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ARTICLE

Coastal and Marine Ecology

Diverse habitats shape the movement ecology of a top marine predator, the white shark *Carcharodon carcharias*

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Abstract

An animal's movement is influenced by a plethora of internal and external factors, leading to individual- and habitat-specific movement characteristics. This plasticity is thought to allow individuals to exploit diverse environments efficiently. We tested whether the movement characteristics of white sharks *Carcharodon carcharias* differ across ontogeny and among habitats along the coast of Central California. In doing so, we elucidate how changes in internal state (physiological changes coinciding with body size) and external environments (differing seascapes and/or diel phases) shape the movement of this globally distributed predator. Twenty-one white sharks, from small juveniles to large adults, were equipped with motion-sensitive biologging tags at four contrasting seascapes: two islands, a headland, and an inshore cove. From multisensor biologging data, 20 metrics characterizing movement (i.e., depth use, vertical velocities, activity, turning rates, and bursting events) were derived and subjected to multivariate analyses. Movement characteristics were most different across seascapes, followed by ontogeny and diel phase. Juvenile sharks, which were only encountered at the cove, displayed the most distinct movement characteristics. Sharks at this seascape remained close to the shore traveling over smaller areas, shallower depth ranges, and with lower levels of tail beat frequencies, when corrected for size, than sub-adult and adult sharks tagged elsewhere. Distinct tortuous daytime versus linear nighttime horizontal movements were recorded from sharks at island seascapes but not from those at the headland or inshore cove. At the offshore islands, the linear nighttime swimming patterns coincided with repeated dives to and from deeper water. The availability of prey and access to deeper water are likely drivers of the differences in movement characteristics described, with varying demographics of pinniped prey found at the subadult and adult aggregation areas and juvenile sharks being piscivorous and their habitat neither adjacent to pinniped haul out areas nor deeper water. This study demonstrates plasticity in the

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movements of a top predator, which adapts its routine to suit the habitat it forages within.

KEYWORDS
biologging tags, megafauna, movement drivers, movement ecology, ontogeny, seascapes

INTRODUCTION

An animal's movement and behavior are intrinsically linked to its biological requirements and surrounding environment. Nathan et al.'s (2008) movement ecology paradigm states that animal movements are shaped by interactions between internal and external processes (see also Martin et al., 2008, 2013). Internal factors influencing the movement of predators include energy requirements and subsequent motivations (such as feeding or resting), as well as ontogeny and reproductive status (Harten et al., 2020; Martin et al., 2013; Sparrow & Newell, 1998). External factors influencing the movement of predators can include environmental conditions (i.e., temperature, diel phase, or landscape/seascape), prey availability, competition, and predation risk (DeMars & Boutin, 2018; Dunford et al., 2020; Levine & HilleRisLambers, 2009; Lima & Dill, 1990), ultimately giving rise to diverse movements and behaviors. The influence of internal or external factors on movement and behavior is expected to change over time, between areas, sex, or age, and is also dependent on how much an individual can adapt to local environmental conditions (Nathan et al., 2008). Understanding these processes, why and how they vary, is important because animal movements governed by internal influences are expected to vary based on factors like size or sex, regardless of where they are found, while animal movements governed by external influences should vary across different areas or conditions regardless of size or sex (Martin et al., 2013). For example, most species of owl are active during the night and only adapt their routines when caring for young (Wu et al., 2016), while deer species have highly plastic movement characteristics and are seen to adapt their activity routines in response to predation risk (Bonnot et al., 2020). However, measuring these effects is difficult because they are complex and can cause movement changes at fine scales, which require collecting high-resolution data on multiple factors during different conditions, such as different times of the day or year, and in different areas to resolve. Motion-sensitive biologgers (Hays et al., 2016) can provide such data across three axes, linking horizontal and vertical movements, uncoupling two- or three-dimensional activities, determining activity cycles, classifying behavioral states, and revealing cryptic predator–prey interactions (Brewster et al., 2018; Gleiss et al., 2017; Hounslow et al., 2020; Mitani et al., 2010; Papastamatiou et al., 2021).

White sharks *Carcharodon carcharias* provide an interesting model species to test the influence of internal and external factors on predator movement ecology. They are endothermic top predators and tagging studies indicate they range across a vast area of subtropical and temperate oceanic environments globally but aggregate with high fidelity around distinct foraging areas often near pinniped colonies (Bruce & Bradford, 2015; Chapple et al., 2011; Huveneers et al., 2018; Klimley & Ainley, 1996; Skomal et al., 2017; Winton et al., 2023). Several factors influence coastal residency periods, movements, and behaviors of white sharks during these aggregations, particularly the presence of a predictable high-calorie prey source at pinniped colonies (Huveneers et al., 2018; Jorgensen et al., 2012; Klimley, Le Boeuf, Cantara, Richert, Davis, Van Sommeran, & Kelly, 2001; Kock et al., 2022; Towner et al., 2013). However, only larger white sharks are able to consistently capture pinniped prey, with young of the year and juvenile sharks reliant on nonmammal diets, making ontogeny an important influence on the species as they grow (Estrada et al., 2006; French et al., 2018). Yet, there remains a significant knowledge gap in understanding why individuals select specific aggregation areas, how their movements and routines vary between areas, and how these variations may be influenced by the size or sex of individuals, or environmental characteristics (Huveneers et al., 2018). This is in part due to the rarity in finding sharks of both sexes and all size classes within the same aggregation areas (Domeier, 2012). However, within Central Californian waters, a newly described aggregation of juvenile and young of the year white sharks occurs close to three other well-known aggregations of subadult and adults (Chapple et al., 2016; Kanive et al., 2021; Tanaka et al., 2021).

In this study, we use multisensor biologging tags to explore how white sharks utilize four distinct habitats. We derive 20 movement metrics, which can be broadly characterized into those representing depth use, vertical

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velocities, activity, turning rates, and bursting events. These metrics are used to describe the movement characteristics of white sharks of various demographics as they aggregate at different seascapes in the Northeast Pacific. Using multivariate analysis, we test for differences in movement characteristics of white sharks by area, size class, sex, and diel phase. We would expect that if movement characteristics were shaped by internal processes, then size class and sex will explain more variation in metrics. Meanwhile, if external processes are shaping movement characteristics, we would expect a large variation in data to be explained by area.

MATERIALS AND METHODS

Study sites

All research took place at known white shark aggregation areas in the Northeast Pacific off the coast of Central California (Domeier, 2012; Jorgensen et al., 2010; Weng et al., 2007). White sharks increase in numbers along the central coast of California (e.g., Monterey National Marine Sanctuary, Farallon National Marine Sanctuary) during summer when juveniles are found in coastal areas (Lowe et al., 2012; Tanaka et al., 2021; White et al., 2019) and in fall and winter when subadult and adults aggregate around pinniped colonies (Anderson et al., 2011; Chapple et al., 2016). Photo identification and telemetry studies conducted over many years have confirmed individuals revisit the same areas seasonally, with some individuals visiting multiple aggregation areas in a season and others exclusively found in one (Anderson & Goldman, 1996; Chapple et al., 2011, 2016; Jorgensen et al., 2010, 2019; Kanive et al., 2019). We tagged sharks in four areas (Figure 1), including a cove at the north end of Monterey Bay where juvenile sharks are found close to shore (Aptos), a nearshore rocky island (Año Nuevo Island), an offshore island outcrop (The Southeast Farallon Islands), and a rocky headland shoreline (Tomales Point). Pinniped colonies of various species are found on each island and rocky shoreline area but are absent from the Soquel Cove area in Monterey Bay (Table 1).

