the surveyed aggregation site. The proportion of individuals ≥ 3m total length (TL) increased in 2021 relative to previous years, comprising 40% of observations - a prevalence of larger sharks higher than was previously observed at these sites.

White shark density was highly variable within and across years, and more sharks were observed at later hours of the day. Sharks < 3 m TL were observed more often during periods of colder water temperature, while the density of larger sharks did not appear to be affected by water temperature. Low visibility and higher tides reduced shark density, while chlorophyll-A levels, sea state, and swell height were not associated with density. Our study highlights the dynamically variable use of near-shore habitat by this top predator and suggests that juvenile white sharks may be more responsive to changes in oceanographic conditions, namely water temperature, than larger individuals. Understanding how temporal patterns and oceanographic predictors of density change over time, and as white sharks age, can help us better predict how this species uses coastal habitats and when they may be more likely to share space with humans and be more exposed to anthropogenic threats. We demonstrated that using UAVs to monitor white shark aggregations can produce useful insights which have both pure and applied value when attempting to better understand how these and other sharks utilize these especially dynamic coastal habitats.

Chapter 1: Characterizing the density, size-structure, and fine-scale distribution of white sharks (*Carcharodon carcharias*) at a southern California coastal aggregation site using two different UAV survey methods

Introduction

Unoccupied aerial vehicles (UAVs) are rapidly becoming more widespread in ecology. UAVs are cheaper and safer to operate than airplanes or helicopters, do not require advanced training to pilot, and are readily available for purchase at a low price point (Chabot & Bird 2015, Christie et al. 2016). In addition, the onboard GPS and video collection abilities of UAVs enables standardization of survey effort, and provides for a verifiable record of sightings of the species of interest (Hodgson et al. 2013, Christie et al. 2016). UAV technology has been implemented in a wide variety of wildlife survey applications, including abundance and distribution surveys of cervids and other large terrestrial mammals (Linchant et al. 2015, Christie et al. 2016, Mangewa et al. 2019).

UAVs have also been used successfully in a host of marine applications - especially in contexts where the focal species is in shallow water or spends significant time near the surface**.** UAVs have been used to determine sex ratios of loggerhead sea turtles (*Caretta caretta*, Schofield et al. 2017), take samples of respiratory vapor ("whale blow") from humpback whales (*Megaptera novaeangliae*, Pirotta et al. 2017), map ocean habitat (Ventura et al. 2018), and measure body condition of whales and pinnipeds (Christiansen et al. 2016, 2018; Krause et al. 2017). UAVs are especially effective in marine settings when the spatial extent of the study is a few square kilometers or less (Colefax et al. 2018, Hensel et al. 2018).

New insights into shark populations have also been enabled by UAVs, with a number of studies addressing questions about predation, social behavior, and detection probability (see review in Butcher et al. 2021). The application of new technology to shark research is crucial because almost one third of all shark species are threatened with extinction (Dulvy et al. 2021), potentially jeopardizing the top-down effects that sharks have on marine ecosystems (Stevens et al. 2000; Ferretti et al. 2010; Heithaus et al. 2010, 2012; Jorgensen et al. 2022). Large-bodied shark species inhabiting shallow waters, where they are exposed to fishing and habitat degradation, are especially vulnerable (Dulvy et al. 2014), but these same factors that put shark populations in jeopardy also make them more available to investigation via UAV. Coastal aggregations of pelagic sharks, for example hammerheads (*Sphyrnidae*), present an opportunity to study habitat use and behavior of otherwise cryptic species (Fortuna et al. 2013, Benavides et al. 2019, Doan and Kajiura 2020).

Aggregations of another large pelagic shark, the white shark (*Carcharodon carcharias*), have been the subject of few UAV-based surveys aiming to characterize temporal or spatial patterns of density and size structure (Colefax et al. 2020a). Applying UAV technology to the study of white sharks at aggregation sites may provide insight into their behavior and ecology, complementing recent studies using satellite and acoustic telemetry (White et al. 2019; Spaet et al. 2020; Anderson et al. 2021a, 2021b; Lee et al. 2021). These methods have yielded extremely valuable insight into migratory patterns and habitat use, especially over regional spatial scales. Satellite tags are sometimes limited by low spatial resolution (Costa et al. 2010). Acoustic detection systems can yield more precise spatial data, but only if multiple sensors are installed at the location of interest (Anderson et al. 2021a, 2022, Spurgeon et al. in review). Furthermore, studies relying on the tagging of individuals only yield data on a subset of the studied population, which may be non-randomly sampled (Anderson et al. 2021b, Lubitz et al. 2022).

In this study, we used UAV survey methods to perform counts and body length estimations of white sharks at an inshore aggregation site off the coast of Carpinteria, California (hereafter "Carpinteria aggregation site") from May 2019 to December 2021. This area is considered to be an aggregation site due to the consistent presence of multiple white sharks within one beach area over multiple consecutive days (Anderson et al. 2021a, 2022; Spurgeon et al. in review; P. Rex unpublished data). In addition to investigating the relative efficacy of two different UAV survey methodologies and the accuracy of length estimations, we characterized: 1) the density of observed sharks at the aggregation site; 2) the size structure of observed sharks; and 3) the spatial distribution of sharks in the near-coastal environment. This research provides insight into the spatial and temporal dynamics of a white shark aggregation site and helps to illuminate the strengths and weaknesses of using UAV methods in similar study contexts.

Methods

Study Site

UAV surveys at the Carpinteria aggregation site were flown from Santa Claus Beach (34°24'33"N 119°33'10"W) in Carpinteria, California. Carpinteria is located along the Southern California Bight (SCB), a nursery area for white sharks (Anderson et al. 2021a). The inshore marine environment in our study area consists of shallow sand bottom habitat < 10 m depth, with no observable rocky substrate or kelp forest habitat (**Figure 1**). Annual sea surface temperature in the study area ranges from 10 - 24 °C (Spurgeon et al., in review).

UAV Operations

Surveys were performed with a Mavic 2 Pro quadcopter (SZ DJI Technology Co., Shenzhen, China) with a 4k resolution camera that films at 30 frames per second (fps). The Mavic Pro 2 uses a barometric sensor to determine relative altitude (height above the takeoff location). Save for a polarizing filter over the camera lens, the UAV was otherwise unmodified. We used a non-modified, consumer-grade UAV with the goal of ensuring that all research outputs could be replicated more widely and that the methods presented could be adopted by other researchers and citizen scientists.

Survey Design

We surveyed the immediate inshore area, from the surf line outwards to a maximum distance of ~600 m from the mean high water line. We flew up to 1 km laterally along the coast to the northwest and southeast from our UAV takeoff location (GPS coordinates 34.4096, -

119.5533; **Figure 1**), following Federal Aviation Administration guidelines for maintaining visual contact with the UAV at all times.

In 2019, we flew three adjoining blocks of four transects parallel to the shore (hereafter, “transect survey”, **Figure 1A**). To ensure consistency and enable the UAV pilot to focus on monitoring the surrounding airspace, the UAV flew automatically along a flight path that was pre-programmed using Litchi autonomous flight software (VC Technology Ltd,). Transects were 510 meters long, with 25 meters between each parallel transect allowing for slight overlap of the field of view, for a search area of 0.17 km^2. The UAV was flown at a speed of 3.4 m/s and an altitude of 20 m above sea level (ASL), which limited the field of view compared to higher altitudes, but enabled higher detection probability of objects in the water and a greater ability to distinguish sharks from non-shark animals and objects. In order to position the innermost transect of each block just offshore of the surf line, we created three different versions of the transect survey at varying distances from the coastline (**Figure S1**). We chose the transect survey version before conducting the survey each day to match the tide and surf height at time of survey.

In order to increase survey efficiency, we modified our transect design for 2020 and 2021 (**Figure 1B**). During these years, the UAV flew two pre-programmed transects: a 1560 m long transect positioned just offshore of the surf zone (“inshore transect”) and a transect of similar length ~200 m farther offshore (“offshore transect”). During these transect surveys, the UAV was flown at an altitude of 40 m ASL and a speed of 5.6 m/s. The total area covered by the 2020/2021 transect survey was the same as the total area covered by the 2019 transect survey.

Beginning in 2020, we also introduced a “roaming survey” (**Figure 1C**), which consisted of one flight under direct control of the UAV pilot. Roaming surveys were introduced in order to compare the efficacy of automated vs human-piloted flights, and to enable the observation and collection of data from individual sharks at a lower altitude upon detection of each individual. During roaming surveys, the UAV pilot flew at an altitude of 40 m over the survey area (delineated by an overlay on the video monitor), attempting to cover as much area as possible during the flight. 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. Roaming surveys ended when the UAV battery was depleted, which occurred after ~20 minutes of flying. The mean search area of roaming surveys was 0.304 km2 (n = 238, SD = 0.134).

Shark abundance

For each day where survey flights were flown, we estimated the number of unique individual sharks observed within the roaming survey (“roaming count”) and the transect survey (“transect count”). We also estimated the number of unique individual sharks between the two survey types (“total count”). We identified unique individuals based on their location within the survey area, their size, and distinguishing characteristics including scarring and presence of previously applied telemetry tags. We used a Kruskall-Wallis test, with a Dunn test for multiple pairwise comparisons, to determine if observed shark density (total count standardized by survey area) varied across years. A Pearson's chi-squared test was used to compare daily presence probability (the likelihood of observing at least one shark during either survey flight) across the three years of the study.

We compared the efficacy of the roaming and transect survey methods using a Wilcoxon signed-rank test, where roaming and transect counts were paired within each day. We ran this test on counts, density (count/km^2), and rate (count/min). All statistical analyses were performed in R (R Core Team, 2022) using RStudio (RStudio Team, 2022). See Supplementary Methods for a description of survey area and duration calculations.

Size Structure

Over-land 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 at our study site to quantify and correct for measurement error (see Supplementary Methods). Analysis of length estimations from these field tests revealed that for a UAV altitude of 20 meters, the same altitude that was used for most length estimations of sharks, a combination of accounting for takeoff elevation and shark depth produced the most accurate length estimations using this UAV platform (**Figure S2**). Correcting for these two factors resulted in a mean length estimate of 193.6 ± 1.1 cm for the 197 cm target that we used in our field calibration test, or a mean error of 1.7%. Mean error for uncorrected length estimates, meanwhile, was 12.8%.

Due to the improvement in length estimation accuracy by accounting for target depth and takeoff elevation, we used this method for all shark length estimations. Takeoff elevation above sea level was taken from the UAV flight log. Shark depth was visually categorized from video data into three 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 midpoint 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 measurements of sharks estimated to be deeper than 3 m due to an inability to accurately identify the tail and snout positions at this depth.

Using 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; and 5) correcting for shark depth by multiplying the total length estimate by the proportion of the shark depth correction factor plus UAV altitude to the UAV altitude. This final step treats shark depth as an increase to the distance between the UAV and the shark. As a means of obtaining preliminary insight into the degree of variability in our measurements of shark length, we compared repeat measurements of one shark, identifiable by a distinct scarring pattern (**Figure S3**), which we observed on five separate occasions between June 17 and July 13, 2021.

Spatial Distribution

In order to determine how white sharks were distributed within the extent of the aggregation site that was surveyed, we compared counts of white sharks from the inshore transect to counts from the offshore transect. We used a Wilcoxon signed-rank test and paired the inshore and offshore counts within each day, thereby standardizing for daily variation in shark density and detectability. We used ANOVA to test if shark length differed between the inner and outer transects. We also compared the proportion of sharks in each transect between 2020 and 2021 using Pearson's chi-squared test. We classified visibility (as influenced by surface glare, sea state, and turbidity) from each transect video as "poor", "medium", or "high" and performed a chi-squared test to determine if our ability to detect sharks differed between the inshore and offshore transects.

