

# Seasonal spatial segregation in blue sharks (*Prionace glauca*) by sex and size class in the Northeast Pacific Ocean

Sara M. Maxwell<sup>1,2</sup>  | Kylie L. Scales<sup>3</sup>  | Steven J. Bograd<sup>4,5</sup> | Dana K. Briscoe<sup>6,7</sup>  | Heidi Dewar<sup>8</sup> | Elliott L. Hazen<sup>4,5</sup> | Rebecca L. Lewison<sup>9</sup> | Heather Welch<sup>4,5</sup> | Larry B. Crowder<sup>6</sup>

<sup>1</sup>School of Interdisciplinary Arts and Sciences, University of Washington, Bothell, Washington

<sup>2</sup>Department of Biological Sciences, Old Dominion University, Norfolk, Virginia

<sup>3</sup>Global Change Ecology Research Group, University of the Sunshine Coast, Maroochydore, Australia

<sup>4</sup>NOAA Southwest Fisheries Science Center, Environmental Research Division, Monterey, California

<sup>5</sup>Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, California

<sup>6</sup>Hopkins Marine Station, Stanford University, Pacific Grove, California

<sup>7</sup>National Institute of Water and Atmospheric Research, Nelson, New Zealand

<sup>8</sup>NOAA Southwest Fisheries Science Center, La Jolla, California

<sup>9</sup>San Diego State University, San Diego, California

## Correspondence

Sara M. Maxwell, School of Interdisciplinary Arts and Sciences, University of Washington, Bothell, WA.  
Email: smmax@uw.edu

## Funding information

Center for Ocean Solutions; Stanford University; NOAA Bycatch Reduction and Engineering Program, Grant/Award Number: NA14NMF4720312; NASA Earth Science Division/Applied Sciences ROSES Program, Grant/Award Number: NNH12ZDA001N-ECOF; University of California

Editor: Clare Embling

## Abstract

**Aim:** Animal tracking can provide unique insights into the ecology and conservation of marine species, such as the partitioning of habitat, including differences between life history stages or sexes, and can inform fisheries stock assessments, bycatch reduction and spatial management such as dynamic management.

**Location:** Northeast Pacific Ocean.

**Methods:** We used satellite tracking data from 47 blue sharks (*Prionace glauca*) from the Northeast Pacific to determine movements and home range along the west coast of North America, and sex–size class (immature females, mature males) specific habitat preferences using boosted regression trees. Using a suite of static and dynamic environmental variables, we determined distribution and habitat preferences across summer and fall for each sex–size class.

**Results:** We found that there was spatial segregation between sex–size classes particularly in the summer months with immature females found largely north of 33°N, and males south of 35°N. In fall, females travelled south, resulting in an overlap in distributions south of 37°N. Sea surface temperature (SST), latitude and longitude were top predictors. However, immature females and adult males demonstrated unique habitat preferences including SST, with immature females preferring cooler

This article has been contributed to by US Government employees and their work is in the public domain in the USA.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2019 The Authors. *Diversity and Distributions* Published by John Wiley & Sons Ltd

temperatures (SST < 15°C) than adult males in summer, and a broader band of SST than adult males in fall. All models performed well, explaining 50%–67% of deviance, and 23%–41% of deviance when predictions were cross-validated.

**Main conclusions:** We provide first insights into coastal movements and habitat preferences of blue sharks in the Northeast Pacific. We found that immature females undergo a seasonal southward migration in this more coastal habitat, similar to patterns observed in the North Atlantic. We also found some overlap between adult males and immature females in fall months, suggesting the importance of more coastal habitat in managing this species, particularly in determining population structure for blue shark stock assessments, and reducing blue shark bycatch.

#### KEYWORDS

dynamic oceanographic variables, fisheries management, habitat partitioning, home range, spatial segregation, species distribution modelling