In this study, Aptos (APT) refers to the aggregation of juvenile white sharks found in the waters of Soquel Cove at the northern end of Monterey Bay. Sharks have been observed in this area from April to October, with increasing detections over years thought to result from warming

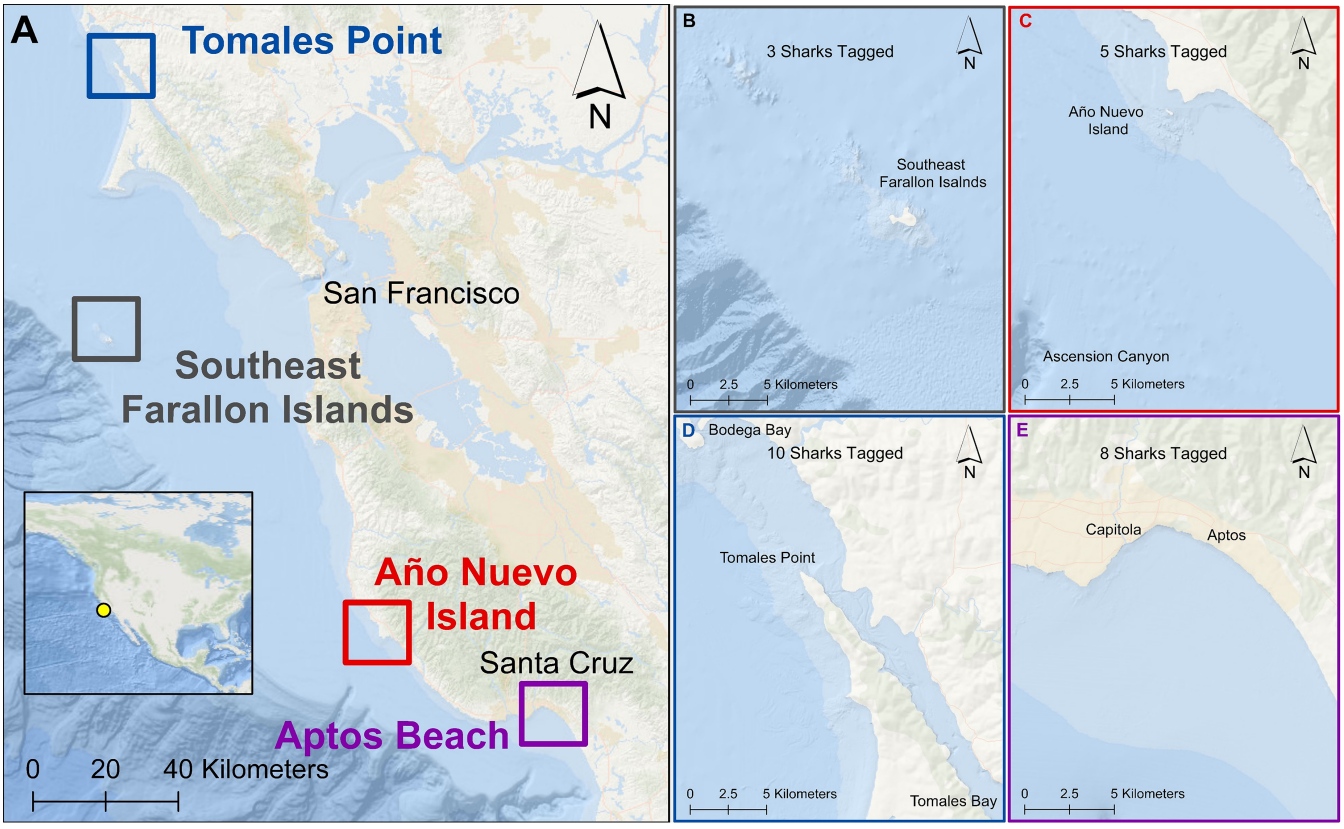


FIGURE 1 (A) The four sites in Central California where white sharks were tagged. Each is a known aggregation area; (B) (gray), The southeastern Farallon Islands (FAR), (C) (red), Año Nuevo Island (ANO), (D) (blue), Tomales Point, and (E) (purple), Soquel Cove off Aptos (APT).

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TABLE 1 Descriptions of the areas and size range of sharks tagged.

Area	Seascape type	Pinnipeds present	Reef present	Kelp present	Total length, range (cm)
Aptos (APT)	Inshore Cove	No	Partial	No	190–260
Año Nuevo (ANO)	Island (nearshore)	Yes	Yes	Yes	380–490
Farallones (FAR)	Island (offshore)	Yes	Yes	Yes	440–550
Tomales Point (TOM)	Headland Point	Yes	Partial	Yes	275–460

ocean temperatures expanding their range northward (Tanaka et al., 2021). The cove is partially protected from prevailing winds from the northwest and has a relatively featureless predominantly sandy seafloor (Plant & Griggs, 1992). Año Nuevo Island (ANO) refers to an island group approximately 30 km north of Santa Cruz, consisting of a main island and several closely attached rocky outcrops approximately 700 m across (Klimley, Le Boeuf, Cantara, Richert, Davis, & Van Sommeran, 2001; Klimley, Le Boeuf, Cantara, Richert, Davis, Van Sommeran, & Kelly, 2001). Kelp forests form to the north of the island, and a large reef and kelp forest are present off its southwestern end. Five species of pinniped haul out on the island: northern elephant seal *Mirounga angustirostris*, harbor seal *Phoca vitulina*, northern sea lion *Eumetopias jubatus*, Californian sea lion *Zalophus californianus*, and northern fur seal *Callorhinus ursinus* (Le Boeuf et al., 2011). The Southeast Farallon Islands (FAR) is an island group approximately 90 km north of Año Nuevo Island and 50 km offshore of the Golden Gate Bridge, San Francisco (Klimley et al., 1992; Klimley & Anderson, 1996). The group consists of two main islands and several rocky outcrops, around 100 ha in size, used as haul out sites for the same five pinniped species as Año Nuevo Island (Ainley et al., 1981, 1985). The islands form many inlets and bays, and several rocky reefs and kelp forest patches surround them (Goldman & Anderson, 1999). Tomales Point (TOM) is the northern end of the Point Reyes headland, ~ 60 km north of San Francisco (Anderson, Becker, et al., 2008). The point consists of a rocky shoreline and cliff face steeply dropping to 20 or 30 m depth within 100 m of the coast (Kanive, 2020). The northern side of the point is formed by the mouth of Tomales Bay, a saltwater inlet containing multiple elasmobranch species, although it is thought white sharks rarely enter this system (Hopkins & Cech, 2003). All five species of pinniped haul out on the Point Reyes shoreline, though considerably more harbor seals are found here than at either Año Nuevo or the Farallon Islands, and this species is thought to be the primarily targeted prey item of white sharks at Tomales Point (Anderson, Becker, et al., 2008; Carlisle et al., 2012).

Data collection

White shark tagging took place between October 2017 and November 2019 at four locations along the central coast of California. Tagging occurred on juvenile white sharks off the coast of Aptos in summer months (July–September) and at Año Nuevo, The Farallon Islands, and Tomales Point sites in fall (October–November). Juvenile sharks at Aptos were located by spotters or a drone while free-swimming at the surface. In contrast, sharks in all other areas were attracted to research vessels under NOAA sanctuary permits using a small piece of marine mammal blubber and a seal-shaped decoy (Chapple et al., 2011). Once close enough, sharks were sexed and photo identified using a GoPro as per Kanive et al. (2019). For each shark, total length (TL_{cm}) was visually estimated by two to three experienced researchers using the known length of the research vessel as a reference as sharks swam close by Kanive et al. (2023), or measured using photogrammetry from drone images taken from above (Tanaka et al., 2021). Generally, experienced researchers are expected to have size estimates within ~20 cm of actual TL, with greater accuracy expected with greater experience (Leurs et al., 2015; May et al., 2019) each of our researchers had at least 10 years of experience with the species during the time of the fieldwork. Traditionally white sharks have been classified into age classes based on sizes associated with ontogenetic shifts in diet and physiology (Carlisle et al., 2012; Estrada et al., 2006). However, these shifts are subject to individual and sexual variation (French et al., 2017, 2018). In this study, two sharks tagged at Tomales were just under 300 cm in total length (TL) (290 and 275 cm TL respectively), while all sharks at Aptos were under 260 cm TL. Therefore, all sharks below 275 cm TL were considered juveniles, sharks between 275 and 360 cm TL for males, and 275 and 450 cm TL for females were considered subadults, and all sharks over these thresholds were considered adults (Estrada et al., 2006). This study used CATS Cam biologging tags (generation 6 or 7, Customized Animal Tracking Solutions, Australia) containing triaxial accelerometers, gyroscopes, and magnetometers (sampling at 20–50 Hz), and light, temperature,

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and depth sensors (sampling at 10 Hz) in similar methods to those described in Chapple et al. (2015) and Jewell et al. (2019). Tags were attached to the first dorsal fins of free-swimming sharks using customized clamps and tagging poles. The authors timed deployments as sharks swam close to research vessels and no sharks were handled in this study. After tagging, research vessels moved away from sharks to allow natural swimming behaviors to return. The tags remained rigidly in place until released by either a galvanic timed release or preprogrammed electronic release; deployment durations were selected based on forecast weather conditions (i.e., to avoid tags being released during adverse weather when they would be difficult to retrieve). All devices were packaged in a buoyant flotation device and fitted with Smart Position Only Tags (SPOT-363, Wildlife Computers, Redmond, USA), which were used to locate and retrieve them once the tags were released and floating at the surface. All tagging took place during daylight hours and in conditions of under 3 m of swell or 40 km/h of wind.

