Vol. 639: 155–167, 2020
https://doi.org/10.3354/meps13271

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 2

Common thresher shark *Alopias vulpinus* movement: Bayesian inference on a data-limited species

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ABSTRACT: Within the fields of biology and ecology, animal movement is arguably one of the most basic, and yet, often one of the most difficult areas of study. Where and why animals migrate, and what patterns can be derived from individual movements in order to make population-level inferences are key areas when attempting to define basic population dynamics. These questions are of equal interest to biologists and managers, with many species assessments identifying improvements in the understanding of population-level movement as a key research need. We aimed to improve our understanding of population level movement for common thresher sharks *Alopias vulpinus* by leveraging the largest satellite tagging dataset available for this species. Using a Bayesian approach specifically designed to address population-level questions with sparse telemetry data, we identified that *A. vulpinus* off the west coast of North America are partial migrators which conditionally migrate, based on a combination of fixed intrinsic states (size, sex) and variable extrinsic states (e.g. season, environment). Waters of the Southern California Bight were identified as an area where, seasonally, a large variety of sizes of *A. vulpinus* can be found. While smaller juveniles can be found throughout the year, larger sub-adults and adults often move out of the Bight during certain seasons (spring and winter). Knowledge of how *A. vulpinus* distribute along the coast, and that season, size, and to some extent sex, play important roles in where and what type of animals are likely to be found, are key pieces of information when attempting to accurately characterize basic biological parameters like age, growth, and reproduction, as well as understanding the effects of variable fishing pressures across the species' range.

KEY WORDS: Bayesian Inference · Eastern Pacific · Ecology · Movement · Satellite tagging · Shark

1. INTRODUCTION

The commercial exploitation of shark species has, in many cases, proven to be a short-lived and unsustainable enterprise (Holts 1988, Camhi 1998, Walker 1998, Stevens et al. 2000). Factors such as slow growth, late maturity, and low fecundity make certain species particularly susceptible to harvest. Additionally, the nature of shark fisheries often requires high catch per unit effort in order to offset the fluctuating commercial value and market demand for shark products (Holts et al. 1998). As a result, maintaining ecologically and economically sustainable shark fisheries requires carefully planned, science-based management (Kacev et al. 2017).

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Like many other targeted shark fisheries, the commercial gillnet fishery for common thresher sharks *Alopias vulpinus* off the US west coast proved to be very sensitive to high removals. Less than a decade of commercial gillnet fishing in the late 1970s and early 1980s resulted in signs of population decline (Hanan et al. 1993, Holts et al. 1998), forcing the adoption of a number of regional conservation measures (Hanan et al. 1993, Holts et al. 1998, PFMC 2011) and the significant contraction of the fishery over time. In retrospect, this result is not surprising given the conservative life history traits of this species, with *A. vulpinus* being the largest member of the family Alopiidae, reaching up to 6 m in total length, maturing at ~5 yr old at lengths around 160 cm, having small litters of 2 to 4 pups, and an estimated maximum reproductive age of 25 yr (Compagno 2001, Smith et al. 2008). Evidence of potential misidentification of pelagic thresher sharks *A. pelagicus* as *A. vulpinus* in these Pacific studies may have biased these estimates on the low side (H. Dewar unpubl.). Evidence from Atlantic common threshers suggests an even older age (12 yr) and larger size (~216 cm) at maturity (Natanson & Gervelis 2013). *A. vulpinus* seem to reproduce on an annual cycle, although evidence from the Atlantic suggests that their reproductive cycle could be biennial or even triennial (Natanson & Gervelis 2013). This species, in comparison to most commercially targeted teleosts, fits the slow-growing, late-maturing, low fecundity picture of a species that is unlikely to be suited for high levels of targeted commercial exploitation, and suggests that *A. vulpinus* are sensitive to overharvesting (Chapple & Botsford 2013).

Regional conservation measures such as the establishment of the Pacific Leatherback Turtle Conservation Area, along with a shift in the primary target of the California drift gillnet fishery from *A. vulpinus* to swordfish *Xiphias gladius* have likely spurred the recovery of the *A. vulpinus* population along the US west coast over the last 2 decades (Teo et al. 2018). Further, a combination of management policies and declining participation in the US west coast gillnet and longline fisheries (Teo et al. 2018) has resulted in the US portion of the Southern California Bight (SCB) acting as a relative refuge from intensive commercial fishing pressure. However, its history of overexploitation has raised concerns over the growing impact resulting from the recent expansion of the recreational *A. vulpinus* fishery in southern California (Heberer et al. 2010), and the continued catch of the species in the California drift gillnet fisheries (PFMC 2011).

Despite logistical challenges associated with studying highly migratory pelagic species, research on *A. vulpinus* along the California coast is increasing, with physiological (Bernal & Sepulveda 2005, Heberer et al. 2010), behavioral (Aalbers et al. 2010), dietary (Preti et al. 2001), and movement studies (Cartamil et al. 2010a,b, 2011, 2016) adding to our understanding of the biology and ecology of *A. vulpinus*. Population-level movement knowledge to date, mostly inferred from catch patterns of the California drift gill net (CDGN) fishery, indicates that *A. vulpinus* migrate seasonally between Baja California (Mexico) and southern California (USA), with large, adult sharks occasionally found as far north as British Columbia (Canada) (Hanan et al. 1993, Holts et al. 1998, Cartamil et al. 2016). Juvenile *A. vulpinus* use the shallower waters over the continental shelf within the SCB as an important nursery area (Cartamil et al. 2010b). However, the drivers behind movements out of the relative safety of the SCB are unknown. Understanding the mechanisms of migration out of the SCB is important in order to gauge which segment of the population is likely to be exposed to higher levels of fishing pressure in less regulated waters such as those outside of the SCB to the south, and whether spatially explicit management should be considered for this species.