Due to uncertainty in the accuracy of our measuring procedure, we grouped observations into two size classes (*sensu* Bruce & Bradford 2012): "small" (< 3 m TL) and "large" (≥ 3 m TL) sharks. These size classes are based on the body length at which prey shifts from primarily fish to marine mammals (Estrada et al. 2006, Hussey et al. 2012, Kim et al. 2012) We used Pearson's chi-square test to determine if the relative proportion of the two size classes changed across years.

Results

Overview of surveys

We conducted surveys on a total of 351 days between May 30, 2019, and December 18, 2021. 2019 field surveys were conducted between May 30 and December 6 (n = 98 days, average of 3.6 days surveyed per week). In 2020, surveys were conducted between June 24 and December 11 (n = 113 survey days, 4.7 per week). 2021 field surveys were conducted between April 20 and December 18 (n = 140 survey days, 4.0 per week). Transect surveys had an average search duration of 31.7 min (SD = 3.4) in 2019 and 10.5 min (SD = 1.0) in 2020 and 2021, due to the updated survey protocol. Roaming surveys, which were only conducted in 2020 and 2021, had a mean search duration of 12.2 min (SD = 3.5).

Shark abundance

We made 912 sightings of white sharks (**Figure 2**) that were identified as unique between the two survey methods ("total count", $\mu = 2.6$ sharks/survey day). 44 total sightings ($\mu = 0.45$) occurred in 2019, compared to 271 sightings ($\mu = 2.4$) in 2020 and 597 sightings ($\mu = 4.4$) in 2021. Observed density (**Figure 3**) increased each year ($\chi^2 = 88.245$, $p < 0.001$). Average observed density was 2.9 sharks/km² in 2019, 5.4 sharks/km² in 2020, and 14.5 sharks/km² in 2021 ($p < 0.001$ for all pairwise contrasts).

We sighted at least one shark between the two surveys (*i.e.*, total count ≥ 1) on 203 days (58% daily presence probability). Daily presence probability differed across years ($\chi^2 = 97.677$, $p < 0.001$), increasing from 17% in 2019 to 62% in 2020 and to 83% in 2021 ($p < 0.001$ for all pairwise contrasts). The maximum total count was 15, on August 4, 2021. The maximum total count in 2020 was 12, on October 29 of that year, and the maximum total count in 2019 was 6, on October 21. Of the 268 sightings where the presence or absence of a telemetry tag was able to be determined (representing 29.4% of the total sightings), 99 sightings (37.1%) were of untagged sharks.

Comparison of Methods

The mean count of white sharks in 2019 transect surveys was 0.45 (SD = 1.24). Mean transect count in 2020-2021 was 2.1 sharks (SD = 2.9), compared to a mean count of 2.3 in roaming surveys (**Figure 4)**. The median difference between roaming and transect counts in 2020 and 2021 was significantly greater than zero ($p < 0.01$, $n = 221$).

Observed shark density (*i.e.*, sharks/km²) across the 2020 and 2021 field seasons did not differ between the two survey methods ($p = 0.286$, $n = 221$). Mean observed density from roaming surveys in these two years was 11.9 sharks/km² (SD = 22.4), compared to a mean observed density from transect surveys of 12.1 sharks/km² (SD = 16.5). Shark observation rate (*i.e.*, sharks/minute) also did not differ between the two survey methods ($p = 0.123$, $n = 221$). Mean observation rate in the roaming surveys was 0.21 sharks/minute (SD = 0.25), compared to 0.20 sharks/min (SD = 0.28) in the 2020 and 2021 transect surveys.

Size structure

We were able to obtain corrected length estimates for 515 of the 919 observations (the majority of unsized sharks were observed only in the transect surveys, where the increased flight altitude often precluded determinations of depth and snout/tail location). Median estimated total length was 2.8 m (range 1.5 - 4.9 m). Repeated measurements ($n = 5$) of the single individual white shark observed on five separate days indicated an error from the mean of -10% to +11.4%, with a range of 90 cm between the lowest and highest length estimates.

Of the 515 observations where length measurements were made, 342 were classified as small individuals < 3 m TL (66.4%) and 173 were classified as large individuals ≥ 3 m TL. Large individuals were sighted on 101 of the 351 survey days (28.8%). In 2019, median TL was 2.8 m (range 1.7 - 3.4 m), in 2020, median TL was 2.7 m (range 1.8 - 4.9 m), and in 2021, median TL was 2.9 m (range 1.5 - 4.7 m). Size class distribution (**Figure 5**) varied across years ($\chi^2 = 10.792$, $p < 0.005$). 29.8% of observations in 2019 were of large sharks and 25.4% of observations in 2020 were of large sharks. In 2021, 39.8% of observations were of large sharks - a significant increase from the year before ($\chi^2 = 9.767$, $p < 0.005$).

Spatial Distribution

On average, we observed more sharks in the inshore transect (*i.e.*, within 50 m of the surf zone) than in the offshore transect located 200 m farther offshore ($p < 0.001$). Across 2020 and 2021, we observed a total of 480 sharks in the inshore transect (daily mean density= 29.4 sharks/km^2), compared to 61 (3.7 sharks/km^2) in the offshore transect. The proportion of sharks in the inshore transect increased from 83.0% in 2020 to 90.9% in 2021 ($\chi^2 = 5.86$, $p < 0.05$). Inner transects had poor visibility on 62.1% of surveys, compared to 38.7% on outer transect surveys ($\chi^2 = 25.308$, $p < 0.001$).

Discussion

The high density of white shark observations at the Carpinteria aggregation provides a valuable and unique opportunity to describe and compare key biological and ecological attributes of this aggregation, namely: how observed shark density varied over time, the size structure of this population, and the fine-scale spatial distribution of these sharks. Furthermore, this dataset permitted the opportunity to compare the performance of two different UAV survey methods.

Shark density

A number of metrics suggest increasing white shark abundance at the Carpinteria aggregation site. Average observed white shark density increased noticeably and significantly across the three years of this study, by a factor of 1.9 between 2019 to 2020, and again by a factor of 2.7

between 2020 and 2021. Daily presence probability also increased nearly five-fold from 2019 to 2021, with a corresponding increase in the maximum number of unique individuals observed in a single day. The increase in density that we observed over the three-year study period is consistent with observed increases in abundance by other researchers at the Carpinteria aggregation during this time (P. Rex & E. Spurgeon, personal communication), and with findings that white shark distribution within the larger Southern California Bight nursery area can be temporally variable (Weng et al. 2007, White et al. 2019, Anderson et al. 2021a). A host of mechanisms have been advanced to explain inter-annual variation in white shark spatial distribution within nursery areas, including temperature, primary productivity, and other oceanographic factors. However, no consensus has been reached as to which of these factors are the most important, and the mechanisms driving distribution may even differ across years (White et al. 2019, Spaet et al. 2020, Anderson et al. 2021a, Lee et al. 2021)

Temporal variability in abundance was also observed within each year, and interestingly, peak densities occurred at different times. In 2019, there was a single peak in density of ~15 sharks/km^2 in late October/early November, and observations tapered off sharply at the end of the field season. In 2020, density oscillated at around 5-10 sharks/km^2 for the majority of the field season (between August and December). Conversely, density in 2021 reached 15 sharks/km^2 between May and June, peaked again from July to September at ~20 sharks/km^2, and reached a nadir in October/November before rising towards the end of the field season in December.

While there are many advantages of UAV surveys, they also confer biases and shortcomings that must be taken into consideration when interpreting the present results. UAV surveys can only detect sharks at or near the surface, surveys may be influenced by factors influencing visibility above (*e.g.*, glare, sea state) and below the water (*e.g.,* turbidity), and once-daily surveys represent only a short snapshot of the population (Colefax et al. 2018; Butcher et al. 2019, 2021). Some of these factors are not dissimilar to issues that affect other shark survey techniques, such as underwater visual census (McCauley et al. 2012) or sighting sharks from a boat (Robbins 2007) or from land (Pyle et al. 1996, Weltz et al. 2013). These limitations are evidenced by the fact that UAV-based detections may not overlap with detections from other methods such as acoustic telemetry (Colefax et al. 2020a), and we expect for there to be differences between our UAV observation data and telemetry-based detections of tagged sharks at the Carpinteria aggregation site.

Future work may be able to help clarify some of these differences by comparing UAV survey data, including the numbers of tagged and untagged sharks, directly to contemporaneous telemetry data. For example, telemetry data at the Carpinteria aggregation suggested a sharp decline in the abundance of tagged sharks in November of 2020 (E. Spurgeon, unpublished data), which we did not observe in our study. This difference could be due to our surveys only covering part of the area within the acoustic array, or we could have been detecting untagged individuals which moved to the aggregation site around the same time as tagged individuals were leaving. At present, therefore, our estimates of density should not be viewed as an attempt to quantify the absolute abundance of sharks at the aggregation site at any one time. Rather, our results are indicative of trends in abundance within the UAV survey area, serve as a baseline for ongoing UAV surveys at the Carpinteria aggregation site, and may provide comparison to other aggregation sites where similar UAV studies could be conducted in the future.

While we are unaware of previous estimates of white shark density at aggregation sites, our white shark counts (*n.b.*, not accounting for area surveyed) are similar to counts from other UAV surveys at the Carpinteria aggregation site and others in the SCB (P. Rex, unpublished data) and with telemetry studies at the Carpinteria aggregation site (Spurgeon et al., in review) Along with white shark capture rates in the SCB (Lowe et al. 2012), these data support our finding that the Carpinteria aggregation site can be frequented by a dozen or more individual white sharks at any one time.

Investigations into the density of other shark species also provide a point of comparison to our findings. UAV surveys of blacktip sharks (*Carcharhinus limbatus*) have yielded density estimates as high as ~1300 sharks/km² at an aggregation site in Baja California, Mexico (Ayres et al. 2021) and as low as 1 shark/km² and 100 sharks/km² (at unprovisioned and provisioned sites, respectively) within a coral reef in the south Pacific (Kiszka et al. 2016). Estimates of shark density at Palmyra atoll, a location known for its high density of top-predator sharks (Stevenson et al. 2007), include 21.3 blacktip sharks/km² from capture-recapture models (Bradley et al. 2017) and 100 reef sharks/km² based on multiple concurrent underwater survey methods (McCauley et al. 2012). Densities between 50-250 sharks/km², depending on the habitat and degree of human interaction, have been observed in the southern Great Barrier Reef (Rizzari et al. 2014). Comparing densities of sharks between different survey methodologies is problematic given inherent biases in such methods (Ward-

Paige et al. 2010, McCauley et al. 2012), and therefore further research of white shark aggregations using UAVs is necessary to determine how the present results compare to densities at other locations.

Size Structure

We frequently observed sharks < 3 m total length at the Carpinteria aggregation site, consistent with studies of YOY and juvenile white shark distribution in the SCB nursery area (White et al. 2019, Anderson et al. 2021a) and supporting the identification of this area as a habitat for immature sharks. In addition, our median TL estimate across years (2.8 m) and our sightings of individuals ≥ 3 m TL on around one-quarter of days surveyed suggest that the Carpinteria aggregation site may be frequented by, on average, larger individuals compared to coastal areas in eastern Australia and in Monterey Bay, California (Colefax et al. 2020b, Tanaka et al. 2021). The apparent presence of larger sharks at this inshore region of the SCB nursery area also contrasts with the lack of larger individuals in the western North Atlantic nursery area (Curtis et al. 2014, Skomal et al. 2017), and with the fact that individuals ≥ 3 m are rarely observed during tagging operations at aggregation sites, including Carpinteria, within the SCB (C. Lowe, personal communication). We do, however, note that our study was unique with regard to the frequency of surveys conducted, therefore giving us a higher chance of detecting larger individuals, and we also conducted surveys later into the year compared to tagging operations. Furthermore, we were unable to determine the period of residency of sharks that we observed. It is likely that larger sharks were more transient and using the aggregation site habitat less on an individual basis than the smaller sharks we observed, which are known to exhibit periods of residency at aggregation sites within the SCB (Anderson et al. 2021a).