Data processing and pretreatment

Biologging data from 21 tag deployments was downloaded and processed on Igor Pro (version 8.04) *Wavemetrics* and the Ethographer package (version 2.04) *University of Tokyo* (Sakamoto et al., 2009; Appendix S1: Figure S1). Two activity metrics were calculated to determine whether sharks were more active in certain areas or times: Vectorial Dynamic Body Acceleration (VeDBA) and Tail Beat Frequency (TBF). VeDBA has been used as a proxy to measure energy expenditure from accelerometer data in previous studies and was calculated from the accelerometer's three orthogonal axes (surge, heave, and sway) in the methods described by Qasem et al. (2012). TBF was estimated from oscillations in the lateral rotation (yaw) of gyroscope data (axis Z) using a Fourier transformation in the methods of Sakamoto et al. (2009). As a wide range of sized white sharks were tagged, the effect of body size on TBF needed to be accounted for Sato et al. (2007). Sato et al.'s (2007) scaling relationship for expected stroke frequency: mass$^{-0.29}$ was used to correct this effect, creating a difference from the expected stroke frequency metric based on size (TBF_Diff). Shark TL was first corrected to expected precaudal length using the equations provided by Cliff et al. (1989) and expected mass using Mollet and Cailliet (1996) before being fitted to Sato et al.'s (2007) scaling rate for stroke frequency (TBF) to mass (Appendix S1: Figure S2). The results were left-skewed, as only the largest white sharks met the expected values on this scale, and so the values were normalized to give an even range of values above and below zero.

Differences in swimming depth and the rate of movement through the vertical environment by marine predators can indicate differences in habitat use (Andrzejaczek, Gleiss, Pattiaratchi, et al., 2019). Pressure sensor data (Depth) and a maximum depth value of each hour of data (Depth_Max) were used to determine the depth use of sharks in different areas and times using the mask analysis in Ethographer. Vertical velocity (VV) was calculated using a 10-s running mean on depth use data and calculating the difference of successive periods using a 1-s interval (Andrzejaczek et al., 2018; Andrzejaczek, Gleiss, Lear, et al., 2019). These values were then converted to an absolute scale (VV_abs).

Predators encountering prey are expected to react by increasing their turning rates and adopting horizontal search patterns (Hays et al., 2016). Therefore, tortuosity of tracks was used to examine whether sharks were swimming with more or less horizontal patterns in different areas or times using the circular package (version 0.4-93) of R (version I386 3.5.1) (Andrzejaczek et al., 2018; Lund & Agostinelli, 2017; R Core Team, 2018). First, the heading of movements was estimated using the dead reckoning package of Framework4, Swansea University (Walker et al., 2015). Accelerometer, magnetometer, and depth data were used to reconstruct three-dimensional pathways away from a shark's tagging location based on estimates of movement (using an assumed constant speed) and direction. Estimated pathways can be validated and adjusted using pitch, roll, and first location of SPOT transmissions post-release, yet may be subjected to significant error from environmental conditions (such as currents). As a result of these errors, dead reckoned paths are not a true representation of where movements took place but accurately predict the shape and angles of movement in three dimensions (Andrzejaczek, Gleiss, Lear, et al., 2019). Three separate time frames were selected, 1, 5, and 20 min, to account for finer (indicative of interactions with prey or habitat features, i.e., Jewell et al., 2019) and larger scale (indicative of residency periods or area-restricted search, i.e., Towner et al., 2016) changes in heading. Second, a value of tortuosity was determined sensu Andrzejaczek et al. (2018) using the mean resultant length of heading, $\overline{R}$, calculated from the concentration of circular heading data (Pewsey et al., 2013). An $\overline{R}$ value approaching one would result if all points clustered around a mean direction and represent a completely straight heading during the period. A value of 0 would result from evenly spread headings over time representing a very tortuous or back-and-forth path (R1, R5, and R20).

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Dynamic activities were used to examine whether there were times or areas where sharks may be feeding, calculated using the bursting rate threshold used in Jewell (2022), 0.6 g of VeDBA. Counts of total bursts per hour in each hour of data collection (BpH) and a binary count of whether a burst event was present during each hour of data collection (BPs) were calculated in Ethographer.

Time series were separated into diel phases (i.e., day, dusk, night, and dawn) to determine the effect of differences in light levels. Diel phases were determined using data on nautical twilight times for each area and date using www.timeanddate.com. Crepuscular phases were classified from an hour after sunrise or before sunset to the beginning or end of nautical twilight. An hour of data was excluded between each diel phase to account for transition periods between phases (i.e., the first and last hours of daytime or night). All data were extracted from the individual deployment time series to give an average and SD for each metric (i.e., VeDBA_Avg, VeDBA_StD, etc.).

Statistical analyses

Multivariate analyses were used to determine the influence of internal (size class and sex) and external (area and diel phase) factors on the fine-scale movement ecology of white sharks. As not all size classes were present in each area (i.e., only juvenile sharks were tagged at Aptos), area and size class were combined (Area-Class). Area-Class contained seven levels: that is, FAR-Adult, FAR-Sub-Adult, ANO-Adult, ANO-Sub-Adult, TOM-Adult, TOM-Sub-Adult, and APT-Juvenile. Data were first checked for autocorrelation and skewness using a Draftsman plot and associated Pearson's correlations. These tests demonstrated that none of the 20 variables were highly autocorrelated (all $r < 0.95$) and were retained, but some required transformation. As a result, VeDBA_StD, Depth_Max_StD, BpH_Avg, and BpH_StD were Ln + 0.00001 transformed and Depth_Avg, Depth_StD, and Depth_Max_Avg were square-rooted. As data for several of the 20 variables were not directly comparable due to their different units of measurement, values were normalized to place them on a common scale. Finally, to account for the fact that different numbers of variables represented different types of movement, each variable was assigned one of five categories, that is, *Activity* (VeDBA_Avg, VeDBA_StD, TBF_Diff, TBF_StD), *Depth use* (Depth_Avg, Depth_StD, Depth_Max, Depth_Max_StD), *Turning* (R1_Avg, R1_StD, R5_Avg, R5_StD, R20_Avg, R20_StD), *Dynamic activity* (BPs_Avg, BPs_StD, BpH_Avg, BpH_StD), and *Vertical velocity* (VV_abs_Avg, VV_abs_StD). A weighting procedure was carried out in which each category was given an arbitrary weight of 100, divided equally among its component variables.