Our work seeks to expand upon the growing body of knowledge about *A. vulpinus* movement ecology by examining the largest satellite tagging dataset available for this species off the coast of California. A Bayesian movement model specifically designed for data-poor telemetry datasets (Kinney et al. 2017) was applied to understand the intrinsic and extrinsic drivers behind *A. vulpinus* movement out of the SCB. Together with the growing pool of *A. vulpinus* research, this analysis can help inform current and future efforts to manage this valuable resource.

2. MATERIALS AND METHODS

2.1. Capture and tagging method

Alopias vulpinus were captured in the waters of the SCB during either the Southwest Fisheries Science Center's (SWFSC) Annual Juvenile Pelagic Shark Abundance Survey, the SWFSC Pre-Recruit Thresher Shark Survey, or during the Pfleger Institute of Environmental Research (PIER) Thresher Shark Survival Study Cruises from 2004–2011. These cruises were carried out onboard the NOAA RV 'David Starr Jordan,' the commercial longline FVs

'Outer Banks' or 'Ventura II,' or small recreational boats used by PIER.

Sharks captured during SWFSC cruises were caught using monofilament or stainless steel longlines and circle hooks baited with dead mackerel *Scomber japonicus* or squid *Loligo opalescens* and left to soak for 3 to 4 h (Runcie et al. 2016). Sharks judged to be uninjured and in good condition were pulled into a specially designed cradle alongside or at the rear of the vessel. A salt-water hose was placed in the shark's mouth to irrigate its gills, and a moist rag was placed over its eyes to keep the animal calm. Strait fork length (FL) was measured to the closest cm, and sex was recorded. Pop-up archival transmitting tags (PAT3, Wildlife Computers; or PSAT X-Tag, Microwave Telemetry), were attached below the dorsal fin with a wooden tagging pole using a nylon anchor inserted into the dorsal muscle. A plastic band (cable tie) was used to keep the transmitter close to the body to reduce drag while swimming. Satellite transmitters with Smart Position and Temperature options (SPOT4, Wildlife Computers), were attached to the first dorsal fin and secured with nylon bolts and stainless steel washers and nuts. Following tagging, the hook was removed when feasible. Otherwise, the fishing line was cut close to the hook and the sharks were released and observed while swimming away from the vessel. Tagging locations were recorded using the vessel's global positioning system (GPS).

Sharks captured on PIER boats were caught using hook and line methods like those used in the current recreational *A. vulpinus* fishery (Sepulveda et al. 2015). Once pulled to the boat, biological measures and tagging operations were the same as onboard SWFSC cruise vessels except for a lack of tissue sampling. All cruises were carried out in the coastal waters off southern California.

2.2. Satellite tags

In total, 25 *A. vulpinus* were tagged from 2004–2011, with SPOT4 or PAT3 tags, and some with both (Table 1). Most tags were sourced from Wildlife Computers, but 7 were from Microwave Telemetry; this affected tag processing, but not the collected data. All PAT3 tags were programed to record ambient temperature, depth, and light levels at either 1 min or 30 s intervals. If the tag was not recovered, data were transmitted to Argos satellites in 12 user-predefined temperature and depth bins (14 for tags in 2008), which represented summarized data over 2 h (2004), 4 h (2005, 2008), or 6 h (2006, 2007, 2009, 2010) intervals. SPOT4 tags were programed to transmit near-real time geolocation data to Argos satellites whenever the antenna and salt-water switch broke the surface of the water long enough to allow data transmission. When recovered, all tag data were downloaded to a computer.

2.3. Geolocation of tag data

Three different geolocation estimates were used to create tracks; light-based geolocation (pop-up archival transmitting PAT or PSAT tags), Argos satellite telemetry (smart position and temperature SPOT tags), and Fastloc® GPS satellite telemetry (SPOT tags with Fastloc® GPS). Light-based geolocation involves the calculation of local noon and midnight based on measurements of light intensity, which can then be used in standard astronomical equations to determine longitude. Day length, assuming the date is known, is then used to calculate latitude. Confounding factors such as negligible differences in day length during the equinoxes, especially at lower latitudes, animal behavior such as diving near dawn or dusk, or simply not returning to the surface on a regular basis, can all significantly affect the accuracy of light-based geolocation estimates. Argos satellite telemetry and Fastloc® GPS are more accurate than light-based geolocation, but Argos in particular can be confounded by the Doppler algorithm used to calculate location during satellite overpasses (Vincent et al. 2002, Maxwell et al. 2011).

Light-based geolocation estimates for Wildlife Computers tags were generated using the 'Trackit' package in R (version 2.15.3) which uses the state-space model developed by Nielsen & Sibert (2007). Tracks were then bathymetrically corrected, where estimated locations with their associated depths were compared to bathymetry charts to correct horizontal locations using the 'analyzepsat' extension to the 'Trackit' package (Galuardi et al. 2010). Microwave Telemetry tags differ from Wildlife Computers tags and consequently were processed using the methods outlined by Cartamil et al. (2016). This approach entailed the use of Arcview GIS, GeoLight, a state-space Kalman filter model, with sea surface temperature matching, and Ocean Data View.