## 1 | INTRODUCTION

Understanding the relationship between animal distribution and environmental features can be useful for determining appropriate management and conservation actions. Information on the spatial and temporal overlap of animal movement and fisheries can highlight potential changes to fishing techniques to reduce bycatch (Carvalho et al., 2015; Dewar et al., 2011; Lewison et al., 2013; Polovina, Howell, Parker, & Balazs, 2003) or can inform dynamic management approaches that allow for changes in human activities in near real-time, based on the habitat of species of concern (Hazen et al., 2016; Hobday, Hartog, Spillman, & Alves, 2011; Howell, Kobayashi, Parker, Balazs, & Polovina, 2008; Lewison et al., 2015; Maxwell et al., 2015). Habitat modelling (also known as species distribution modelling) allows for an understanding of the factors that drive animals' habitat preference (Elith et al., 2006) which can include physiological limitations, requirements for reproduction, avoidance of predators or likely locations of prey (Torres, Read, & Halpin, 2008; Whitlock et al., 2015; Wingfield et al., 2011). While it is rare to know the mechanisms underlying habitat preference, determining what defines habitat through modelling provides insight into the influence of the physical environment in habitat selection and provides the potential to predict species distribution in areas or seasons beyond the sampled region (Becker et al., 2014; Mannocci, Monestiez, Spitz, & Ridoux, 2015). In addition to providing insight into the drivers of distribution, habitat modelling can give unique insights into species' ecology. For example, habitat modelling can highlight differences in habitat and potential niche separation between different species, or between sexes or age classes of the same species (Ficetola, Pennati, & Manenti, 2013; Jegliński, Goetz, Werner, Costa, & Trillmich, 2013; Kappes et al., 2010; Vandeperre, Aires-da-Silva, Lennert-Cody, Serrão Santos, & Afonso, 2016).

In the marine environment, niche habitat separation is common for a number of sharks including blue sharks (*Prionace glauca*). Blue sharks are a highly mobile, circumglobally distributed species, which

are incidentally caught in a number of fisheries around the world, and in some fisheries are the predominant shark bycatch species (King et al., 2015; Nakano & Seki, 2003; Walsh & Kleiber, 2001). As a result of fisheries interactions, they are a priority species for the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean and managed domestically. Information on how mortality is distributed across sex and size classes is critical for making proper assumptions in fisheries stock assessments, as well as other fishery management techniques such as closed areas, gear restrictions and dynamic management (Sippel et al., 2015).

Blue sharks are hypothesized to be spatially segregated by both sex and size class. In the North Pacific, Nakano (1994) proposed that juvenile males are largely located between 30–35°N, juvenile females north of 35–40°N and adults located throughout the North Pacific, with mating taking place between 20–30°N; this distribution is known as the “north–south model” (hereafter “N–S model”; Nakano, 1994; Nakano & Seki, 2003). Strong evidence for this pattern in the Central Pacific is provided by bycatch data (Walsh & Teo, 2012), and evidence of a similar pattern exists in the North and South Atlantic from bycatch and tracking data (Montealegre-Quijano & Vooren, 2010; Vandeperre, Aires-da-Silva, Fontes, et al., 2014a; Vandeperre, Aires-da-Silva, Santos, et al., 2014b). However, the N–S model described by Nakano (1994) has not been explored in more coastal regions where much commercial fishing occurs (Hazen et al., 2018; Scales et al., 2018), leading to uncertainty in our understanding of near-shore blue shark distributions. Observer data from the swordfish drift gillnet fishery off the west coast of the United States, which has considerable blue shark bycatch (over 100,000 individuals between 1999–2006 (NOAA, 2008)), suggest that this N–S model may extend into more coastal waters of the California Current Large Marine Ecosystem (Urbisci et al., 2013). Observer data, however, is limited to only where fishing occurs and does not follow individuals through time, thus limiting inferences regarding habitat preference to snapshots that correspond to fishing. A robust satellite tracking dataset, however, can help to identify drivers