The pretreated data were used to construct a Euclidean distance matrix and subjected to three-way PERMANOVA to test whether movement metrics differed significantly ($p < 0.05$) between Area-Class, Diel Phase and Sex, and interactions between the main effects (Anderson, Gorley, et al., 2008). Note that in this preliminary test, data from sharks of unknown sex (5) were excluded. The results demonstrated that while significant differences were detected between Area-Class ($p = 0.001$) and Diel Phase ($p = 0.016$), Sex was not influential as a main effect ($p = 0.078$) and in any two- and three-way interactions ($p = 0.103$–0.788). Thus, Sex was removed as a factor, and the analyses were rerun as a two-way PERMANOVA. The percentage contribution made by the MS for each factor and interaction to the corresponding total MS in each PERMANOVA test was calculated to estimate the relative importance of each factor and interaction in that test (Crisp et al., 2018). When a significant difference was detected, pairwise PERMANOVA was employed to determine which levels of a factor were responsible.

The Euclidean distance matrix was subjected to the Bootstrap Averages Routine (Clarke & Gorley, 2015) to bootstrap those samples in metric multidimensional scaling (mMDS) space. The averages of repeated bootstrap samples (bootstrapped averages) for each group of samples were used to construct an mMDS ordination plot. Superimposed on each plot was: (1) a point representing the group average (i.e., the average of the bootstrapped averages) and (2) the associated, smoothed, and marginally bias-corrected bootstrap region, in which 95% of the bootstrapped averages fell. This process was repeated for each main effect.

The values for each variable were averaged across their component levels (i.e., separately for each of the seven location and size classes and for the four diel phases) and standardized by the maximum average value for each variable to show which variables were responsible for any differences in movement ecology for each main effect. These percentages were used to construct a shade plot (Clarke et al., 2014). The depth of the shading for each variable denotes the percentage of the maximum value recorded. The levels of each factor (i.e., area-size class or diel phase, *y* axis) were arranged based on a dendrogram derived from hierarchical agglomerative cluster analysis with variables (*x* axis) arranged in optimal serial order constrained by their category.

RESULTS

Description of shark movements

We tagged 21 white sharks from four areas off the Central Californian coast. Deployments lasted between

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2.5 and 148.5 h (deployment duration 43 ± 33 h; mean ± SE), producing a total of 908 h of biologging data (Table 2). All sharks were tagged during daylight and appeared to stay within the tagging areas for at least the remainder of the day post tagging. Sharks at the Farallon Islands appeared to move further from the island systems during the night as indicated by swimming into deeper water with straighter movements before returning to shallower water, of similar depth as tagging locations during the daylight (Figure 2A). At Año Nuevo Island and Tomales Point, there were fewer movements to deeper waters observed. Instead, movements close to Año Nuevo Island during the day and back and forth across the surrounding continental shelf during other times were identified (Figure 2B), while back-and-forth movements across the Point Reyes headland were identified in dead reckoned paths of sharks tagged at Tomales during both daylight and night (Figure 2C).

TABLE 2 Meta data of tagging efforts.

Log ID by location	Date	TL (cm)	Sex	Size class	Reference ID	Duration (h)
Tomales Point						
TOM01	10/11/2018	460	F	Adult	TOM_CC0705_20181110	54.1
TOM02	18/11/2018	400	M	Adult	TOM_CC0705_20181118	44.1
TOM03	05/10/2017	400	M	Adult	TOM_CC0705_20171005	36.6
TOM05	15/10/2017	426	M	Adult	TOM_CC0705_20171015	29.0
TOM06	25/10/2017	400	F	Subadult	TOM_CC0704_20171025	10.3
TOM08	05/11/2017	290	F	Subadult	TOM_CC0704_20171105	6.2
TOM22	29/10/2019	275	F	Subadult	TOM_CC0704_20191029	57.2
TOM23	03/11/2019	320	M	Subadult	TOM_CC0707_20191103	66.8
Total of eight deployments						304.3
Año Nuevo						
ANO07	07/11/2019	400	F	Subadult	ANI_CC0617_20191107	29.4
ANO08	10/11/2019	460	F	Adult	ANI_CC0704_20191110	5.2
ANO09	11/11/2019	380	F	Subadult	ANI_CC0706_20191111	52.8
ANO10	12/11/2019	380	U	Subadult	ANI_CC0704_20191112	9.6
ANO11	13/11/2019	490	U	Adult	ANI_CC0707_20191113	74.4
Total of five deployments						171.4
Aptos						
APT01	18/07/2018	215	F	Juvenile	APT_CC0705_20180718	148.5
APT03	10/08/2018	215	U	Juvenile	APT_CC0705_20180810	29.6
APT04	22/08/2019	260	U	Juvenile	APT_CC0705_20190822	3.8
APT05	29/08/2019	190	U	Juvenile	APT_CC0706_20190829	92.4
APT06	29/08/2019	220	F	Juvenile	APT_CC0704_20190829	5.5
APT07	30/08/2019	230	U	Juvenile	APT_CC0704_20190830	41.6
APT08	20/09/2019	250	M	Juvenile	APT_CC0704_20190920	2.5
Total of seven deployments						323.9
Farallon Islands						
FAR01	16/10/2018	485	F	Adult	FAR_CC0704_20181016	44.2
FAR02	21/10/2018	550	F	Adult	FAR_CC0737_20181021	31.5
FAR03	11/10/2019	440	F	Sub-adult	FAR_CC0704_20191011	33.1
Total of three deployments						108.8
Overall totals	2017–2019	190–550			21 deployments	908

Note: Twenty-one sharks were tagged with CATS Camera biologging tags in four areas off Central California between October 2017 and November 2019, totaling 908 h of usable data.
Abbreviation: TL, total length.

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At Aptos, no sharks appeared to travel far from their tagging locations, all biologgers popped up in the vicinity of their deployment locations, and this was also suggested from dead reckoned paths, highly tortuous movements, and depth traces (Figure 2D). In all areas, metrics describing tortuosity and activity of movements indicated high levels of linear swimming and lower levels of activity at night compared with during the day (Appendix S1: Figure S3). Depth use was highest at the Farallon Islands (22.4 ± 13.6 m during day and 33.7 ± 17.5 m during night), followed by Año Nuevo (17.13 ± 10.3 m during day, 16.0 ± 7.7 m during night), Tomales (8.8 ± 4.8 m during day, 10.2 ± 4.8 m during night), and Aptos (3.2 ± 2.1 m during day, 2.8 ± 1.3 m during night). The Farallon Islands and Año Nuevo had comparable vertical velocities, with VV peaking at dawn at the Farallon Islands (0.13 m/s) and Day in Año Nuevo (0.14 m/s); meanwhile, Tomales and Aptos had lower levels of VV, with Tomales peaking during the day (0.07 m/s) and Aptos at dusk (0.04 m/s). There were no clear patterns in dynamic activities, with values of bursting at Aptos slightly higher than other areas, although a value of 2.9 bursts per hour at dusk was primarily driven by one individual that performed 39 burst swims in a single hour.