By combining tracking data from both Wildlife Computer tags and Microwave Telemetry tags, the error structure around location estimates differed due to the disparate approaches used to produce each tag's 'most probable' track. Despite these differ-

Table 1. Common thresher sharks *Alopias vulpinus* tagged with pop-off satellite archival tags manufactured by either Wildlife Computers or Microwave Telemetry. Tag number refers to satellite tag number; tags with an asterisk were recovered. Tag type indicates what types of tags were affixed to the animal. Sex was determined when possible by visual observation of presence or absence of claspers between the pelvic fins. Fork length was measured as straight fork length. Deployment lat/long are GPS coordinates of tag attachment locations, last tracking date is the date a tag detached from a shark, and pop-up lat/long are the coordinates of tag detachment locations; some pop-up locations could not be accurately determined and so were omitted. Tracking days are the number of days between tag deployment and detachment. Geolocation methods used to reconstruct most probable track for each tagged animal were A: arcview GIS/GeoLight, L: light-based geolocation, B: bathymetric correction, F: Fastloc GPS, or T: 'Trackit' model

Tag no.	Tag type	Sex	Fork length (cm)	Deployment			Last tracking date	Pop-up latitude (°N)	Pop-up longitude (°W)	Tracking days	Geolocation methods
				date	latitude (°N)	longitude (°W)					
44386*	PAT3/ SPOT4	M	107	04-May-04	33.57	117.85	15-Sep-04	33.57	117.81	134	L, B, T
44388	PAT3/ SPOT4	M	141	05-May-04	33.57	118.00	10-Sep-04	38.01	123.00	128	L, B, T
44390	PAT3/ SPOT4	F	200	03-Jul-04	33.80	119.17	31-Dec-04	32.63	118.78	181	L, B, T
52236	PAT3	F	150	24-Jun-05	33.26	117.65	08-Sep-05	29.49	115.83	76	L, B, T
52237*	PAT3	M	110	26-Jun-05	33.33	117.62	25-Sep-05	33.51	117.94	91	L, B, T
61936	PAT3	M	89	01-Sep-06	32.64	117.16	22-May-07	33.46	117.68	263	L, B, T
61957	PAT3/ SPOT4	F	110	07-Sep-06	34.28	119.37	14-May-07	33.74	120.01	249	L, B, T
61932	PAT3	M	~150	09-Sep-06	34.46	120.29	09-May-07	32.75	120.85	242	L, B, T
61921	PAT3/ SPOT4	M	122	12-Sep-06	34.03	118.67	12-May-07	33.21	121.05	242	L, B, T
61925*	PAT3	M	93	21-Sep-06	32.62	117.15	21-Mar-07	33.11	117.42	181	L, B, T
63975	PAT3	F	98	22-Sep-06	32.61	117.15	18-Apr-07	34.32	119.46	208	L, B, T
63977	PAT3	M	130	10-Sep-07	33.57	117.88	08-May-08	33.19	117.55	241	L, B, T
61938	PAT3/ SPOT4	F	105	11-Sep-07	33.53	117.82	12-May-08	32.33	117.11	244	L, B, T
52238	PAT3	M	114	15-Sep-07	32.65	117.16	14-Mar-08	–	–	181	L, B, T
87565	PAT3	F	125	06-Sep-08	34.33	119.43	20-Dec-08	34.38	121.04	105	A
41494*	PSAT	F	86	20-Sep-08	32.60	117.15	20-Mar-09	28.69	114.85	181	A
41512*	PSAT	F	87	21-Sep-08	32.60	117.15	21-Mar-09	32.53	117.14	181	A
95150*	PSAT	M	76	04-Sep-09	34.29	119.53	04-Mar-10	33.99	118.78	181	A
95139*	PSAT	F	95	05-Sep-09	34.41	119.57	05-Dec-09	34.37	119.85	91	A
95141*	PSAT	M	92	05-Sep-09	34.41	119.57	04-Jan-10	34.70	121.34	121	A
95153*	PSAT	M	82	05-Sep-09	34.41	119.57	05-Jan-10	33.94	118.581	122	A
95155*	PSAT	F	81	06-Sep-09	34.41	119.57	06-Mar-10	34.22	119.492	181	A
100949	PAT3/ SPOT4	F	164	24-Sep-10	33.50	117.76	21-May-11	–	–	239	F,T
60641	PAT3	M	140	22-Jun-11	33.18	117.50	20-Sep-11	33.38	117.59	90	L, B, T
60639	PAT3	M	130	24-Jun-11	33.18	117.50	22-Sep-11	32.32	117.11	90	L, B, T

ences, each type of tag produced Argos location quality codes for estimated locations. Using these codes and estimates produced by Vincent et al. (2002), we produced an average error for both latitude (4.61 km) and longitude (11.29 km) which could be applied to all of our tagging data uniformly for extracting relevant environmental data and to help identify the appropriate scale of the population-level question of interest. More advanced methods for dealing with spatial error, such as the multiple imputation approach (Johnson et al. 2011, Buderman et al. 2016), have been used by others to describe the error around location estimates. However, with the numerous geolocation estimation approaches, constrained latitudinal range, and mixture of 2 different tagging systems (Wildlife Computer and Microwave Telemetry tags) in our analysis, a uniform approach to dealing with spatial error was deemed more desirable then the added complexity of a multiple imputation approach.

2.4. Kernel density defined area

The SCB has been described in numerous studies but with mutable boundaries in many cases (Butler et al. 2003, Pondella & Allen 2008, Nasby-Lucas et al. 2019), often relative to the specific questions or scale of the studies themselves. Our interest in the SCB relates specifically to nearshore areas commonly used by *A. vulpinus* throughout life. To help define such a common access area, we used a 50% kernel density polygon generated around estimated *A. vulpinus* locations, a bandwidth that encompassed coastal water from Point Conception down to just south of the Mexican border, an area common to all definitions of the SCB (Fig. 1). The plasticity of this area was tested via cross validation, by which the kernel was generated multiple times, each time with a single animal's locations removed, to ensure that the kernel was relatively stable and not overly influenced by any single animal. Several variations of differing kernel densities were investigated (25, 40, 60, 95%); however, a 50% kernel proved to be stable following cross-validation tests, while also encompassing a large portion of the area common to all definitions of the SCB. This area is not meant to define a 'home range' or 'core usage area' or any of the other myriad of ecological monikers which carry with them pre-defined descriptions outlining specific uses to a population, thus avoiding the baggage those terms carry from years of misuse due to a lack of standardization (Hall et al. 1997, Laver & Kelly 2008). Rather, our defined kernel is simply a commonly used area that can help identify and understand the intrinsic and extrinsic drivers surrounding *A. vulpinus* movements in and around the coastal waters of California and Mexico.