Given the surprising nature of our findings and the novelty of our photogrammetric approach, it is possible that our length estimations were biased towards overestimating shark length. Despite our field tests serving as a partial validation for our measurement approach, the range of size estimates from repeat measurements of one uniquely marked individual shark in the field revealed the limitations of using a consumer-grade UAV, with no modifications, for performing length estimates. These limitations, discussed at length in the Supplementary Material, introduced a degree of uncertainty into our determinations of a shark's length, and precludes the use of length data procured by our methods in calculations of length-to-girth ratios, body condition, or growth rates, which require more precise estimates (Tanaka et al. 2011, Natanson & Skomal 2015, Logan et al. 2018). A larger sample of repeated length estimations would be needed to determine more precisely the accuracy of our length measurement process.

As with density, size structure appeared to vary across years. We found that the proportion of sharks ≥ 3 m increased in 2021. Also, the largest shark observed in 2019 was estimated at 3.4 m TL, compared to maximum length estimates of over 4 m in 2021 and 2021. We emphasize that these observations do not suggest that the aggregation site is being used equally across size classes, as evidenced by the decrease in median TL in 2020 compared to 2019. As discussed above, we also acknowledge the potential for overestimates of shark length, but these relative increases in maximum and average length are nevertheless notable given that our sizing methodology was consistent across years. This apparent increase in larger sharks is, furthermore, consistent with the observed decrease in the proportion of sharks carrying tags, from 95% to 62%, as tagging studies in this region have primarily included smaller (*i.e.*, YOY and juvenile) individuals (White et al. 2019; Anderson et al. 2021a, 2021b, 2022; Spurgeon et al. in review). We may have observed sharks which were not included in these telemetry studies, namely larger sharks which may only be present at the aggregation site for a brief period as they move between other areas. If average shark length did, in fact, increase between 2020 and 2021, it may have be due to resident individuals growing larger, as the estimated 7.1% increase in mean TL that we observed between 2020 and 2021 is within the range of many estimates of yearly growth rates of white sharks (Cailliet et al. 1985, Tanaka et al. 2011, Natanson & Skomal 2015).

Spatial distribution

We observed almost eight times as many sharks within 50 m of the surf zone compared to ~200 m offshore. There are at least two explanations for this elevated observation rate closer to shore: 1) white sharks were more easily detected in the shallow inshore transect, and simply harder to observe when at depth in the offshore transects, or 2) the more inshore habitat was preferred by more sharks in this aggregation. While we cannot rule out the possibility that sharks were present on the offshore transect at depths too deep to be detected via UAV survey, we do note that the inshore area had comparatively worse visibility (twice as many days where visibility was classified as “poor”), due primarily to cresting waves and associated turbidity. Data on distributions of white sharks and other marine species at this fine spatial scale are limited, but some fish species do discriminate between nearshore habitats at this scale (Munsch et al. 2016). Fine-scale vertical migration patterns of white sharks, furthermore, are likely related to foraging activity (Weng et al. 2007, Domeier et al. 2012, White et al. 2019), so higher abundance of prey just outside of the surf zone could translate to the preference of white sharks for these areas as well.

Future investigation will be required to properly evaluate the mechanisms explaining the putative elevated density of white sharks in the inshore area of this aggregation site. Taken at face value, these patterns would suggest that sharks in this aggregation area are, coincidentally, selecting habitats that have them sharing more marine space with beachgoers. We were not able to distinguish differences in spatial distribution between size classes due to measurement error, but future studies may be able to determine if the potential safety risk posed by a high density of white sharks close to shore is mitigated by these sharks typically being smaller. From a methodological perspective, our UAV survey results would suggest that others wishing to assay or monitor white shark presence at similar aggregation site for management or research applications should consider prioritizing UAV survey effort in areas more proximate to the surf break.

Comparison of UAV Methods

There were no significant differences between the density or observation rate measures for white sharks between the roaming and transect UAV surveys. This finding was somewhat surprising given the differences between analogous visual underwater census methods used to survey fish (Murphy & Jenkins 2010, Beck et al. 2014, Rassweiler et al. 2020). This observed similarity would provisionally suggest that either method can be employed effectively to measure shark abundance at this location and under these conditions, and that choice of methodology can be tailored to the requirements of each study.

Each survey type confers strengths and weaknesses, with transect surveys providing consistency and roaming surveys allowing for more flexibility. In the context of shark research, a pre-programmed transect survey would be more appropriate for research where many different UAV pilots are collecting video data, or when surveys are being compared between multiple locations. The use of automated transect surveys in this context would ensure consistent survey effort and standardize other parameters such as flight speed and altitude, thereby reducing bias due to differences between UAV pilots. Citizen science initiatives can leverage these features and make use of the large base of UAV hobbyists to increase the scope of data collection (Pucino et al. 2021, Theuerkauf et al. 2022) and adapt, for example, to any shifts that may occur in white shark distribution (Tanaka et al. 2021). UAV surveys do have the potential to overestimate (*i.e.* re-count individuals) or underestimate shark density, not unlike methods for estimating fish density such as underwater visual census (Edgar et al. 2004, Harvey et al. 2004, MacNeil et al. 2008), so the same caution with which we addressed the above estimates of density must be applied to estimates from future studies until these biases are better understood and quantified.

Roaming surveys, which had a higher average search area, did have a significantly higher total count of white sharks than transect surveys on average. While counts unstandardized by time or area may not be informative for comparing densities between studies, as we have above, there may be contexts in which maximizing the number of individual sharks on a flight is beneficial. For example, surveys wishing to collect more individual-centric data on sharks to resight uniquely marked individuals (Anderson et al. 2011, Towner et al. 2013, Kanive et al. 2021) or obtain morphometric data (Colefax et al. 2020b, Whitehead et al. 2022) might benefit from utilization of roaming surveys. The result of our methodological comparison would suggest that these types of count data can potentially be collected via roaming survey without necessarily compromising the comparative value of density measures obtained.

Conclusion

Using a UAV, we observed an apparent year-over-year increase in white shark density at a nearshore aggregation site. Density also varied dynamically within years, and the pattern of that intra-annual variation was not consistent across years. The Carpinteria aggregation was composed mostly of juveniles, but the proportion of larger sharks may have increased in 2021. This possibility deserves closer attention given the paucity of observations elsewhere regarding temporal changes in the sharing of habitat across size classes for white sharks. We also observed distinct fine-scale partitioning within the aggregation site itself, with more observations of sharks in the nearshore transect.

Density measures did not vary between methods, potentially opening up more opportunities for flexible application of these methods under various research contexts including citizen science monitoring. While these results provide useful initial insight into the ecology of this aggregation, future work is needed to understand the mechanisms driving temporal and spatial variability at aggregation site. Our findings stand as further validation of the utility of UAVs for performing high frequency observation of shark populations and gathering data of value to marine scientists and coastal managers alike.

Figures

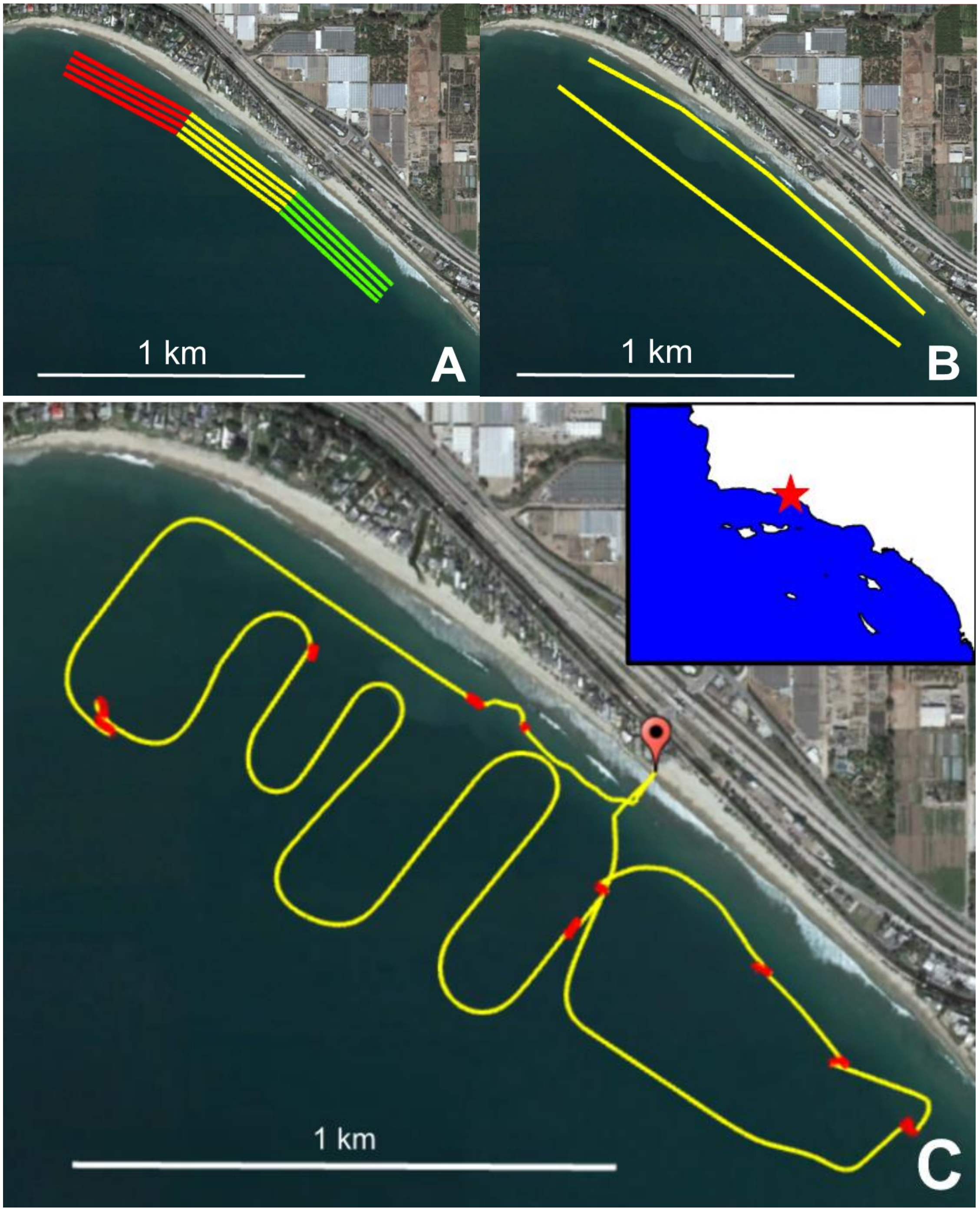

Figure 1. UAV flight paths for A) transect surveys conducted during the 2019 field season, B) transect surveys conducted during the 2020 and 2021 field seasons, and C) roaming surveys conducted during 2020 and 2021, with inset map showing the location of the Carpinteria aggregation site (red star) within the Southern California Bight. For 2019, the red, yellow, and green lines denote the three separate blocks of transects. 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 nine portions of the roaming survey flight path shown in red indicate where the UAV pilot observed a shark and lowered the altitude of the UAV, and the red marker indicates the typical takeoff/landing location. Maps produced in Google Earth, satellite image © 2022 TerraMetrics.