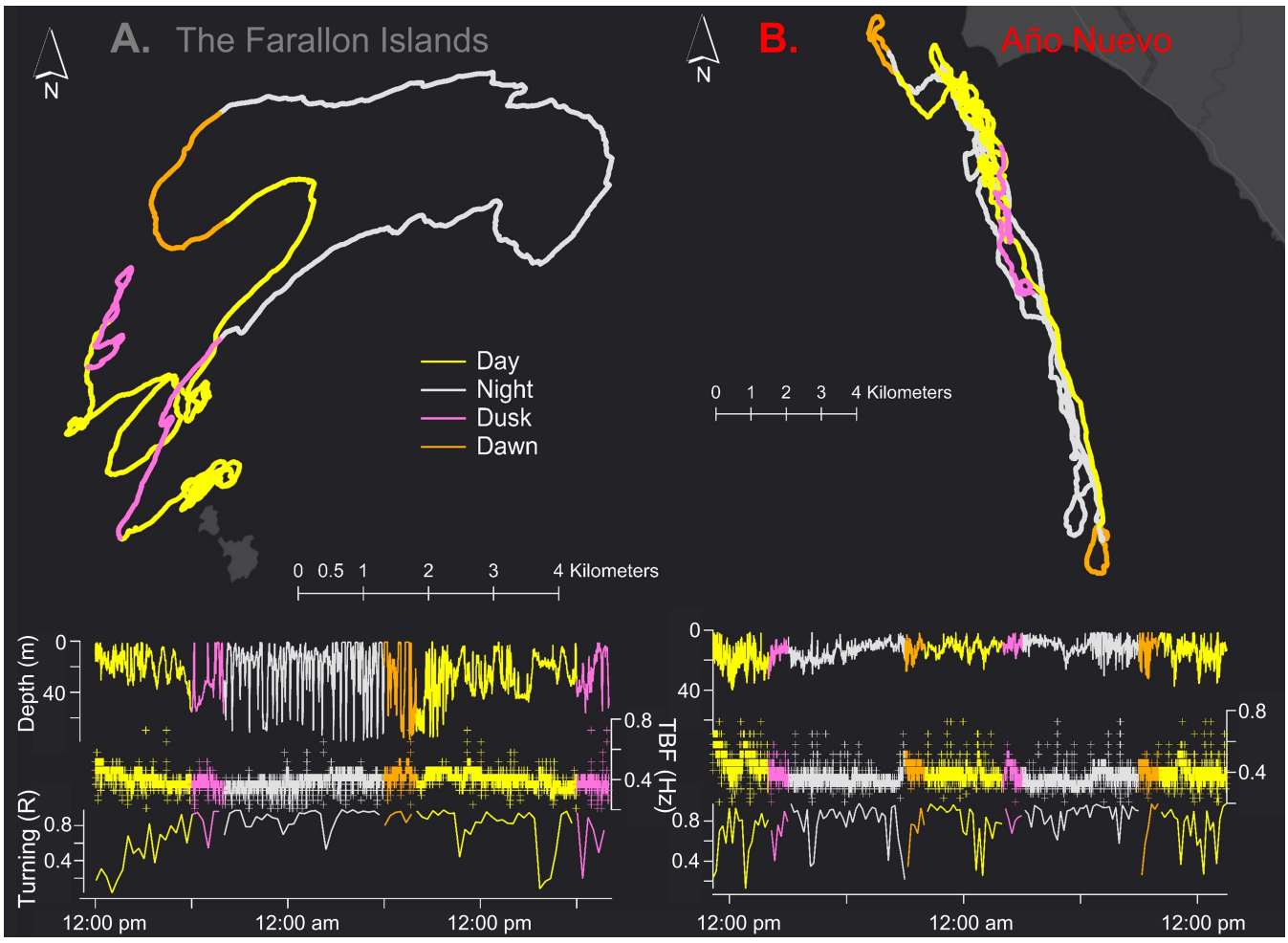


FIGURE 2 Representative tracks and activities from each aggregation area. Estimated pathways made with deduced reckoning are drawn in color, indicating day (yellow), night (gray), dusk (pink), and dawn (orange). While depths, tail beat frequencies (TBF), and turning rates over 20-min intervals (R_20) are displayed in time series and colored by the same periods below. Four examples are given: (A) a deployment from a 440-cm total length (TL) female white shark tagged at the Farallon Islands that swam to deeper water by night before returning to the islands by day (confirmed by sightings and detachment SPOT location). (B) A deployment from a 400-cm TL male white shark at Año Nuevo Island with a similar movement pattern away from the island at night before returning during the day. (C) A 440-cm female white shark at Tomales Point that does not demonstrate nighttime movements away from the aggregation area. (D) A 230-cm unsexed juvenile white shark at Aptos. This shark also stayed close to the coastline during the day and night, although it did move straighter and into slightly deeper water during the night compared with shallow tortuous daytime movements.

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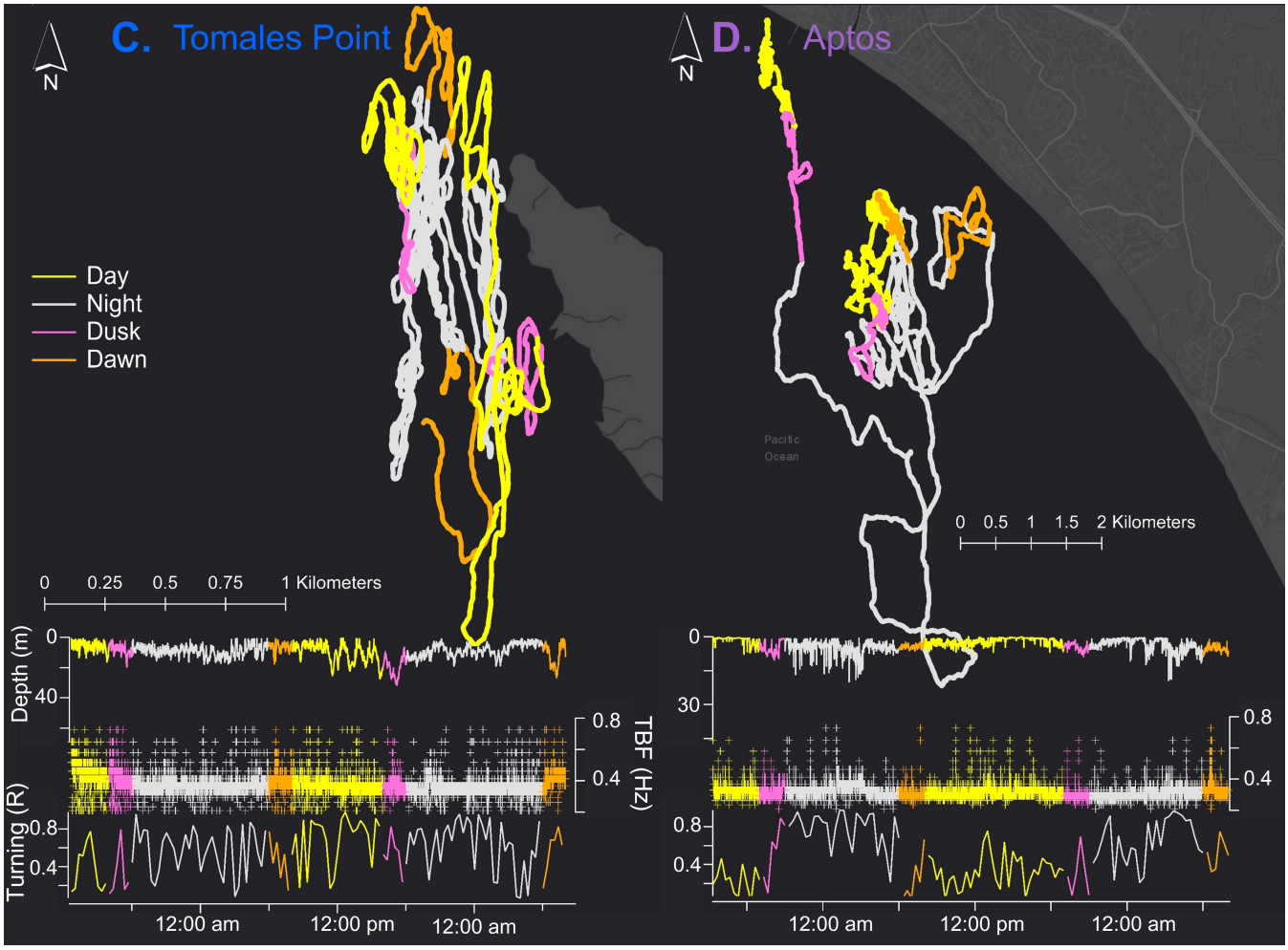


FIGURE 2 (Continued)

Multivariate analyses of movement characteristics

The movement characteristics of the sharks differed significantly between Area-Class (the combined factor incorporating location and demographic), Diel Phase, and their interaction was also significant (Table 3). Area-Class exerted the biggest influence on shark movement characteristics, explaining over 80% of the variation, followed by Diel Phase at 11%. The Area-Class × Diel Phase interaction accounted for less than 5% of the variation and was caused by different patterns in response to changing diel phases, with sharks of all sizes at the Farallon Islands exhibiting a greater shift in movement between diel phases, swimming significantly deeper than those at Año Nuevo Island, Tomales Point, and Aptos, particularly at night (Appendix S1: Figure S3).