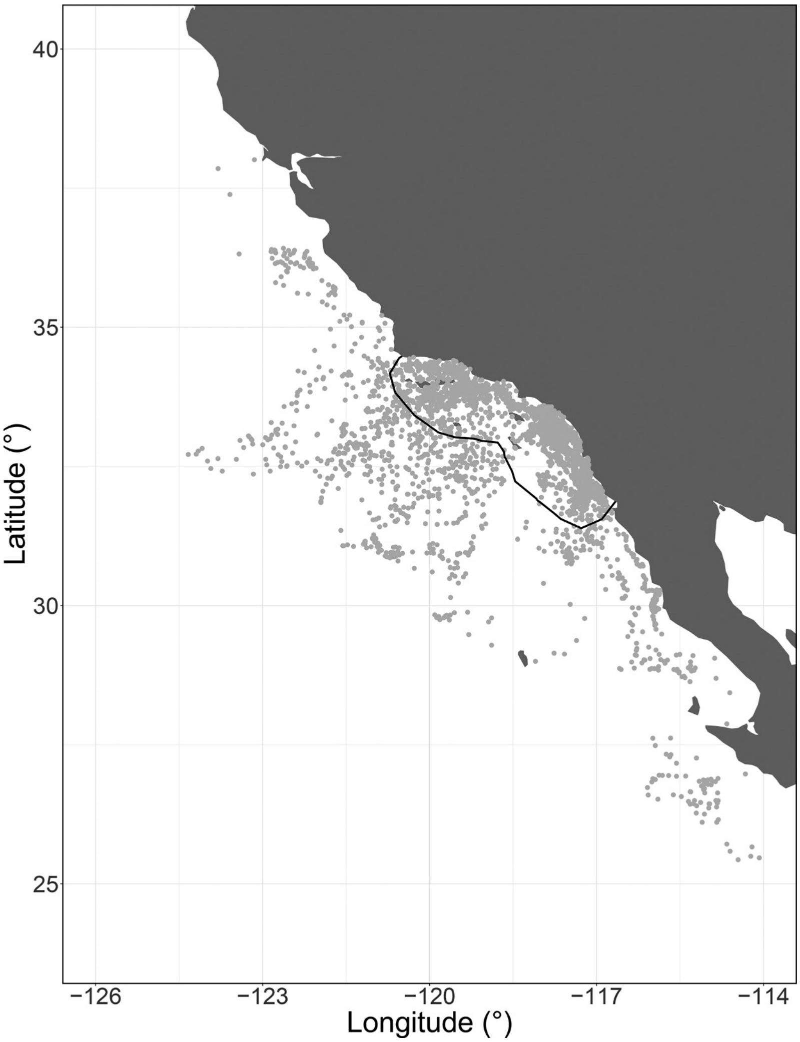

Fig. 1. Common thresher shark *Alopias vulpinus* locations in and around the Southern California Bight: aggregated pop-up archival transmitting tags representing 25 individual *A. vulpinus* (>2500 total locations, grey dots) from 2004–2011. Black line indicates the derived 50% kernel density polygon generated around estimated *A. vulpinus* locations

2.5. Movement model analytical approach

Using the 'most probable' track derived from 'Trackit,' movement data for *A. vulpinus* were turned into a binomial response variable, which identified at any given point whether an animal was inside (0), or outside (1) the defined kernel, the same approach outlined by Kinney et al. (2017). After defining our response variable, the first step was to identify potential variables of interest that may influence *A. vulpinus* movement in and out of the SCB. We considered fork length, sex, season (as defined by the solstices and equinoxes), moon phase, and several potential environmental indices (North Pacific Gyre Oscillation [NPGO], Pacific Decadal Oscillation [PDO], and Multivariate ENSO Index [MEI]).

Sea surface temperature (SST) and biological productivity (using chlorophyll [chl] *a* concentration as a proxy) were also investigated as potentially influential variables; however, as discussed by Kinney et al. (2017), spatial and temporal scales of environmental covariates and tagging data need to be comparable. SST and biological productivity were extracted for each tag's most probable track locations using the R function 'xtracto' (package 'xtractomatic') (Mendelssohn 2018) and the satellite data in the Environmental Research

Division's Data Access Program (ERDDAP) server at the Environmental Research Division of the National Marine Fisheries Service, SWFSC (Simons 2019). Data were extracted from an area around each location defined by the average x and y errors discussed above, thus matching the scales of the position estimate errors with those of SST and biological productivity. Data used were monthly composites of MODIS chl *a* and daily multi-scale ultra-high resolution (MUR) SST. Monthly composite MODIS chl *a* was the only available source of chl *a* data that covered the entire area used by *A. vulpinus* in this study. It was decided that the coarseness of a monthly scaled variable was preferable to combining chl *a* data from multiple sources, each with its own caveats, in an attempt to improve the temporal scale of the chl *a* data. Due to the high variability of these 2 metrics within the spatial error of the position estimates, we investigated these parameters cautiously by comparing, when possible, estimates with tag-recorded readings of SST, and mapped chl *a* values from surrounding areas, since such variability could result in conditions (temperature and biological productivity) being inappropriately applied to location estimates without proper regard for the inherent error of the estimated location.