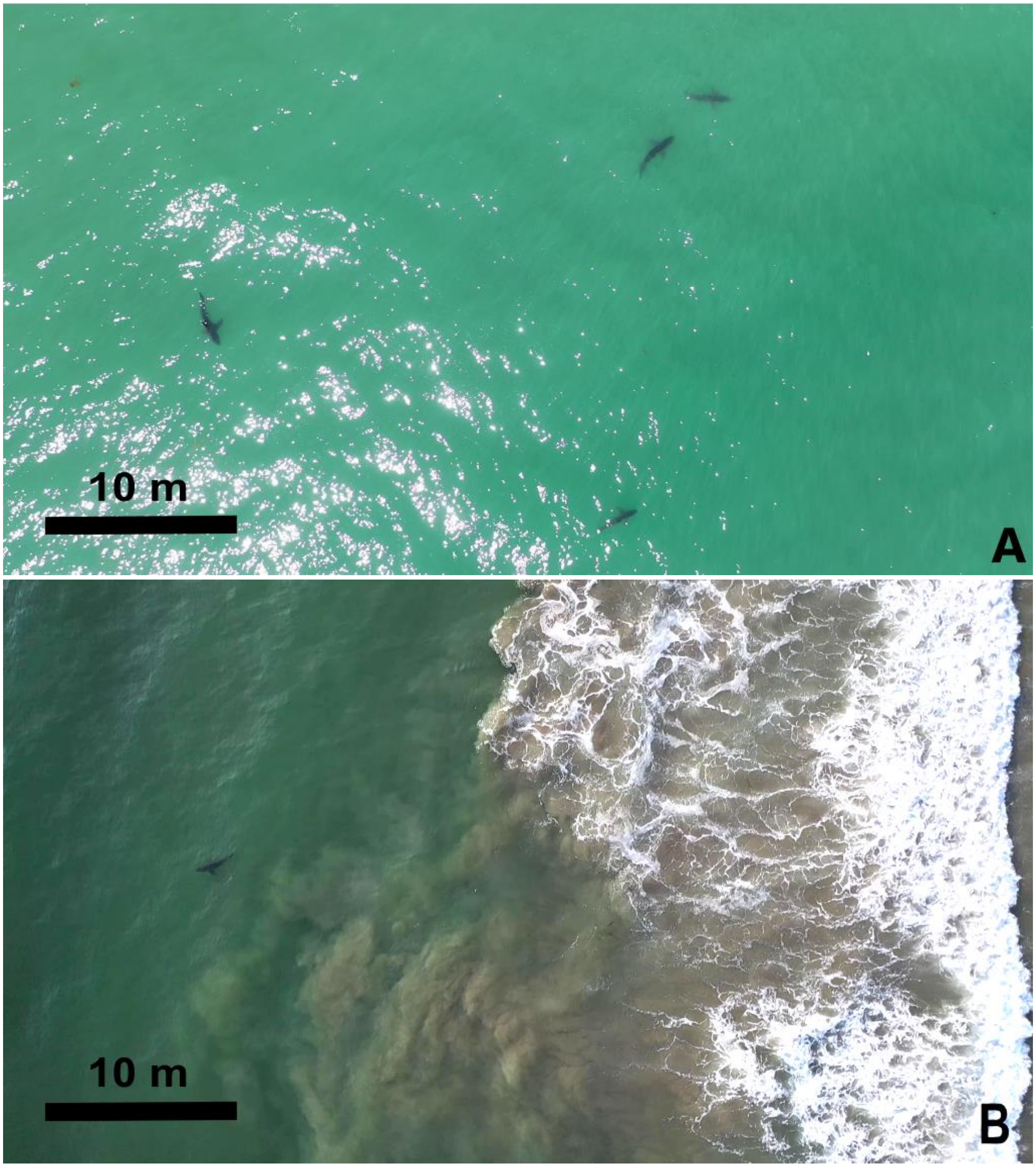

Figure 2. UAV images from the Carpinteria aggregation site of A) four white sharks in close proximity to one another and B) one white shark (center-left of frame) just outside of the surf zone, with the shore to the right of the frame.

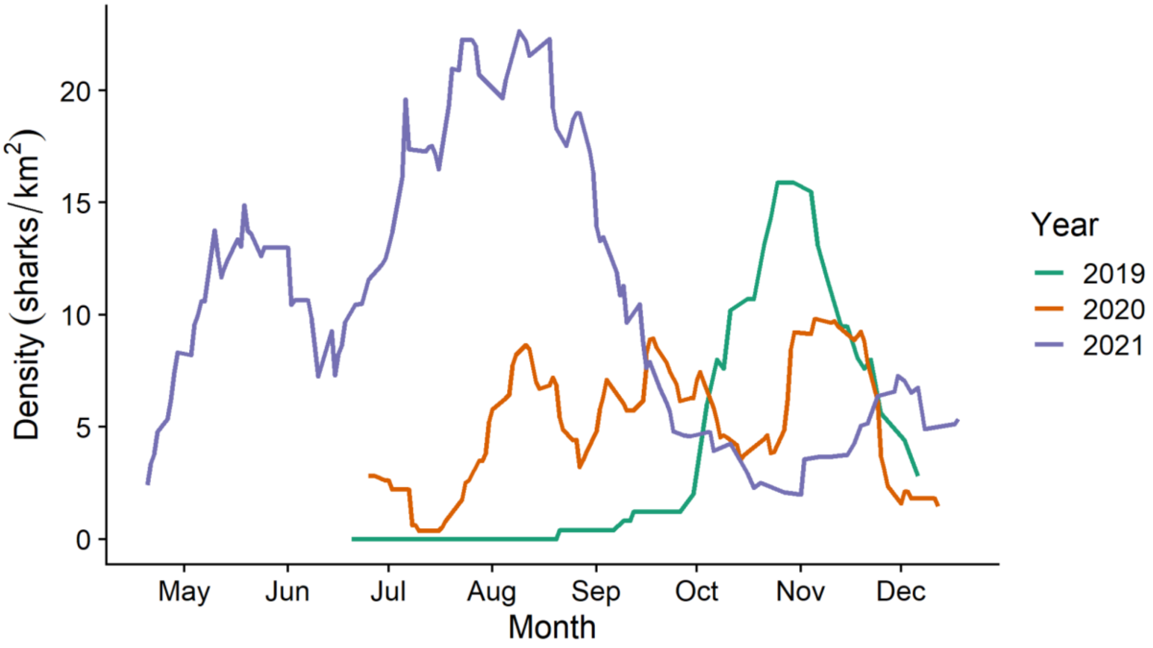

Figure 3. 14-day rolling mean of total white shark density (individuals that were identified as unique across the roaming and transect surveys, per km²) as observed via UAV in 2019 (n = 98 survey days), 2020 (n = 113), and 2021 (n = 140).

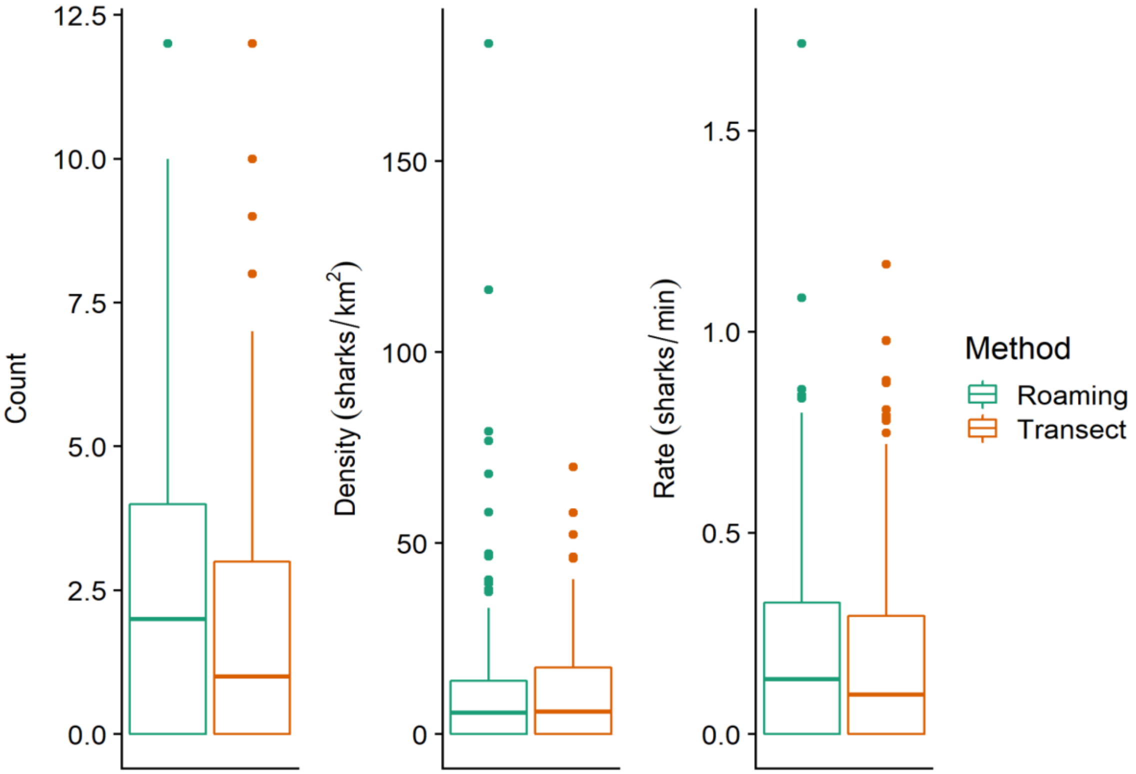

Figure 4. Comparison of shark count, density (count/km²), and rate (count/minute) between roaming and transect surveys (n = 221 for each metric/method combination). The median difference between roaming and transect counts from surveys conducted on the same day was significantly greater than zero (paired Wilcoxon signed-rank test, $p < 0.01$). There was no significant difference between roaming and transect surveys with regards to density or rate.

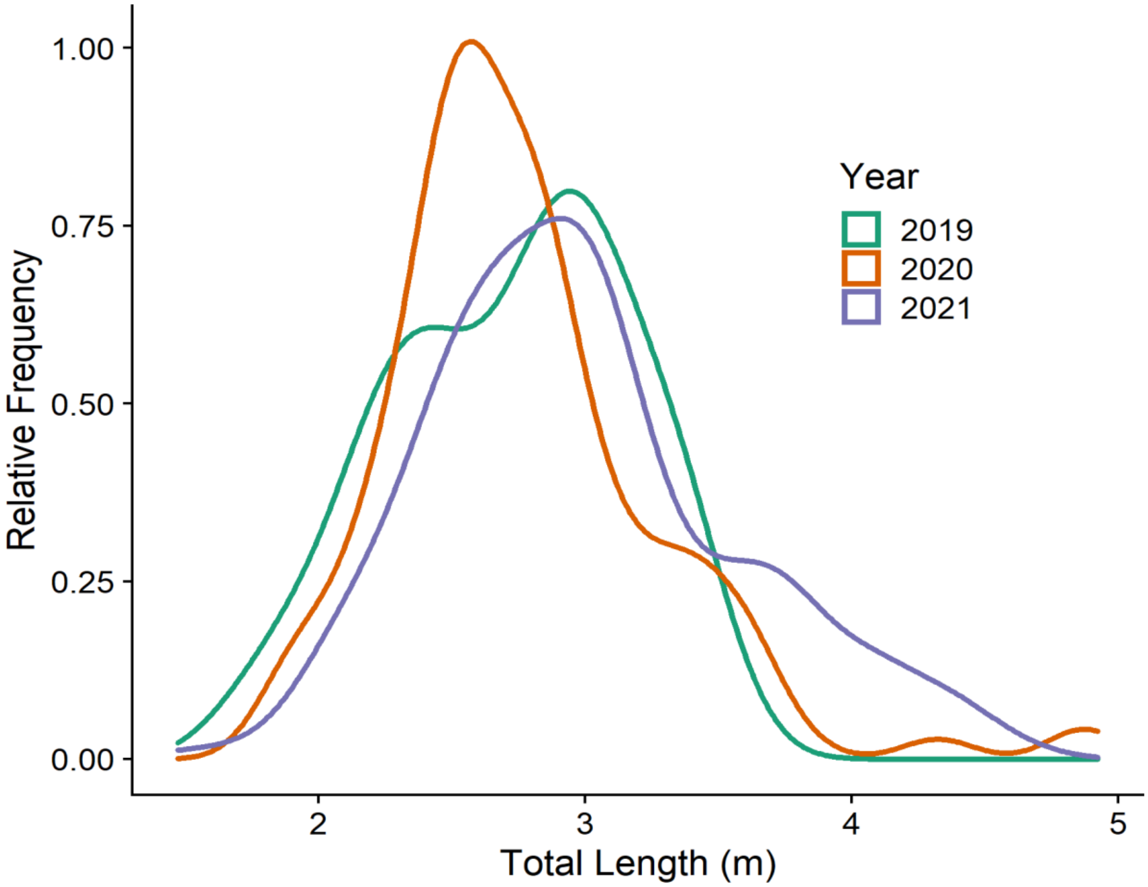

Figure 5. Frequency distribution of white shark total body length estimates, by year.