Pairwise PERMANOVA tests detected significant differences between all combinations of areas and size classes ($p = 0.001$–0.036) except for that between adults and subadults at the Farallon Island ($p = 0.287$; Table 4). The largest differences were between Aptos juveniles and sharks in all other areas and size classes ($t = 7.75$–5.50) except for Tomales Point subadults ($t = 4.01$), meaning Aptos juveniles had the most distinct movement characteristics. The next most distinct movements were undertaken by both size classes of sharks at Tomales Point ($t = 4.66$–2.90). In contrast, the most similar movement characteristics were between sharks of different size classes within the same aggregation areas ($t = 1.14$–1.94), although there were similarities between both size classes at Año Nuevo Island and the Farallon Islands ($t = 1.93$–2.5). These differences are also seen on the mMDS ordination plot, where juvenile sharks from Aptos appear on the left and sharks of both size classes at Año Nuevo Island and the Farallon Islands on the right (Figure 3A).

A shade plot was constructed to visualize the differences in each of the 20 movement metrics among sharks in each Area-Class group. The associated cluster dendrogram grouped those area-classes that were most similar, and in all cases where multiple size classes were present

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TABLE 3 Results of two-way PERMANOVA test on the movement characteristics of white sharks in California waters between Area-Class and Diel Phase.

Source	df	MS	%MS	pF	*p*
Area-Class	**6**	**166,940**	**80.71**	**23.62**	**0.001**
Diel Phase	**3**	**23,466**	**11.35**	**3.32**	**0.001**
Area-Class × Diel Phase	**18**	**9355**	**4.52**	**1.32**	**0.035**
Residual	130	7067	3.42		

Note: Percentage MS (%MS), pseudo-F (pF), and significance values (*p*) are shown. Significant differences appear in boldface.

TABLE 4 *T*-statistic values derived from a pairwise PERMANOVA on the movement characteristics of Californian white sharks from different area and size classes.

Area and size class	APT-Juv	TOM-sub	TOM-Adt	ANO-sub	ANO-Adt	FAR-sub
TOM-Sub	4.07					
TOM-Adu	5.53	1.94				
ANO-Sub	6.47	2.95	2.90			
ANO-Adt	7.35	4.06	3.93	1.75		
FAR-Sub	5.86	3.64	3.74	2.29	2.29	
FAR-Adt	7.75	4.50	4.66	2.48	1.93	1.14*

Note: All pairwise tests were significant except the different size classes at the Farallon Islands (FAR-Adt to FAR-Sub) as denoted by an asterisk. See Table 1 for an explanation of location abbreviations. Size classes are: Sub, subadult; Adu, adult; Juv, juvenile.

in an area, it grouped them together first, thus providing evidence that area rather than size class was the greatest factor influencing movement. Depth use and TBF were two of the main contributing factors to the differences between Area-Class (Figure 3B). For instance, juvenile sharks at Aptos spent little time in waters below 10 m, whereas all sharks from both size classes at Año Nuevo and the Farallon Islands averaged swimming depths of greater than 10 m regardless of diel phase.

Nighttime movement characteristics of sharks of all classes and in all areas were significantly different from all other diel phases (PERMANOVA; $p < 0.01$; Table 5). There were only marginal insignificant differences between day versus both dawn and dusk ($p = 0.07$ and 0.06, respectively) and no significant difference between dawn and dusk ($p = 0.850$). Metric MDS visualizations followed the same trend, with night widely separated from other phases, but with the 95% confidence regions of the other three phases overlapping (Figure 4A). Activity metrics were the main contributors to this difference between night and the other phases. All four metrics (TBF_Diff, VeDBA_StD, VeDBA_Avg, and TBF_StD) were the highest ranked, indicating that daytime activity was higher and more variable than night. Vertical velocities were also higher during the day, and turning metrics indicated sharks swam straighter and less variably during the night (Figure 4B). The depth and bursting metrics were similar across all phases, with variability in (Depth_StD) lowest at night (Appendix S1: Figure S5).

DISCUSSION

White sharks are large endothermic predators that utilize specific coastal locations as foraging areas for periods each year. Adult sharks are known to specialize on marine mammal prey, and their specific foraging areas are usually associated with pinniped colonies, while young of the year specialize on piscivorous prey and transitional periods occur as individuals grow through juvenile and subadult stages of life (French et al., 2018; Kanive et al., 2021). Central California provides an interesting location to test how these ontogenetic changes may affect the movement ecology of the species, as it is one of the few known places in the world where white sharks of all stages of life can be found. Animals with movement characteristics that are shaped by internal process have less ability to adapt to external factors and have less plasticity in their movement and behavioral routines as a result (Martin et al., 2013; Nathan et al., 2008). For instance, Port Jackson sharks *Heterodontus portusjacksoni* display similar nocturnal behaviors wherever they are found (Kadar et al., 2019; Kelly et al., 2020). If that were the case with white sharks, we would expect to see similar daily routines

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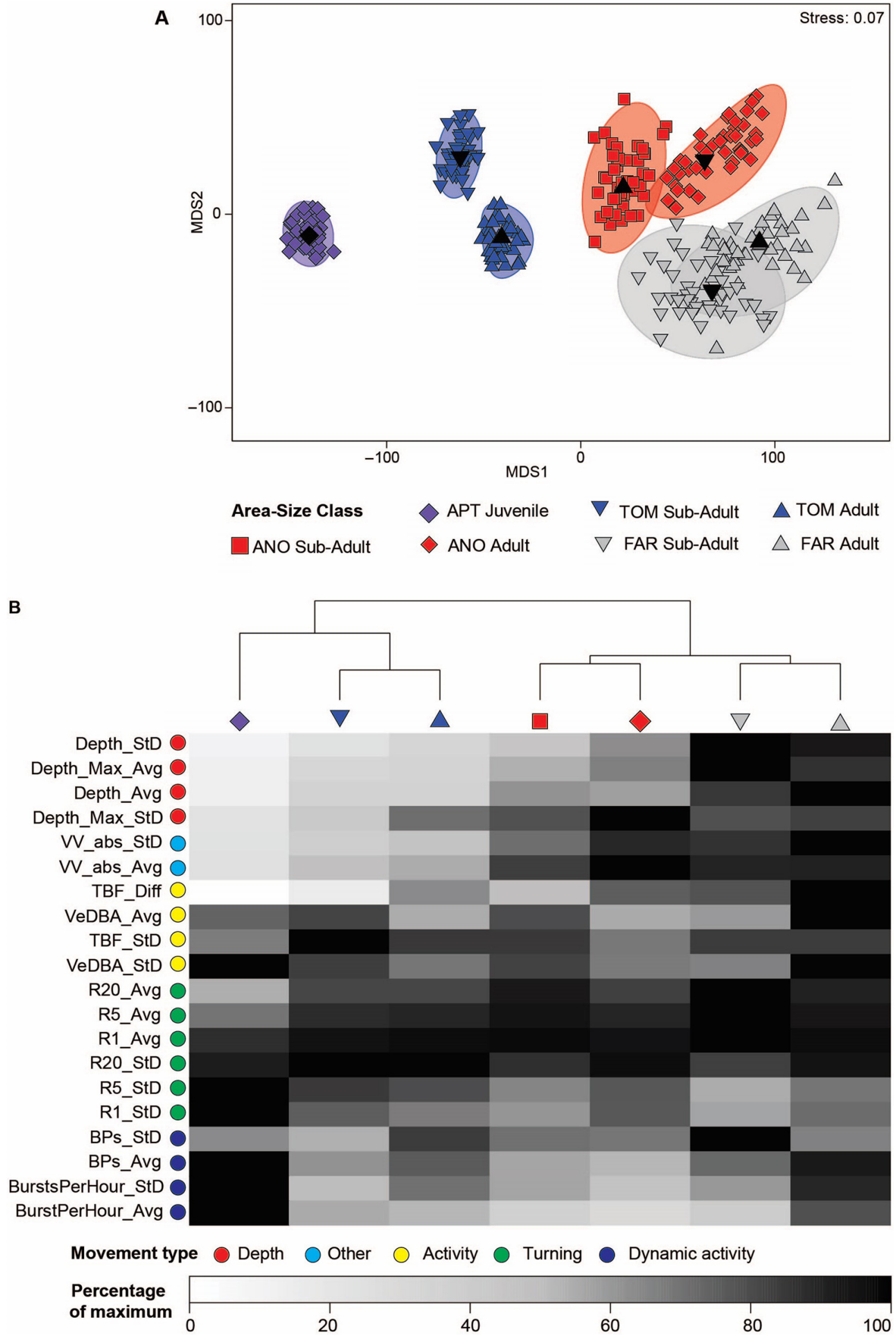


FIGURE 3 Legend on next page.