We used a random forest to identify which of our considered variables influenced the movement of *A. vulpinus* in and out of the SCB. We used the R package 'rfPermute' (Archer 2013) since it contains a permutation-based function to provide both variable importance and significance for each predictor, thus allowing us to carry forward only significant variables. We then used a generalized additive mixed-effects model (GAMM) to test each variable for linearity to ensure that a linear model would be appropriate, and finally applied a modified version of the hierarchical Bayesian model described by Kinney et al. (2017) to investigate the magnitude of environmental and biological effects on movement and habitat occupancy. The model was fit using 'Just Another Gibbs Sampler' (JAGS) and had the following basic structure:

$$\mu = \beta_0 + \beta_1 \times \text{Spring} + \beta_2 \times \text{Summer} + \beta_3 \times \text{Winter} + \beta_4 \times \text{FL} + \beta_5 \times \text{Sex} + \beta_6 \times \text{NPGO} \quad (1)$$

where μ is the response variable and β_0 through β_6 are the parameters associated with each data input. The model was initialized with vague priors and included tagged individuals as the random effect. Since the response variable is binomial, the model is set with a logit link function and the response variable 'μ' is drawn from a Bernoulli distribution, just as in Kinney et al. (2017). β_0 is the model intercept, which is the parameter associated with the fall season. This manifests itself in the model as every other season's parameter needs to be evaluated relative to the fall (e.g. model convergence was evaluated by visually assessing the trace plots and calculating Gelman and Rubin's convergence diagnostic; Brooks & Gelman 1998). This diagnostic is analogous to ANOVA, comparing the pooled within-chain variability to the among-chain variability. A score of 1 to 1.1 is deemed acceptable for establishing convergence.

2.6. Spatial and temporal autocorrelation

We recognize that in many cases, spatial and temporal autocorrelation can have major impacts on analyses and inferences from tagging studies (Rooney et al. 1998, De Solla et al. 1999, Aarts et al. 2008, Nathan et al. 2008). Often, where an animal is at time x affects where it will be at time $x+1$. Much time and effort have been spent grappling with this issue, and no single method for dealing with it has yet been accepted in the scientific literature. Following the framework outlined by Kinney et al. (2017), we built a version of our model that accounts for autocorrelation (see 'The model' in the Supplement at www.int-res.com/articles/suppl/m639p155_supp.pdf. After running the autocorrelated model, we compared the results with the non-autocorrelated model described in this paper and found that they were comparable (Fig. S1 in the Supplement). Due to the increased simplicity of the non-autocorrelated model, easier to interpret results, and reduced running time, we opted to focus on the simpler model. We suggest that anyone interested in applying these models to telemetry data should consider if the autocorrelated model is more appropriate for their dataset. If unsure, the results of both models should be compared. All statistical analyses in this study were performed in R (version 2.15.3 or 3.3.2, R Core Team 2016).

3. RESULTS

Over the course of the study, 25 tags were deployed; 14 of the tags that reported data were attached to male *Alopias vulpinus*, 11 to females (Table 1). Tagged *A. vulpinus* ranged in size from 76–200 cm FL (mean ± SD: 114 ± 30 cm), with the majority under the estimated size at maturity (~160 cm, [females: 160 cm, males 155–165 cm]) for this species (Smith et al. 2008). Within this size range, we classified individuals at or above 120 cm as subadults or adults, and those below 120 cm FL as juveniles, following the definition of Cartamil et al. (2011). However, as stated above, evidence of potential misidentification by Smith et al. (2008) could mean that the Atlantic size at maturity (Natanson & Gervelis 2013) is more appropriate for these *A. vulpinus* (~216 cm), which would mean that all *A. vulpinus* in the study (apart from males identified to have calcified claspers) would be immature. Over 2500 locational estimates were recorded since 2004. The longest tag record was 263 d, whereas the shortest record was 76 d (Table 1). The average number of tracking days was 170 ± 71. Of the 25 tags released, 4 were recovered.

3.1. Random forest and GAMM

The initial random forest with all 3 environmental indices (NPGO, MEI, and PDO) yielded an out-of-bag error rate of 4.17%. A simplified model with only 1 environmental index (NPGO) performed better, yielding an out-of-bag error rate of 4.11%. The Gini importance measure of the single index model, which measures how each variable contributes to the homogeneity of the nodes in a random forest, indicated that in terms of creating pure terminal nodes, FL is the most important, followed by NPGO, season, and sex (Fig. 2). It is important to note here that the Gini measure of parameter importance does not deal with individuals in the same way as the hierarchical Bayesian approach, thus the ranking of parameter importance is likely to differ between the 2 methods. Chl *a* concentration, SST, and moon phase were statistically insignificant and were therefore dropped from further analyses. Results from the GAMM indicated that all remaining variables (Table 2) had a single degree of freedom, indicating linear relationships with the response variable.

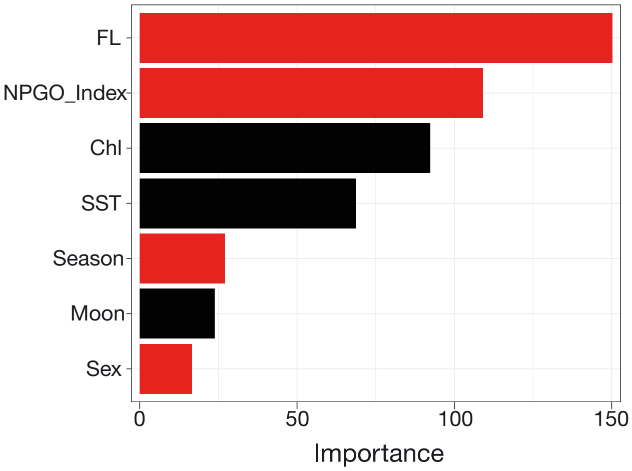

Fig. 2. Gini index of importance scores for all of the potential parameters in the ultimate permuted random forest run (including only the single most influential environmental index, the North Pacific Gyre Oscillation [NPGO]). This index was generated using 'rfPermute' and contains indicators (red) that a parameter significantly partitions the data and thus would be of interest in further analysis. Tested variables: fork length (FL), NPGO, chlorophyll *a* (Chl), sea surface temperature (SST), season, moon phase, and sex