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Chapter 2: Temporal and oceanographic factors differentially affect two size classes of white shark at a Southern California aggregation site

Introduction

Many marine species demonstrate ontogenetic shifts in habitat use, driven by changes in physiology, predation pressure, and diet (Pittman and 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 1992, Baeza & Stotz 2001, 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 approximately one-third 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 2021a).

White sharks (*Carcharodon carcharias*) are a prime example of a large-bodied shark that exhibits ontogenetic shifts in its distribution and faces conservation threats (Rigby et al. 2022). Specifically, juvenile white sharks have been described to utilize 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 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). White shark nurseries meeting some or all of these criteria have been identified in the Southern California Bight (hereafter “SCB”, Weng et al. 2007, White et al. 2019, Anderson et al. 2021a); 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 different biotic and abiotic factors have been called upon to explain the abundance and distribution of juvenile and adult white sharks, with temperature often believed to be among the most important. 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 a transition to a diet more heavily comprised of marine mammals occurs at around 300 cm TL (Tricas & McCosker 1984, Estrada et al. 2006, Hussey et al. 2012, Kim et al. 2012). Chlorophyll-A, a proxy for primary productivity, has been shown to correlate positively with immature white shark detections in eastern Australia (Spaet et al. 2020, Lee et al. 2021).

In addition to creating nursery areas, age-specific habitat requirements cause white sharks to form aggregation sites with high densities of immature individuals within nursery areas (Anderson et al. 2021a, Spurgeon et al. unpublished data). Most research of white shark aggregations, however, has focused on larger individuals at foraging grounds outside of nursery areas (Domeier & Nasby-Lucas 2007, Robbins 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 correlates of density at aggregation sites within nursery areas are poorly understood. Because white sharks across a range of size classes have been observed at at least one aggregation site within the SCB (see Chapter 1), these sites provide a useful context for studying if and how environmental factors shape the local abundance of different white shark life stages. Uncovering the mechanisms which drive the formation of, and abundance at, these critical habitats is a key directive for white shark research (Huveneers et al. 2018).

Despite demonstrated correlations between the aforementioned factors 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. Spaet et al. (2020), for example, found that month, time of day, water temperature, tidal height, swell height, and lunar phase collectively explained only 1.8% of deviance in a model of white shark acoustic detections in eastern Australia. Temperature, while well-supported as a driver of basin-scale movement, may not be useful for predicting occupancy at individual locations: a study of high-density aggregation sites within the SCB nursery found that temperature influenced YOY density in only four of the nine years of the study, and that other variables such as chlorophyll-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 2021a, Jorgensen et al. 2022).

Unoccupied aerial vehicles (UAVs) can provide valuable complementary insights to traditional methods and technologies (*e.g.*, telemetry) for studying the factors that shape white shark abundance in these high-density aggregation habitats (see Chapter 1). Advantages conferred by UAVs include: they provide a snapshot view of the surface waters of an entire aggregation site (e.g., Ayres et al. 2021a); they can be used to track the abundance of tagged and untagged individuals (see Chapter 1); 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, disadvantages of UAVs for these applications are also many: they do not permit observation of sharks at depth, they cannot track individuals or populations for prolonged periods and over significant distances, and they often cannot aid with identification of specific individuals in a population. 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 also needed about the efficacy of UAV surveys as compared to other methods, as well as the oceanographic factors that may introduce bias or otherwise affect UAV-derived shark counts (Elphic 2008, Williams et al. 2017, Butcher et al. 2021). 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). Other survey methods have also shown that variables such as tidal height, swell height, water clarity, and time of day may be associated with white shark sightings and behavior (Pyle et al. 1996, Robbins 2007, Weltz et al. 2013, Papastamatiou et al. 2022), and the effect of these factors on UAV estimates of density should also be considered.

In this study, we analyzed a 3-year (2019-2021) dataset 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, chlorophyll-A, tide, swell height, visibility, sea state) factors on shark density estimates. We conducted equivalent modeling procedures on YOY/juvenile (< 3 m) and sub-adult/adult sharks (≥ 3m, *sensu* Bruce & Bradford 2012) independently, to explore whether the relationship between temporal and oceanographic factors and observed shark density was mediated by ontogeny.

Methods

White shark UAV surveys were conducted off the coast of Carpinteria, California, at the northwest extent of the SCB. Surveys took place over the immediate inshore area, covering around 2 km of coastline and extending up to 600 m from shore (~1.2 km^2). Sea surface temperatures are warmest in July and August (20-30 °C daily maximum), and are generally coldest from November to January when daily maximum SST can be below 15 °C, although similarly low temperatures were also observed in May of 2021 (Spurgeon et al., unpublished data).

UAV surveys at the Carpinteria aggregation site were conducted between May 30 and December 6 in 2019, June 24 and December 11 in 2020, and April 20 and December 18 in 2021. Two UAV surveys were performed each day that surveys were conducted, one an automated survey with an inshore and offshore flight path (similar to a belt transect), and the other manually operated by the UAV pilot in a “roving” manner. We compared the video record from each survey to determine the number of unique sharks that were sighted between the two surveys, based on body length, distinguishing features such as scarring, and whether a previously-sighted shark could have moved to the location of a subsequent sighting. This count of unique sharks observed on a daily basis is hereafter referred to as “daily unique shark count”. A comprehensive description of survey flights and the photogrammetric measurement procedure can be found in Chapter 1.

Modeling shark density

We constructed generalized additive models (GAMs) to determine the association between temporal and oceanographic variables (**Table 1**) and the density of observed white sharks. GAMs were constructed 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 count (hereafter “overall model”), the subset of sharks included in the daily unique shark count that were less than 3 m TL (hereafter “small shark” model), and the subset of unique sharks included in the daily unique shark count that were 3 m TL or longer (hereafter “large shark” model). We used both SFT data, which was available for all three years, and SST data, which was only available in 2020 and 2021, giving us a total of 6 GAMs. In order to model density (daily unique shark count per unit area surveyed), survey area was included as an offset term. The overall models were included to determine if a larger sample size would significantly change the patterns of density compared to the small shark and large shark models.

We used restricted maximum likelihood (REML) smoothing parameter estimation, with a negative binomial family distribution due to overdispersion. Rather than performing backwards 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 and Wood 2011). Knots for each smooth function were set at 10 to avoid overfitting (Anderson et al. 2021a).

Smooth functions for oceanographic variables included sea surface temperature (SST), averaged across two sensor locations at the Carpinteria aggregation site in 2020 and seven locations in 2021, along with sea floor temperature (SFT), averaged across five locations in 2019 and seven locations in 2020 and 2021 (E. Spurgeon, in review); satellite-derived chlorophyll-A levels, averaged across the three most proximal 0.0125° grid cells (coastwatch.noaa.gov); tidal height from the nearest NOAA tide station ~12 km to the west (tidesandcurrents.noaa.gov Station 9411340); and swell height from the nearest offshore

NOAA swell buoy ~31 km to the southwest (ndbc.noaa.gov Station 46053). We used hourly averages 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. These variables were included in the GAM as parametric terms. Due to few survey days at the extremes of each scale, we binned sea state into two levels (0-1 and 2+) and visibility into three levels: 1-2 ("low"), 3 ("medium"), and 4-5 ("high").

We accounted for seasonality using a continuous "day of year" smoothing spline, rather than a categorical "season" (*e.g.,* Anderson et al. 2021a) or "month" (*e.g.,* Spaet et al. 2020) term, to test for temporal non-linearity in shark density. Day of year was modeled separately for each year, to account for variance in the intra-annual temporal pattern of environmental factors. The other temporal factors in the GAMs were year (categorial) and the time of day (binned hourly) at which the surveys were conducted.

The model structure was thus:

Shark count ~ year + s(day of year) + s(hour) + s(temperature) + s(wave height) + s(tidal height) + s(chlorophyll-A) + sea state + visibility + offset(survey area)

where *s()* denotes that a smoothing function was used.

We tested for significant associations between each term and shark density using ANOVA and compared levels of significant parametric variables using post-hoc Tukey comparison. 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.

Results

The effects of each term in the model were, for the most part, consistent between the models using sea floor temperature and those where sea surface temperature was used (**Table 3**). There were no differences in the terms that were significantly associated with density between the overall model with SFT and the overall model with SST. The results below are from the models using SFT, and we note where using SST changed the effects of terms in the small and large shark models. Differences between the effects of SST and SFT themselves are also discussed below.

We modeled overall observed shark density using sea floor temperature across 284 survey days, with 774 observations of white sharks. The small and large shark models included survey data from 276 days, with 275 and 144 shark observations, respectively. 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. The factors associated with observed shark density were broadly consistent across the overall, small, and large shark models (**Table 2**). The overall model explained 53.7% of deviance in density, compared to 33.4% and 33.0% for the small and large shark models, respectively.

Year and *day of year* were the variables most highly associated with density in all three models. Year explained 22.5% of deviance in the overall model ($p < 0.001$), 14.7% in the small shark model ($p < 0.05$), and 11.2% in the large shark model ($p < 0.001$). Holding all other factors equal, the peak in density shifted earlier each year, from October-November in 2019, to August-October in 2020, and to May-July in 2021. Within each year, the seasonal trend in density (**Figure 1**), represented by day of year, was similar across the overall, small shark, and large shark models. However, seasonality explained over twice as much deviance in the overall and small shark models (15.7%, $p < 0.001$; and 15.8%, $p < 0.05$; respectively) as in the large shark model (7.5%), where day of year was only significantly associated with density in 2021($p < 0.05$). In the SST model, day of year was not significantly associated with density in either 2020 or 2021.

Time of day explained 4.4% of deviance in overall shark density ($p < 0.001$). Density increased throughout the day, peaking from 16:00 to 18:00 h (the latest hour at which surveys were conducted). Similar trends were observed in the small and large shark models, but the associations between time of day and density only explained 1.4% ($p = 0.059$) and 0.6% ($p = 0.053$) of deviance, respectively. Time of day was, however, significantly associated with small shark density in the model using SST data (4.4% DE, $p < 0.005$).

Sea floor temperature (**Figure 2**) was associated with overall density (3.7% DE, $p < 0.005$), small shark density (3.5% DE, $p < 0.001$), and large shark density (2.3% DE, $p < 0.05$). In the adult model, the association was non-linear, and modeled density peaked between 17 and 18 °C SFT. Small shark density exhibited a negative relationship with SFT, with the model predicting maximum small shark density at the lowest temperatures (< 12 °C) and minimum density at the highest temperatures (> 22 °C). Overall density, consequently, was higher at sea floor temperatures below 16 °C and lower at 18 °C and above.

Relationships between sea surface temperature and observed density (**Figure 3**) were similar to those between sea floor temperature and density. In the overall model, the relationship was stronger (6.9% DE, $p < 0.001$), and the peak of density was at a slightly colder temperature (15 °C) with SST than with SFT. In the small shark model, SST also explained more variation in density (6.3%, $p < 0.001$) than SFT, and with the same negative relationship. Deviance explained by temperature in the large shark model dropped to 0.8% ($p < 0.001$) when SST was substituted for SFT, but observed density still peaked between 17 and 18 °C.