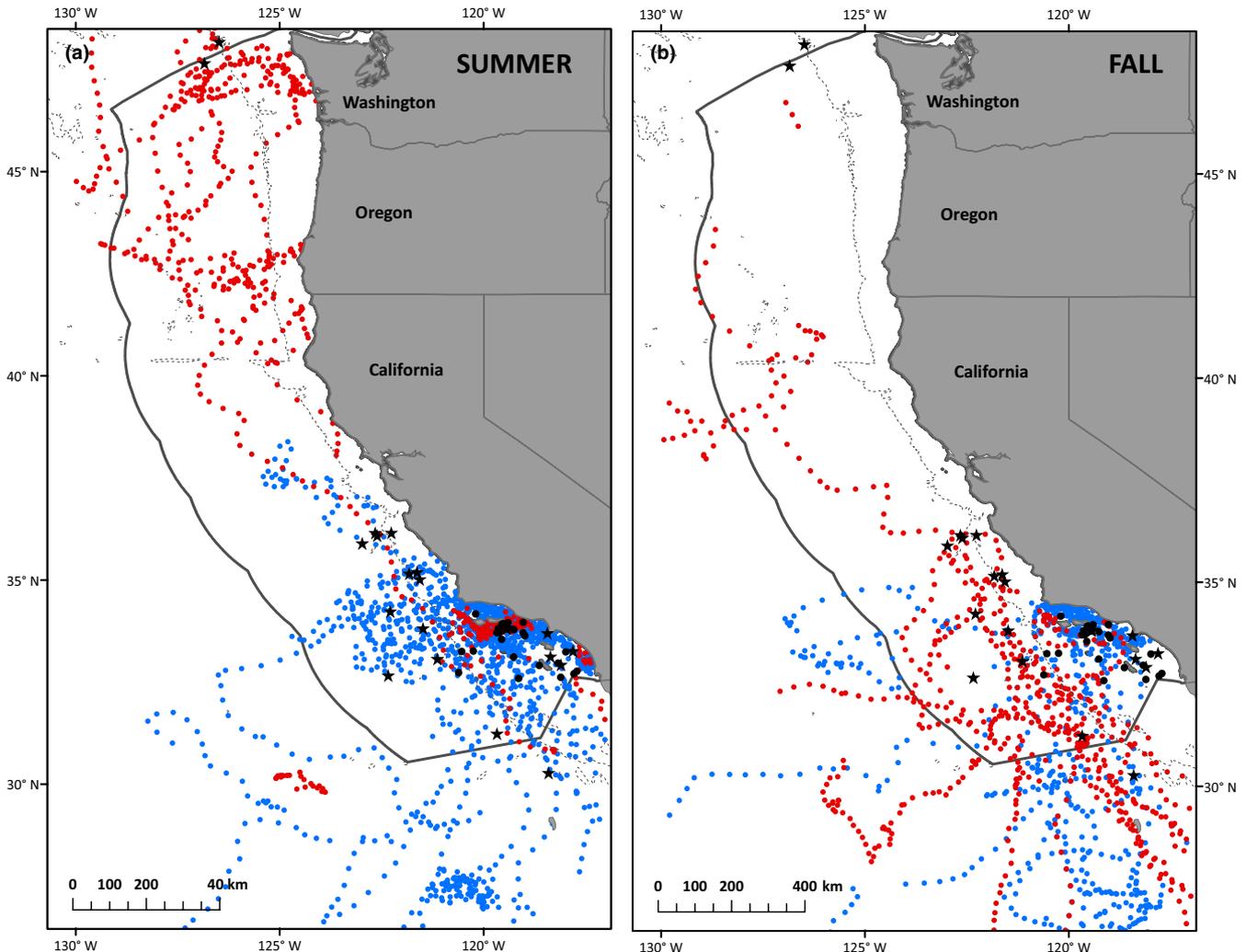
behind blue shark distribution and thereby refine our understanding of population structure in more coastal waters.

While aspects of blue shark habitat preferences have been explored in the Atlantic (Adams, Flores, Flores, Aarestrup, & Svendsen, 2016; Campana et al., 2011; Carvalho et al., 2015; Howey, Wetherbee, Tolentino, & Shivji, 2017; Queiroz, Humphries, Noble, Santos, & Sims, 2012; Queiroz et al., 2005; Vandeperre, Aires-da-Silva, Fontes, et al., 2014a), the influence of the physical environment on regional blue shark distributions in the North Pacific has not yet been characterized outside of exclusively pelagic environments far from coastal influence. Here we use blue shark satellite tracking data and habitat modelling to address this knowledge gap through (a) identifying seasonal home range and key habitat areas in more coastal waters in the Northeast Pacific; (b) exploring the physical drivers of habitat selection across seasons; and (c) examining how the influence of these drivers varies among sexes and size classes across seasons. We then discuss the implications of these findings for the management of blue shark populations along the US west coast.