3.2. Bayesian analysis

As in Kinney et al. (2017), vague priors were used for all model parameters. Priors were given a normal distribution with a mean of 0, and a variance broad enough to keep them vague (between 10 and 1 000 000). The model resulted in smooth, normally distributed posterior distributions (Fig. 3) with rea-

Table 2. Parameters of interest identified by random forest and included in the final model outlined in Eq. (1). 'Scaled' refers to whether a variable was standardized to account for it being much larger or smaller than other values; in such a case, a *z*-score standardization was used. NPGO: North Pacific Gyre Oscillation

Model parameter	Name	Data type	Scaled (Y/N)	Description
β_0	Fall	Binary	N	Indication of data point occurrence after the fall equinox but before the winter solstice
β_1	Spring	Binary	N	Indication of data point occurrence after the spring equinox but before the summer solstice
β_2	Summer	Binary	N	Indication of data point occurrence after the summer solstice but before the fall equinox
β_3	Winter	Binary	N	Indication of data point occurrence after the winter solstice but before the spring equinox
β_4	Fork length	Continuous	Y	Measurement of fork length in centimeters
β_5	Sex	Binary	N	Sex, indicated as Female (0), Male (1)
β_6	NPGO	Continuous	N	An index that measures changes in the North Pacific gyre circulation

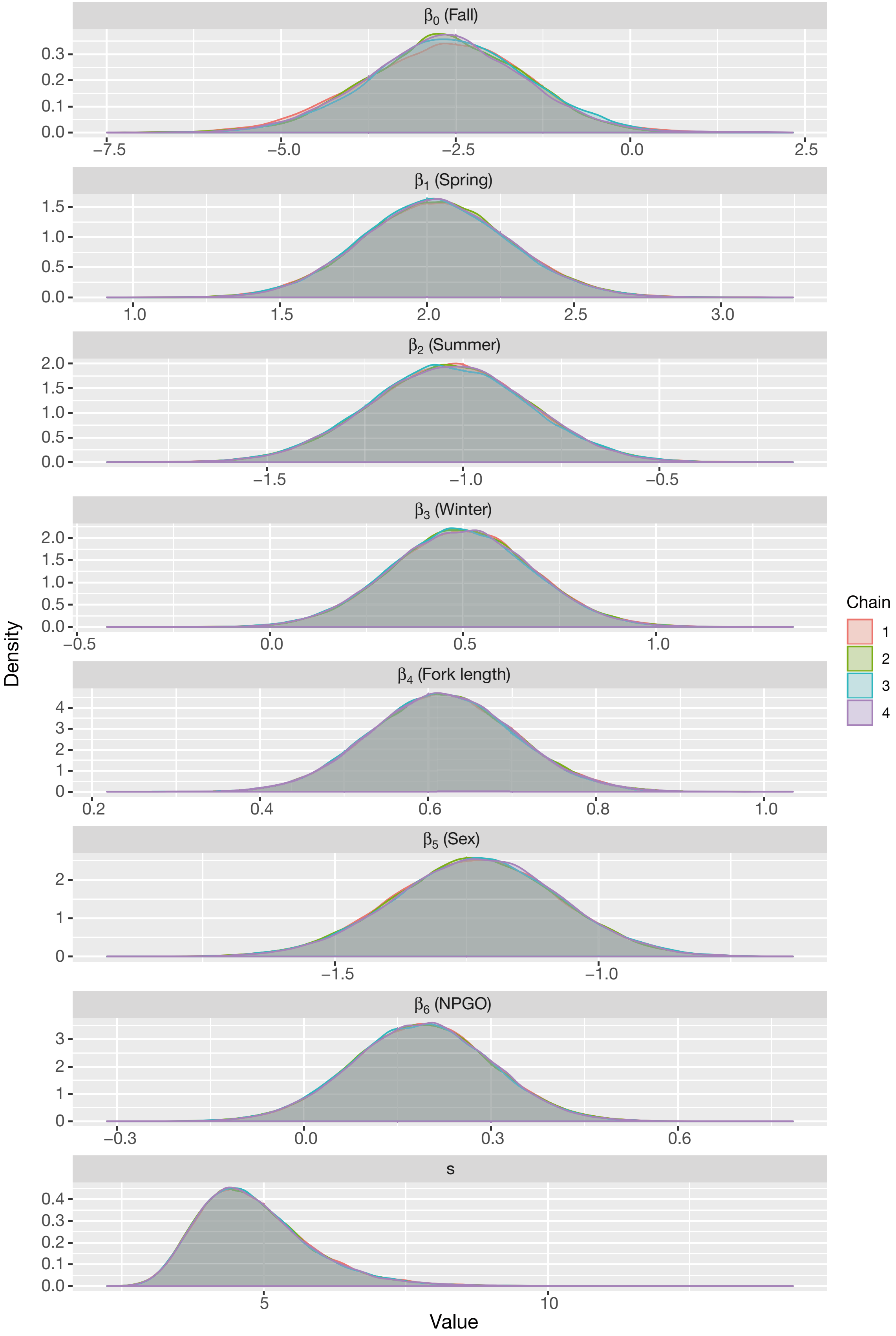
β0 (Fall)
0.3
0.2
0.1
0.0
–7.5
–5.0
–2.5
0.0
2.5
β1 (Spring)
1.5
1.0
0.5
0.0
1.0
1.5
2.0
2.5
3.0
β2 (Summer)
2.0
1.5
1.0
0.5
0.0
–1.5
–1.0
–0.5
β3 (Winter)
2.0
1.5
1.0
0.5
0.0
–0.5
0.0
0.5
1.0
β4 (Fork length)
4
3
2
1
0
0.2
0.4
0.6
0.8
1.0
β5 (Sex)
2
1
0
–1.5
–1.0
β6 (NPGO)
3
2
1
0
–0.3
0.0
0.3
0.6
s
0.4
0.3
0.2
0.1
0.0
5
10
Density
Value
Chain
1
2
3
4

Fig. 3. Posterior distribution plots indicating parameter estimates produced by the model, with positive values suggesting that a covariate is associated with μ values of 1, i.e. a greater probability of being outside the defined kernel. The further shifted away from 0, the greater the parameter influence. Variables with 95% credibility interval which include 0 are considered not statistically significant. Parameters are described in Table 2; chains are the MCMC chains (see Section 3.2 and Fig. S2). 's' is the model error term

sonable trace plots, indicating model convergence and mixing among the 4 Markov chain Monte Carlo (MCMC) chains (Fig. S2). Additionally, Gelman and Rubin scores of 1 for all model parameters confirmed convergence.