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TABLE 5 *T*-statistic results derived from a pairwise PERMANOVA on the effect of diel phase on movement characteristics of Californian white sharks.

Diel phase	Day	Dawn	Dusk
Dawn	1.55		
Dusk	1.53	0.65*	
Night	2.41	1.92	1.83

Note: All pairwise tests were significant except between dawn and dusk, as denoted by an asterisk.

and movement characteristics from individuals of similar size and sex, regardless of the area they occupied. However, in our results, over 900 h of movement data from 21 sharks ranging in size from 190 to 550 cm found that area had the greatest influence on movement characteristics, with white sharks tagged at the offshore islands (the Farallones) where surrounding waters are of deeper depths, differing from those at inshore islands (Año Nuevo) or the headland (Tomales Point) where bathymetry might constrain movements, regardless of shark size. It is worth noting that individual sharks are not restricted to any single area of the region and are often found to visit multiple aggregation sites in a single year (Chapple et al., 2016; Jorgensen et al., 2010, 2019; Kanive, 2020). These results support the hypothesis that white sharks have plastic foraging behaviors that are adapted to prevailing conditions (Benoit-Bird et al., 2013; Bradford et al., 2020). This plasticity is further supported by their diverse diets (Carlisle et al., 2012; French et al., 2018), and swimming strategies (Andrzejaczek et al., 2022; Kock et al., 2018; Watanabe et al., 2019b). Adopting plasticity in their behavioral routines would enable white sharks to take advantage of local foraging opportunities or prey adaptions, such as seen in South Africa, where in some areas Cape fur seals *Arctocephalus pusillus* are more easily caught at dawn and sharks are more active then, while in others they refuge in and around kelp forests where sharks are active throughout the daytime (Jewell et al., 2014; Kock et al., 2013).

By comparing the movements of sharks at four locations with similar biologging tags, we identified significant differences in movement characteristics between size classes, but also consistent effects of diel phase, suggesting internal factors, particularly physiology, constrain at least some aspects of white shark movement ecology and behavioral routine. Stronger jaws and more cuspid teeth make larger sized sharks better adapted to predating on the large marine mammals present at these sites (Ferrara et al., 2011). However, white sharks of all sizes are also considered visual predators, using eyesight to detect their prey, meaning changes in ambient light levels through diel phase or local oceanographic conditions may determine optimal times for these predations to take place regardless of prey targeted (Laroche et al., 2008).

The differences in movements between day and night were stark, particularly in island systems. At night, movements of sharks tagged at the Farallon Islands were away from the island group toward deeper waters, and at Año Nuevo they were away from the island rookery along the continental shelf. During the day, sharks were, in general, more active, engaged in more vertical movement, and swam in more tortuous paths (Figure 4), all of which have been linked to foraging behavior in other species of sharks where increased searching/encounter behavior is suggested by this type of locomotion (Andrzejaczek, Gleiss, Lear, et al., 2019; Gleiss et al., 2013; Lear et al., 2021). However, there were areas where crepuscular periods had similar patterns in locomotion, with sharks at the Farallon Islands and Aptos more active and tortuous at dawn and dusk, respectively. Andrzejaczek et al. (2022) concluded that white sharks in Central California may focus foraging efforts in morning hours, while there is also evidence that white sharks forage for pinnipeds at night in other locations (Moxley et al., 2020; Watanabe et al., 2019a; Winton et al., 2021). More research is needed to determine what movement characteristics correspond to foraging behaviors and how these shape the diel routines of white sharks, yet it is likely localized swimming strategies of pinnipeds, depth and complexity of habitats, and ambient light levels all play a role.

Swimming away from island pinniped colonies at night may indicate foraging on prey other than pinnipeds. White shark retinas have an increase in retinal cones from the periphery to the center, indicating specialization for day and night vision (Gruber & Cohen, 1985), and while offshore, they are thought to forage at depths in the "twilight zone" within the deep scattering layers, where

FIGURE 3 White shark movement characteristic differences by location (area) and size class. (A) Two-dimensional metric multidimensional scaling (mMDS) ordination plot constructed from the bootstrapped averages from 45 iterations of the movement characteristics of Californian white sharks of different sizes at different areas. The group average (black symbols) and approximate 95% region estimates (shaded areas) are fitted to the bootstrap averages for each Area-Class. (B) Shade plot of the standardized value of each 20 movement characteristics (i.e., % of the maximum value) for shark in each Area-Class. The order of the area-classes (*x* axis) is determined by hierarchical agglomerative clustering and the characteristics (*y* axis) are determined by seriation constrained by their categories. Box plots of the values are provided in Appendix S1: Figure S4. ANO, Año Nuevo Island; APT, Aptos; FAR, Farallon Islands; TOM, Tomales Point.

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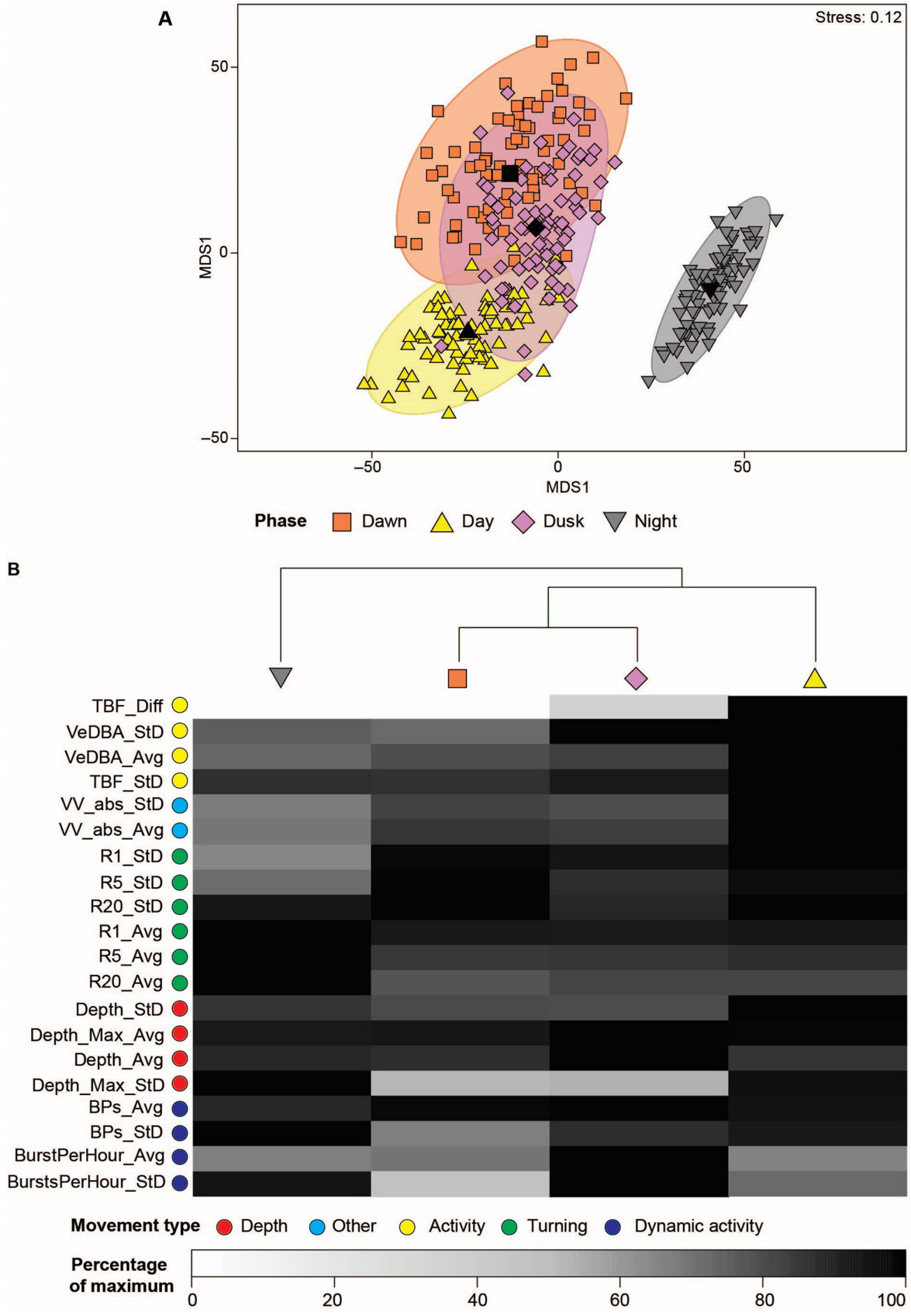