Visibility was associated with density in all three models, explaining 3.1% ($p < 0.001$), 2.6% ($p < 0.05$), and 0.4% ($p < 0.05$) of deviance in the overall, small shark, and large shark models, respectively. Observed density was higher with medium and high visibility than with low visibility in the overall model ($p < 0.05$ for both contrasts), and the low-high contrast in the small shark model ($p < 0.05$) and low-medium contrast in the large shark model ($p < 0.05$) were also significant. Visibility was not significantly associated with observed density in the large shark model where SST was used, likely due to a reduction in sample size.

Tidal height explained just 0.3% of deviance in the overall model ($p < 0.05$) and was not associated with the density of small or large sharks in those models. Higher tides corresponded to lower observed density.

Chlorophyll-A, *wave height*, and *sea state* were not significantly associated with density in any of the three models, with each term explaining 1.5% of deviance at most in any one model.

Discussion

Our study conferred the opportunity to observe and attempt to explain the factors potentially shaping white shark behavior 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, 2021b). UAV surveys are also disadvantaged by imperfect detection probability (Koski et al. 2009, Hodgson et al. 2017, Butcher et al. 2019, Ayres et al. 2021a) and the requirement to determine if each sighting is of a unique individual (this study), and therefore may be biased towards overestimating or underestimating density compared to other methods (Hodgson et al. 2016, Williams et al. 2017). We discuss these and other limitations below.

We included a subjective 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 associated with lower observed shark density. Interestingly, this result contrasts with UAV studies of large predatory sharks (Colefax et al. 2020a) and mock-shark targets (Hensel et al. 2018), where no effect of visibility on detections was found. The high number of observations in this study and the proximity of the UAV surveys to the surf break, where visibility can be very poor due to suspended sand, may have allowed us to uncover this relationship. Accounting for availability of detection, at least in part, by including the effect of visibility in our models enhances the validity of the following conclusions about factors influencing shark density at the Carpinteria aggregation.

Seasonality, the most consistent predictor of YOY white shark density across a multitude of aggregation sites in the SCB from 2010-2018 (Anderson et al. 2021a), played a primary role in explaining shark density at the Carpinteria aggregation using these UAV methods as well from 2019-2021. This was the case not only for smaller sharks, but in the large shark and overall models. Seasonal peaks and troughs were broadly aligned across the three models, but day of year did have twice as strong an association with the density of small sharks compared to large sharks. While the factors that affect size classes, therefore, may be similar or temporally co-varying (Curtis et al. 2014) smaller sharks seem to be more sensitive to variations in these factors.

In addition to density varying profoundly within each field season, modeled density (i.e., holding all other variables constant) peaked at different times each year. Therefore, there may be seasonally variable factors other than those that we included in our model (e.g., not temperature or chlorophyll-A) and that are not consistent across years (e.g. not day length) that affect white shark presence at the Carpinteria aggregation site and/or their availability to detection via UAV. However, it is also possible that the aforementioned abiotic variables do affect sharks, but that the spatial resolution of this data (especially for chlorophyll-A, which was derived from satellite data) precluded us from detecting these relationships. Prey availability is one such factor that could have caused the inter-annually variable effect of seasonality. Since the movement of white sharks and their prey (especially other elasmobranchs) are influenced by a suite of overlapping variables (Kupschus & Tremain 2001, Pittman & McAlpine 2003, Schlaff et al. 2014), it can be difficult to disentangle the physiological effects of seasonal variables on sharks themselves from the effects of these same factors on prey distribution. Incorporating contemporaneous data on prey abundance is therefore an important avenue for future research (Huveneers et al. 2018).

We also observed a diel pattern in overall density, where surveys conducted later in the day were associated with higher density estimates. The diel pattern of UAV-observed density at the Carpinteria aggregation site is likely driven by the fact that white sharks in this location exhibit deeper swimming depths in colder water around dawn and transition to shallow or surface swimming to thermoregulate in the afternoon (Anderson et al. 2022), thereby becoming more available to detection from the UAV platform. Similar diel patterns 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, and are also thought to be the result of behavioral thermoregulation (Ayres et al. 2021a, 2021b).

Both juvenile (Weng et al. 2007, Anderson et al. 2022) and sub-adult to adult (Domeier et al. 2012) white sharks in the eastern North Pacific exhibit diel patterns in vertical movements, but diel patterns of density at specific locations have not been previously demonstrated in the SCB, and juvenile white shark distribution in coastal waters off of eastern Australia shows little response to time of day (Spaet et al. 2020). As with visibility, diel patterns have direct implications for the planning of research and public safety surveys. Our findings demonstrate, for example, that conducting UAV surveys in the early morning (which may otherwise be an appealing time for lifeguards to determine shark presence before the arrival of beachgoers) is likely to give a lower count of sharks than if surveys were conducted later in the day.

Of any factor that we investigated, the effects of sea floor and sea surface temperature exhibited the most variation between the small shark and large shark models. Higher observed density of large sharks occurred when SFT was between 16 and 18 °C, while the density of observed small sharks had a negative relationship to SFT. Observed density responded similarly in each case to SST. However, SST had a larger effect than SFT on observations of smaller sharks, and the association between SST and large shark observations was very low. This difference in the magnitude of the effect of SST is consistent with findings that smaller white sharks tend to occupy a narrower range of temperatures than larger individuals (Boustany et al. 2002, Weng et al. 2007, Curtis et al. 2014).

In the SCB, estimates for the preferred thermal envelope of juvenile white sharks have centered around 18-19 °C (Klimley et al. 2002, Dewar et al. 2004, Weng et al. 2007, White et al. 2019). Similar preferences have been observed globally, with immature sharks preferring temperatures between 18-20 °C in eastern Australia (Bruce & Bradford 2019, Lee et al. 2021), and YOY and juvenile white sharks in the northwestern Atlantic Ocean preferring 19.5 and 18 °C, respectively (Curtis et al. 2014). In apparent contrast to this well-supported thermal preference, we observed sharks < 3 m at the Carpinteria aggregation site most frequently when average SFT was at its lowest, between 12-14 °C. These colder sea floor temperatures likely increased detection probability by prompting shallower swimming behavior (Weng et al. 2007, White et al. 2019) due to the strong thermocline, rather than being the preferred temperature envelope for sharks to inhabit. Behavioral thermoregulation has been demonstrated at the Carpinteria aggregation site using fine-scale temperature and shark location data, which also revealed that white sharks prefer temperatures warmer than those that were associated with high observed density in our study (Anderson et al. 2022, Spurgeon et al. in review).

Our results with regards to temperature, therefore, may be indicative of when UAV surveys might detect higher densities of sharks at an entire-beach scale, but do not capture how the thermocline affects vertical movements of sharks. Furthermore, the magnitude of the effects of sea floor and sea surface temperature on observed density were relatively low compared to those of inter- and intra-annual variation, indicating that average water temperatures across the aggregation site are not strongly associated with shark presence as detected by UAV. We are therefore unable to make strong conclusions about the association between water temperature and shark presence at the Carpinteria aggregation site.

Based on the data we collected, we were also unable to determine why sharks were using the Carpinteria aggregation site. 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), and our lack of observations of hunting behavior does not rule out that such activity does occur within the Carpinteria aggregation site. Observed density in our study was not associated with chlorophyll-A levels, but the spatial resolution of satellite-derived chlorophyll-A data may not be indicative of local prey density, which can also be driven by water temperature, wave climate, and spawning pattern (Olds et al. 2018, Gutiérrez-Martínez 2021). We did observe bat rays (*Myliobatis californica*) and schools of other unidentified fish during our UAV surveys. 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. 2021a, 2022; Spurgeon et al., unpublished data), suggest that sharks are indeed foraging in the area. Other potential drivers of density at the aggregation site include intraspecific interactions (Schilds et al. 2019, Anderson et al. 2021b), and refuge from predation, namely from killer whales (*Orcinus orca*) which are known to depredate and displace white sharks (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 directly confirm this use of the aggregation site.

Conclusion

We demonstrated that many factors, namely time of day, water temperature, and visibility, are associated with white shark density as estimated via UAV survey. Ontogeny may 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 sea surface temperatures. Researchers and safety officials alike should take diel variability in density into account when planning the time of day that surveys are to be conducted and consider that intra-annual variability in density estimates means that long-term data may be needed to accurately capture patterns of shark abundance. Relationships between temporal and oceanographic factors and observed density (e.g., lower density estimates when water visibility is poor or SFT is high) can also inform determinations of actual shark abundance based on UAV survey data. However, these determinations should also be informed by future studies using data on prey availability and information on how oceanographic variability within aggregation sites influence fine-scale white shark distribution in these areas.

UAV surveys are limited by the short-duration, snapshot nature of density estimates and the inability to simultaneously collect ancillary oceanographic data at the same fine spatial scale at which sharks choose habitat, but these limitations do not prevent them from establishing useful benchmarks of shark density at local scales - especially if UAV research is made accessible to a larger number of academic researchers and interested members of the public alike. Our findings may enable citizen science and other research initiatives to better monitor marine habitat use by white sharks (Jorgensen et al. 2022) and other threatened species such as sea otters (Nicholson et al. 2018, Moxley et al. 2019). UAVs are a powerful tool to enable high-quality data collection by the general public, and properly implemented UAV surveys can circumvent the challenge of standardizing records collected by citizen scientists (Matutini et al. 2021, Pucino et al. 2021, Tanaka et al. 2021, Theuerkauf et al. 2022,). Involving more people in the study of white sharks can increase both scientific knowledge and public interest in conservation (Sullivan et al. 2017, Butcher et al. 2021, Garcia-Soto et al. 2021,).

Broadening the scope and reach of marine research is especially important as climate change shifts the range of top predators, including white sharks, and many other species (Burrows et al. 2011, Hazen et al. 2013, Hastings et al 2020, Osgood et al. 2021). As a result of increasing water temperatures in the SCB (Rasmussen et al. 2020), new aggregation sites may form (Tanaka et al. 2021) and current aggregations may shift or, as appeared to be the case at the Carpinteria aggregation site during the course of our study, become more densely populated. In addition to bringing white sharks into potential conflict with fisheries and human recreation, range shifts are important to understand for this species because white sharks are large-bodied, generalist predators and have the potential to trigger trophic cascades (Estes et al. 1998, Halaj & Wise 2001) and affect other species through non-consumptive attacks (Tinker et al. 2016). These ecosystem-level processes highlight the importance of understanding where and when white shark aggregations form and the mechanisms behind their choice of habitat.