The model indicated that season was the strongest driver of *A. vulpinus* movement out of the defined kernel. With fall as the intercept, when evaluating seasonal parameters, a negative value indicates that *A. vulpinus* are more likely to be found within the SCB for a given season when compared to fall (the parameter is negatively correlated with μ values of 1). In summer, *A. vulpinus* were more likely to be inside the defined kernel, with the estimate of β_2 being −1.0142 with the 95% credibility interval (CI) of the posterior distribution not crossing 0 (CI: −1.4181 to −0.618). This result makes sense, as, due to the increased appearance of thresher sharks in the SCB, the above mentioned SWFSC Pre-Recruit Thresher Shark Survey took place around August each year. Spring, on the other hand, indicated that *A. vulpinus* were more likely to exit the defined kernel (β_1: 2.0657; CI: 1.567–2.573). Similarly, during the winter, animals were more likely to venture outside the defined kernel when compared to the fall, but with the 95% CI approaching 0, this relationship is weaker than in the spring (β_3: 0.5176; CI: 0.1549–0.881).

Demographic parameters also affected *A. vulpinus* movement out of the defined kernel. Length showed the second-largest effect on movement, with larger animals more likely to move out of the defined kernel than smaller individuals (β_4: 0.6221; CI: 0.4555–0.7939). Sex was also an influential factor for *A. vulpinus* movement, with females more likely to leave the area than males (β_5: −1.2276; CI: −1.5393 to −0.921).

Statistically, longer-term climatic cycles did not affect *A. vulpinus* movement out of the defined kernel. Increases in the NPGO index increased the likelihood of *A. vulpinus* moving outside of the SCB, but the relationship is weak, with the 95% CI including 0 (β_6: 0.1941; CI: −0.0236 to 0.4146).

4. DISCUSSION

To date, the horizontal movement of *Alopias vulpinus* along the west coast of North America has been inferred primarily from catch patterns of the CDGN fishery. This has suggested that *A. vulpinus* overwinter off Baja California, Mexico, before migrating north in the spring to the SCB (Hanan et al. 1993, Smith & Aseltine-Nielson 2001). No long-term, fisheries-independent data on the horizontal movements of large sub-adult and adult *A. vulpinus* in either the SCB, the Pacific Northwest, or off Baja California have been published. Further, none of the fine-scale movement studies of young *A. vulpinus* during the spring in California waters have identified a consistent pattern of migration (Cartamil et al. 2010a,b). Juvenile *A. vulpinus* use the waters over the continental shelf within the SCB as an important nursery area (Cartamil et al. 2010b); however, it is still unclear what drivers, whether intrinsic or extrinsic, influence the movement of *A. vulpinus* out of the SCB.

Despite nearly a decade of satellite tagging efforts within the SCB, poor location quality estimates, patchy data, insufficient sample size, and a lack of analytical methods with which to analyze such data have relegated efforts to understand *A. vulpinus* movement to more descriptive individual-based accounts. However, with recent advancements in analytical tools for 'data-limited' cases (Kinney et al. 2017), it has become feasible to begin making population-level inferences for *A. vulpinus* movements from satellite tagging data.

Applying the method outlined by Kinney et al. (2017), we were able to use a hierarchical Bayesian model to make population-level inferences which indicate that common thresher sharks are partial migrators that conditionally migrate based on a combination of fixed intrinsic states (size, sex) and variable extrinsic states (e.g. season, environment). Our analysis identified the waters of the SCB as an area where smaller juveniles can be found throughout the year, while larger sub-adult and adult *A. vulpinus* often move out of the SCB during certain seasons (spring and winter).

4.1. Biological and fisheries topics

In many animal populations, including some sharks (Papastamatiou et al. 2013), only a subset of the whole population migrates, with the decision of migration or residency made at the level of the individual. This process is referred to as partial migration (Brodersen et al. 2008, Jahn et al. 2010, Chapman et al. 2012). *A. vulpinus* seem to be partial migrators which conditionally migrate based on a combination of fixed intrinsic states (size, sex) and variable extrinsic states (e.g. season, environment). Of the factors investigated in this research, size appears to be the strongest intrinsic driver of *A. vulpinus* movement out of the SCB. Such size-related range expansion has been observed in several species and, for larger individuals, is often related to dietary changes or physiological restrictions imposed by changes in environmental conditions (Feldheim et al. 2002, Heupel et al. 2007, Carlisle & Starr 2009, Grubbs 2010, Knip et al. 2010). In contrast, range expansion of smaller individuals is often related to predator avoidance and expansion of the home range within nursery areas, with key driving forces including changing water temperatures or juveniles reaching a minimum critical size for predator release (Holland et al. 1993, Simpfendorfer & Heupel 2004, Heupel 2007).

In addition to size, sex also seems to be an influential intrinsic factor in the movement of *A. vulpinus*. A few smaller females (<87 cm) showed movements uncharacteristic for their size (outside of the defined kernel), indicating that sex may warrant further investigation. We do know that sex influences growth rates and length at maturity (Cailliet et al. 1983, Smith et al. 2008, Gervelis & Natanson 2013) and thus may have an indirect effect on movement. A larger sample size may help resolve the influence sex has on the movement of *A. vulpinus* out of the SCB.