FIGURE 4 Legend on next page.

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illumination is highly limited (Jorgensen et al., 2010; Le Croizier et al., 2020). The timing of northern elephant seal mortality, inferred from the cessation of satellite tag transmissions, suggests that some predation, possibly by white sharks, may occur at night (Beltran et al., 2021). At night, seals forage on small fish and cephalopod prey, particularly in deep waters (Adachi et al., 2021); white sharks may feed on similar prey in deeper waters off the Farallon Islands at night, or on foraging elephant seals at depth. Alternatively, the repeated diving we observed during the night may be a cost-efficient swimming strategy during conditions that are suboptimal for foraging on pinnipeds (Gleiss, Norman, et al., 2011; Gleiss, Wilson, et al., 2011). Meanwhile, the continental shelf waters off Tomales Point and Año Nuevo Island may offer the opportunity to encounter other pinniped species, such as harbor seals in the water column regardless of time of day. Such strategies would explain why sharks swam away from the island foraging areas at night and returned during the day when pinniped predations are observed at the surface, while at Tomales, no significant difference in area usage between day and night was apparent (Klimley et al., 1992; Laroche et al., 2008).

White shark movement characteristics from Aptos were the most unique of our results (Figure 3); the sharks tagged here were also the least variable in size, with almost all white sharks found here being either young of the year or juvenile (Tanaka et al., 2021). The movements from Aptos also had the highest rates of tortuosity and the most limited depth range, particularly during day, dawn, and dusk, suggesting that the sharks there may be highly residential despite there being no focal foraging location, such as a pinniped colony in the other studied areas. Juvenile animals are expected to be more constrained by internal influences because they have high mass-specific metabolic rates and are, in general, smaller and less experienced (Byrnes et al., 2021; Martin et al., 2008). Additionally, juvenile white sharks also have a different foraging ecology and lower thermal inertia (Anderson et al., 2022; Harasti et al., 2017; Tamburin et al., 2020). The influence of these physiological factors is thought to limit juvenile white sharks to warmer coastal areas in the Northeast Pacific (Anderson et al., 2021; Lowe et al., 2012; Spurgeon et al., 2022), which means they are only present at Aptos from late spring to early fall. Such constraints are likely drivers of the differences between movement behaviors of sharks tagged at Aptos and all other areas. Furthermore, this may also contribute to the different behavior recorded between subadults and adults at Tomales Point and Año Nuevo Island. Among diverse predator taxa as well as elasmobranchs, larger individuals are expected to exclude smaller competitors from preferred foraging areas (Carbone et al., 2011; Lear et al., 2021; Wacker & Amundsen, 2014), particularly conspecifics (Goldman & Anderson, 1999; Jewell et al., 2013). Some elasmobranch species partition aggregations to limit competition between size classes (Papastamatiou et al., 2018), yet subadult white sharks are often present in the same areas as adults (Kanive et al., 2019). When present at the same foraging areas as adults, subadults may be learning how to forage on pinniped prey while being excluded from prime feeding locations or times by adults. Bites from conspecifics are well documented in white shark aggregation areas (Domeier & Nasby-Lucas, 2007), and smaller individuals have been observed waiting for larger individuals to leave before feeding on whale carcasses (Dicken, 2008; Dudley et al., 2000). A transitional period is therefore likely occurring (French et al., 2018), where subadult white sharks are occupying adult foraging habitat, while not being fully reliant on pinniped prey due to competition by larger individuals, which could therefore give rise to distinct movement characteristics.

Differences in sex, particularly during reproductive periods, can become an important internal factor influencing movement and routine (Martin et al., 2008; Nathan et al., 2008). Sexual dimorphism, segregation, and behavioral differences are common in shark species (Jacoby et al., 2010; Mucientes et al., 2009; Sims, 2005). In white sharks, sexual differences in demographics at aggregation sites have been linked to environmental conditions, prey preferences, and location (Bruce & Bradford, 2015; Kanive et al., 2019; Robbins, 2007; Towner et al., 2013). Differences in migration patterns and movement strategies have also been described (Domeier & Nasby-Lucas, 2012; Spaet et al., 2020; Towner et al., 2016). Yet, there were no significant differences found in our study, potentially due to low statistical power because males were tagged at Aptos and

FIGURE 4 Differences in white shark movement characteristics by diel phase. (A) Two-dimensional metric multidimensional scaling (mMDS) ordination plot constructed from bootstrapped averages from 45 iterations of the movement characteristics of Californian white sharks by phase of the day. The group average (black symbols) and approximate 95% region estimates (shaded areas) are fitted to the bootstrap averages for each phase of the day. (B) Shade plot of the standardized value of each 20 movement characteristics (i.e., % of maximum value) for sharks in each phase of the day. The order of the phase of the day (*x* axis) is determined by hierarchical agglomerative clustering and the characteristics (*y* axis) are determined by seriation constrained by their categories. Box plots of the values are available in Appendix S1: Figure S5.

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Tomales Point but not at Año Nuevo Island and the Farallon Islands.

Conclusions and future directions

The use of biologging tags and multivariate analysis in this study revealed differences in the movements and routines of adult and subadult white sharks at different habitats and provided evidence for plastic responses to local conditions in this species. Such responses may have helped white sharks to become a top predator that is widely distributed in temperate marine ecosystems across the globe (Huveneers et al., 2018). However, these differences may also result from long-term specializations of older individuals that may have developed by foraging in the same areas for multiple years, sometimes decades (Anderson et al., 2011). If the latter is true, it would explain why white sharks are now only reliably found in a limited number of aggregations that are often located in protected areas with abundant pinniped prey, highlighting the importance of maintaining or expanding the protection of these sites and the species that inhabit them. The differences detected across ontogeny, and evidence of a conserved circadian rhythm (Jewell, 2022), are examples of internal influences that may constrain the species' movements and routines, further highlighting that white sharks may be vulnerable to changing environments.

AUTHOR CONTRIBUTIONS

Oliver J. D. Jewell, Taylor K. Chapple, Salvador J. Jorgensen, and Adrian C. Gleiss conceived the study. Oliver J. D. Jewell, Taylor K. Chapple, Salvador J. Jorgensen, Paul Kanive, Jerry H. Moxley, Scot Anderson, and Barbra A. Block took part in fieldwork, either to program instruments, tag animals, or retrieve units' post-deployment. Oliver J. D. Jewell, Taylor K. Chapple, Salvador J. Jorgensen, and Jerry H. Moxley curated data. Oliver J. D. Jewell, James R. Tweedly, and Adrian C. Gleiss performed analysis and produced visualizations. Oliver J. D. Jewell led the manuscript write-up. Taylor K. Chapple, Salvador J. Jorgensen, and Adrian C. Gleiss supervised the manuscript write-up. All authors contributed to drafting and revisions of the manuscript and approved each submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Jewell et al., 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.10676876.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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