Figures and Tables

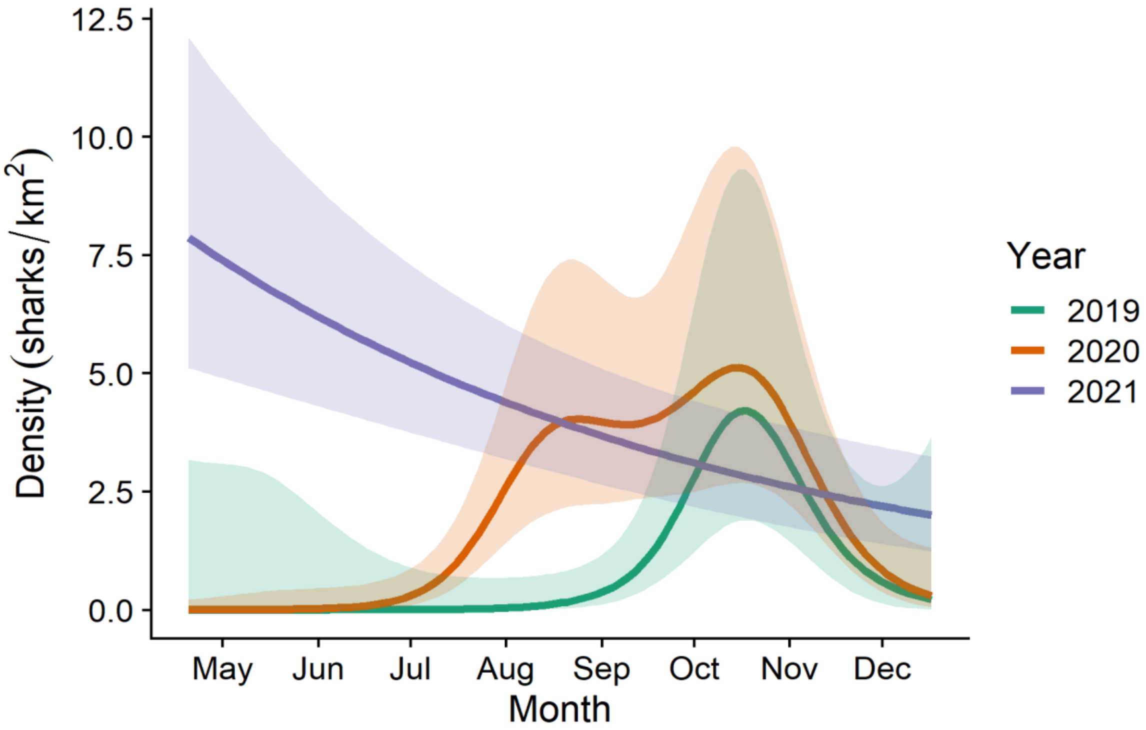

Figure 1. Intra-annual variation in observed white shark density by year, as determined by the smooth function for “day of year” in the generalized additive model. Results shown are on the response scale, with all other parameters held constant. Shaded regions represent the 95% confidence interval for each year.

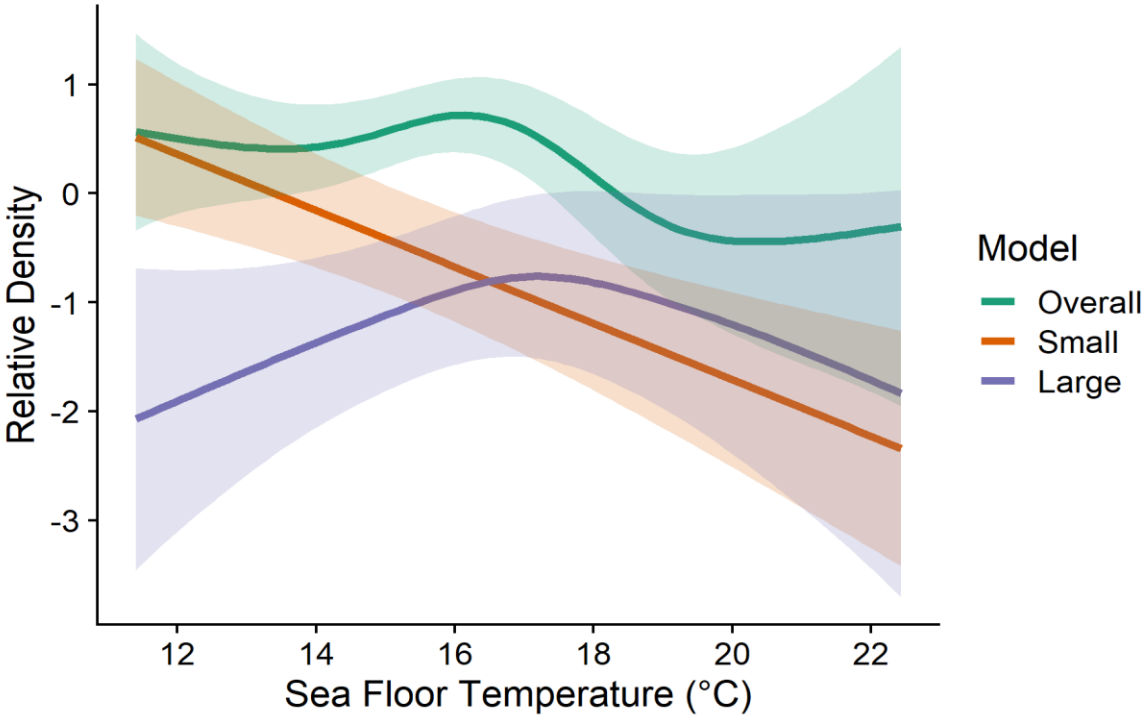

Figure 2. Relationship between sea floor temperature and relative modeled density in the overall (all observed sharks), small shark (< 3 m), and large shark (> 3 m) generalized additive models, with data from 2019, 2020, and 2021. Shaded regions represent the 95% confidence interval for each model.

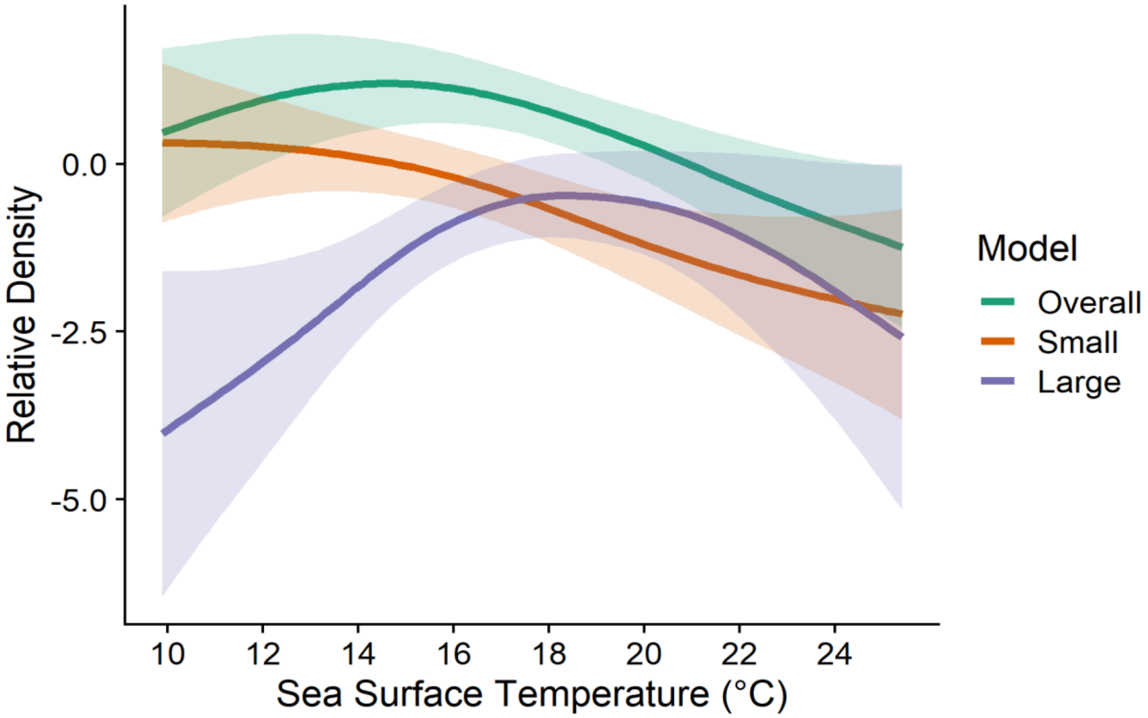

Figure 3. Relationship between sea surface temperature and relative modeled density in the overall (all observed sharks), small shark (< 3 m), and large shark (> 3 m) generalized additive models, with data from 2020 and 2021. Shaded regions represent the 95% confidence interval for each model.

Explanatory Variable	Source	Parameterization
Temporal		
Year	Calendar	Categorical (df = 2)
Day of year	Calendar	Thin plate regression spline
Time of day (h)	PDT/PST	Thin plate regression spline
Oceanographic		
Water temperature (°C)	CSULB Shark Lab temperature loggers*	Thin plate regression spline
Chlorophyll-A (mg/m^3)	NOAA “S-NPP NOAA-20, VIIRS, Near Real-Time, Global 4km, 2019-present, Daily” dataset (0.0125° grid cell)	Thin plate regression spline
Tidal height (m)	NOAA Station 9411340	Thin plate regression spline
Swell height (m)	NOAA Station 46053	Thin plate regression spline
Sea state (Beaufort scale)	UAV survey video	Categorical (df = 1)
Visibility (qualitative)	UAV survey video	Categorical (df = 2)

Table 1. Explanatory variables used in the generalized additive models of white shark density. Sea state was categorized as “low” (Beaufort scale 0-1) or “high” (2+), and visibility was categorized as “low”, “medium”, or “high”.

*Temperature loggers included the Innovasea Rx-LIVE acoustic receiver (0.01°C resolution, +/- 0.2°C accuracy), Innovasea aquaMeasure sensor (0.01°C resolution, +/- 0.2°C accuracy), ElectricBlue EnvLogger (0.1°C resolution, +/- 0.2°C accuracy), HOBO Stowaway TidbiT (0.1°C resolution, 1°C accuracy), and Innovasea VR2Tx (0.1°C resolution, +/- 0.5°C accuracy).

	All sharks	Small sharks	Large Sharks
Year	**22.5**	**14.7**	**8.3**
Day of year	**15.7**	**15.8**	**7.5***
Time of day	**4.4**	1.1	1.2
Sea Floor Temperature	**3.7**	**3.5**	**2.3**
Chlorophyll-A	1.5	0.0	0.1
Tidal height	**0.3**	0.3	0.8
Wave height	0.0	0.0	—
Sea state	0.0	0.4	—
Visibility	**3.1**	**2.6**	**0.4**
Total DE	53.9%	33.4%	33%

Table 2. Total deviance explained (DE) and DE of each temporal and oceanographic term in Generalized Additive Models of observed density of all sharks (n = 284 survey days) and density of observed small (<3 m) and large (>3 m) white sharks (n = 276 survey days) using sea floor temperature data. Data included in these models was from 2019, 2020, and 2021. DE in bold type indicates that a term was significantly associated with density ($p < 0.05$ in the ANOVA of the model). DE is not reported for wave height and sea state in the adult density model because total DE was higher in the reduced models than in the global model.

*Day of year was significantly associated with large shark density in 2021 only.

	All Sharks	Small Sharks	Large Sharks
Year	**20.1%**	**12.6%**	**2.7%**
Day	**19.8%**	**17.5%**	1.5%
Hour	**11.0%**	**4.4%**	1.3%
Sea Surface Temperature	**6.9%**	**6.3%**	**0.8%**
Chlorophyll	0.0%	0.0%	0%.
Tide	**1.7%**	0.7%	1%
Wave height	0.0%	0.0%	0.7%
Sea state	0.0%	0.3%	0.6%
Visibility	**4.0%**	**4.9%**	3.9%
DE	44.8%	22.7%	23.5%

Table 3. Total deviance explained (DE) and DE of each temporal and oceanographic term in Generalized Additive Models of observed density of all sharks (n = 207 survey days) and density of observed small (<3 m) and large (>3 m) white sharks (n = 199 survey days) using sea surface temperature data. Data included in these models was from 2020 and 2021. DE in bold type indicates that a term was significantly associated with density ($p < 0.05$ in the ANOVA of the model).

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Appendix

Supplementary Methods

Determination of Survey Effort

In order to obtain density estimates for observed sharks, we calculated the area and duration of each survey flight. Transect area was calculated from the length of each transect and the width of the field of view of the camera (Kiszka et al. 2016). Because roaming flight paths were non-linear, we generated “field-of-view rectangles” for every GPS point 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 total area surveyed during each roaming flight was calculated as the area of union of these field-of-view rectangles.

Survey duration for roaming flights was also calculated from the GPS flight log, by summing the intervals during which the UAV was at the 40 m search altitude. Since video recording only occurred along each transect during transect surveys, the total duration of video recorded was used as the survey duration for these surveys.