While our results did not strictly identify local extrinsic factors such as SST or biological productivity (chl *a*) as primary factors in the movements of *A. vulpinus*, season, a more broad-scale extrinsic factor, did show an influence on movement. It could be that *A. vulpinus* movement is more affected by extrinsic factors other than SST and chl *a* which are captured in broad factors like season and, to some extent, environmental indices like NPGO. Alternatively or it could be that the nature of *A. vulpinus* movement data (patchy with large confidence intervals for individual locations) diminishes the effect of these point-source extrinsic factors in preference for more global ones. Regardless, it seems clear that *A. vulpinus* predominantly remain within the SCB throughout the year at small sizes, and as they increase in size they become more likely to venture out of the SCB at certain times of year (spring and winter) and under certain environmental conditions (higher values of the NPGO index, i.e. El Niño conditions).

Understanding the influence of length (or possibly age) on movement is important for fisheries demographic analyses (i.e. stock assessments) (Lee et al. 2015, 2017, McDaniel et al. 2016). Knowledge of how *A. vulpinus* distribute along the coast, and knowing that season, size, and to some extent sex, play important roles in where and what type of animals are likely to be found, can improve our understanding of key model parameters and assumptions. For example, consider a scenario in which a population of *A. vulpinus* undergoes a population assessment in which the majority of samples are gathered from Mexican waters, an area expected to contain a less than representative proportion of smaller juvenile fish, and a greater proportion of larger adult fish. Assume that our findings of the influence of season, size, and sex are unknown and that fisheries samples taken from anywhere in the population's range are considered appropriately random, and as such, the samples from Mexico are seen as representative. In this scenario, the stock's growth, estimated size at 50% maturity, and maturity ogives would be biased by an overrepresentation of larger animals. Additionally, with our preliminary findings on sex it might also be true that the population sex ratio could be skewed. This is, of course, an extreme example, but it is meant to emphasize the importance of accurate population-level movement information, especially in terms of identifying potential issues with assumptions of randomness in fisheries samples.

Important biological parameters for *A. vulpinus* would certainly be most accurate if samples were taken throughout the year and from across the animals' entire range; however, given the results of our analysis, representative samples could be obtained by sampling *A. vulpinus* from the SCB during the summer and fall when individuals of a large variety of sizes and maturity status are available. Samples taken from different seasons and/or from waters outside the SCB should be scrutinized since they may only represent a subset of size classes, potentially leading to the kinds of issues outlined above.

4.2. Conservation topics

In addition to the fisheries demographic issues discussed above, our results also indicate potential conservation concerns. While there is evidence of *A. vulpinus* in the waters of the Pacific Northwest and even Canada, limited catch and scant tag records suggest that movements north of the SCB are less prevalent than movements south, into Mexico. A harvest guideline of 340 t is currently in place for *A. vulpinus* in US waters (Teo et al. 2018). This provides an upper limit for the sustainable commercial harvest of *A. vulpinus* along the US west coast. The waters off Mexico, however, do not have a harvest guideline. Instead they have a 50 nautical mile sportsfishing-only zone which was established in 1983, but was routinely violated by commercial fishing operations (Holts et al. 1998), and there is little evidence to suggest this has changed over the last 20 yr. This would suggest that the commercial fishing mortality for *A. vulpinus* in US waters is at least bounded by a harvest guideline (although recent catch is well below this bound), while commercial fishing mortality in Mexican waters is potentially unbounded, although somewhat restricted due to a permit system for the artisanal fishery (pangas). Our results provide greater context to this discrepancy by indicating that the fishing pressures in US and Mexican waters are unlikely to be affecting the same segments of the *A. vulpinus* population in equal measure. Commercial *A. vulpinus* catch in Mexican waters is likely to be more concentrated on larger individuals with fewer small animals represented, something that can be seen when comparing the gillnet and longline length compositions of Mexico's catch with those of the US (Teo et al. 2018). An understanding of this disparity is significant in terms of making informed management decisions. Kinney & Simpfendorfer (2009) suggested that for some shark species, the protection of early life habits may be insufficient if other measures protecting larger mature animals are not also in place. The stock of *A. vulpinus* in the waters off the western coast of North America is currently estimated to not be in an overfished condition nor to be experiencing overfishing (Teo et al. 2018), indicating that concerns over its conservation are negligible. However, as indicated above, advancements in our understanding of the movements of this population of *A. vulpinus* can improve both our knowledge of the animal and the fisheries that impact it, leading to reduced uncertainty in determining its stock status.

4.3. Conclusions

It is important to see this study as a first step. A wealth of electronic tagging data has been produced for numerous species throughout the world, and many of these datasets have been under-analyzed (qualitatively instead of quantitatively), or, as is the case here, not analyzed at all due to perceived limitations in the dataset. Our results show that these datasets can be quantitatively analyzed and can produce population-level inferences. Additionally, since these data have been analyzed in a Bayesian framework, future tagging studies can use the information provided here to define informative priors, thus allowing past data to increase the power of current analyses and helping to alleviate one of the most common shortcomings of satellite tagging projects, namely limited sample size.

Acknowledgements. We thank Jay Barlow and Brice Semmens for sharing their modeling expertise and helping to spark the idea for this project, along with the numerous individuals who gave their time and knowledge during all stages of this work, including Eric Archer, Charlotte Boyd, Jim Carretta, Alex Curtis, Kevin Piner, and Stephen Stohs. We also thank an internal reviewer, Trevor Joyce, for his helpful edits and comments.

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Editorial responsibility: Romuald Lipcius,
Gloucester Point, Virginia, USA

Submitted: November 13, 2019; Accepted: February 20, 2020
Proofs received from author(s): March 28, 2020