Size estimation field tests

To improve the accuracy of the shark length estimations, we conducted in-water field tests with target objects of known length placed in the water at our study site. With the target at the surface, we flew the UAV at altitudes between 10 and 60 m at 10 m intervals, recording 30 seconds of video at each altitude. We then repeated this procedure with the target submerged on the seafloor at a depth of 1.5 m. Based on results from these trials, we compared the accuracy of three different length estimation methods. Treating both takeoff elevation and target depth as increases to the distance between the UAV and target, we calculated target length using 1) UAV altitude above takeoff only, 2) UAV altitude plus takeoff elevation, and 3) UAV altitude plus takeoff elevation and target depth.

Evaluation of sizing methodology

We demonstrated that obtaining accurate estimates of length from UAV video footage is feasible, as long as the appropriate factors are taken into consideration. Perhaps the most important step in calibrating a UAV-based photogrammetric approach to length estimation is determining the characteristics of the UAV and camera being used in a field setting (Whitehead et al 2022), such as camera FOV.

Results from our photogrammetric calibration trials offer some useful insight into methods that can improve the precision of shark size estimations generated with this common and accessible UAV hardware platform. Our analyses would suggest that including takeoff elevation above sea level and the depth of the shark or other target being measured should also be incorporated into the length calculation for these estimates to be accurate. An interesting caveat to this conclusion is that these factors, which are fixed values, become relatively less important at higher altitudes. This is demonstrated by the high accuracy of uncorrected length measurements from 50 and 60 m in our field tests (**Figure S3**). Therefore, a tradeoff must be considered between the relative importance of correction factors, which decreases with increasing flight altitude, and the ability to distinguish and measure the animal of interest, which becomes more error prone as altitude increases. This error is exemplified in the overestimation of target size at altitudes of 40, 50, and 60 m, where the corrected size estimates were, on average, 6.5, 8.2, and 9.5 cm too long **(Figure S3)**. Pixel ground length at

40 m altitude is 1.9 cm, and increases to 2.9 cm at 60 m altitude, so our overestimates correspond to an error in the roaming image-measurement process of one or two pixels on either side of the target.

The most likely source of the variation in our repeat measurements is inaccuracy in the UAV altitude reading. We obtained this value from the UAV barometer, whereas studies using LIDAR to measure UAV altitude have reported measurement errors (of whales) smaller than ours by an order of magnitude (Dawson et al. 2017, Christiansen et al. 2018). However, Durban et al. (2016) also used the UAV's factory barometer and reported variability in whale length measurements of < 5%, and LIDAR systems also can contribute to photogrammetric error (Dawson et al. 2017).

Our field tests were conducted on a day with high water visibility and with a white PVC target, so higher altitude measurements were relatively accurate. The reduced ability to identify objects in the water at high altitudes is offset by the increased duration that an object remains in the frame at a given flight speed and higher-altitude flights also cover more area for a given UAV flight speed. Therefore, we recommend that UAV surveys be conducted at the highest altitude (within FAA and local regulations) that allows for detection of the animal or object of interest, which for white sharks at our research site was around 60 m. When visibility is poor, reduced altitudes may be necessary to make accurate photogrammetric measurements, and correction factors must therefore be determined with tests conducted with the specific UAV to be used in the study, and at the study site. Furthermore, very low altitudes tended to underestimate target length, possibly because of lens distortion (Burnett et al. 2018). We did not explicitly correct for this in our study, but any lens distortion would have been constant between our FOV and length calibration field tests and our measurements of sharks, and was therefore unlikely to have affected measurement accuracy. Studies focusing on smaller organisms or where conditions such as water visibility necessitate low altitudes should also account for this effect.

Supplementary Figures

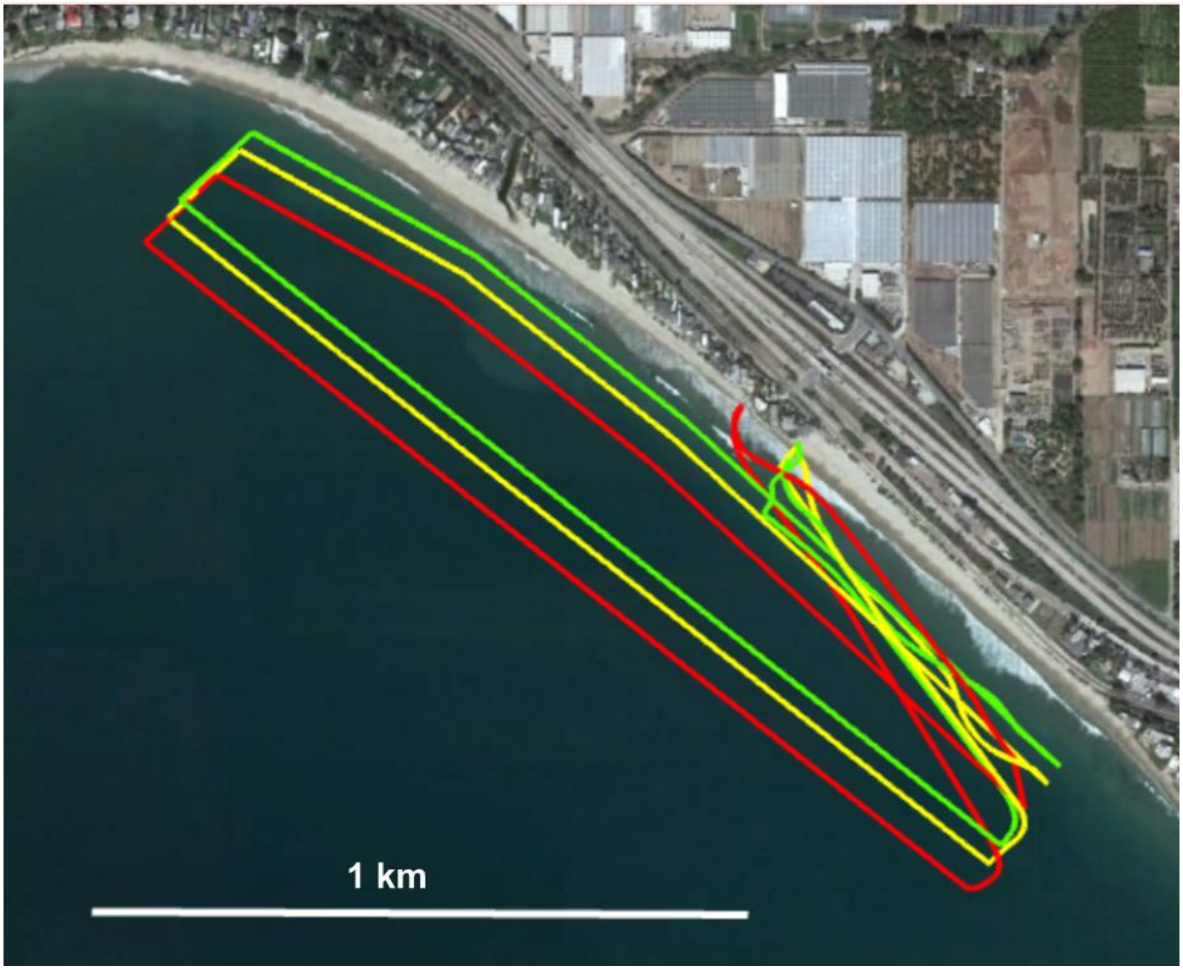

Figure S1. GPS flight paths from the three transect survey versions: high tide/low swell (green lines), medium tide/medium swell (yellow), and low tide/high swell (red). The survey version was selected on a daily basis to position the inner transect just offshore of the surf line. Map created in Google Earth, satellite image © 2022 TerraMetrics.

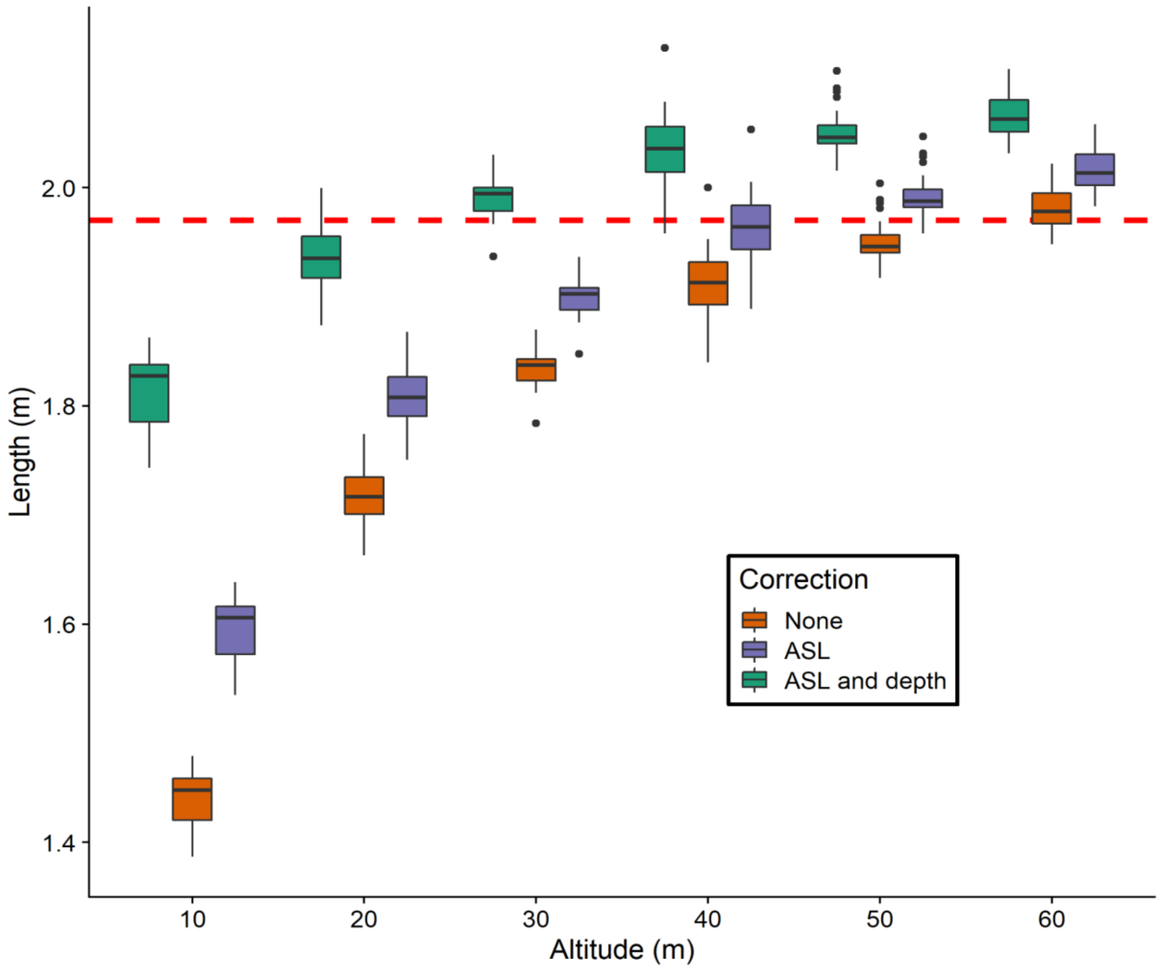

Figure S2. Results of length estimation field testing, showing the effect of altitude and correction method on length estimates of a 1.97 m target (true length indicated by the red dashed line) submerged 1.5 m below the ocean surface. Correction method “None” used only the altitude of the UAV above the takeoff point in the length calculation, while “ASL” incorporated the altitude above sea level of the takeoff point and “ASL and depth” incorporated both altitude above sea level of the takeoff point and the depth of the target (see Methods). Box plots are generated with length estimates from 30 still frames of each altitude/correction method combination.

Figure S3. White shark observed on five separate occasions between June 17 and July 13, 2021. The pattern of scarring between the snout and dorsal fin enabled us to re-identify this shark after the initial sighting. From lowest to highest, our length estimates for this individual were 378, 399, 415, 440, and 468 cm total length (mean = 420, SD = 35).