## 2 | METHODS

### 2.1 | Tracking data

A total of 54 blue sharks were tagged between 2004 and 2012 using fin-mounted Smart Position-Only Tag (SPOT) satellite transmitters (Wildlife Computers Inc.). All sharks were caught using commercial longline gear either (a) off California during the NOAA Southwest Fisheries Science Center's annual juvenile shark survey (Runcie et al., 2016), (b) on commercial vessels operating in Mexican waters off the Baja Peninsula or (c) during surveys conducted by the Department of Fisheries and Oceans of Canada off British Columbia (Figure 1). Sharks were pulled onto a cradle, their eyes were covered with a soft cloth, the hook removed, and the gills irrigated with seawater. For each shark, a DNA sample was taken and sex and length were recorded. Maturity was inferred based on length and sex; females were considered immature if fork length was <182.5 cm, and males were considered immature if fork length was <177.5 cm (Nakano &



**FIGURE 1** Blue shark tracks for (a) summer (red = immature females; blue = mature males) and (b) fall. Dashed line indicates the 200 m bathymetric contour, and the solid black line indicates the US Exclusive Economic Zone. Black stars indicate the locations of immature female tagging; black circles indicate the locations of mature male tagging [Correction statement added on 31 May 2019 after first online publication: Figure 1 and Figure 2 were previously incorrect and have been corrected in this version]

Seki, 2003; Urbisci et al., 2013). SPOT tags were mounted on the dorsal fin using 3 nylon or stainless steel bolts inserted through holes drilled through the fin. In most cases, a conventional tag was inserted in the dorsal musculature below the first dorsal fin. Total time out of the water was typically <10 min.

Transmissions were detected and processed by the Argos satellite system. Tracks of <20 days duration ( $n = 7$ ) were removed from the analysis to reduce tagging location bias, resulting in a total sample size of 47 tagged individuals (Table 1). Average track length for the 47 individuals remaining was 124 days (range: 25–614; Table 1). Twenty-three tagged sharks were immature females, and 24 were mature males; there was an insufficient number of immature males or mature females in the study to include in the analyses. We limited our study to the region where the majority of tracking data were located (between  $-130$  and  $-117^\circ\text{W}$  and  $25$  and  $53^\circ\text{N}$ ) to isolate habitat inferences to areas with sufficient data.

We used a hierarchical Bayesian state space model (SSM) to regularize tracks, remove erroneous points and estimate error associated with each location (Breed, Jonsen, Myers, Bowen, & Leonard, 2009; Jonsen et al., 2013) using the “bsam” package (version 0.43) (Jonsen, Flemming, & Myers, 2005) in R (version 3.0.1) (R Core Team, 2016). The time step between successive modelled locations (18 hr) was determined using the mean length of time between tracking locations in the entire dataset (Maxwell et al., 2011). If gaps of more than 20 days duration existed in tracks (likely due to a lack of surfacing), track segments were treated separately (Bailey et al., 2008). We ran two Markov chain Monte Carlo chains for 40,000 iterations after a burn-in of 20,000 and further thinned the iterations by 10 to estimate the mean and variance for each location. Model output included behavioural estimation, however, given the infrequent surfacing of blue sharks, and the spatial scale of behaviour was not sufficiently resolved to meet our research objectives and, as a result, behaviour was not included in the analysis.

Satellite tracking data are presence-only; thus, we generated pseudo-absences by simulating tracks using correlated random walk (CRW) models (Hazen et al., 2016; Johnson, London, Lea, & Durban, 2008; Willis-Norton et al., 2015). CRWs were generated using the “adehabitatLT” package (version 1.8.12) in R (Calenge, 2006, 2007), and each simulated track maintained the same start location, total distance, turning angle and track duration as the real track. Ten CRW simulations were generated for each real track.

## 2.2 | Environmental data

A combination of static and dynamic remotely sensed data was used to create habitat models. Remotely sensed data were extracted for both real and CRW tracks. Variables were downloaded via ERDDAP (Simons, 2016) or if unavailable via ERDDAP, directly from the data provider (see Table 2 for details) using a combination of Xtractomatic (Simons, 2016) and custom scripts in R. For each variable, data were extracted over a radius, with both the mean and standard deviation across the radius returned. For real tracks, the 95% credible limit in both latitude and longitude generated by the SSM for each point was

used as the radius (credible limits: latitude: mean  $0.16^\circ \pm 0.15^\circ$ ; longitude: mean  $0.15^\circ \pm 0.15^\circ$ ), while for CRW tracks, a standard radius of 0.1 degrees was used. Remotely sensed variables included sea surface temperature (SST) and its standard deviation (SSTsd), surface chlorophyll-*a* (chl<sub>a</sub>), the *v* component of the surface wind vector as a proxy for upwelling (wind), mean sea level anomaly (SLA) and its standard deviation (SLAsd). We included a measure of Eddy Kinetic Energy (EKE), calculated using the *u* and *v* components of geostrophic currents as  $1/2 (u^2 + v^2)$  (Cayula & Cornillon, 1992). Bathymetry (bathy) was extracted along with the standard deviation of bathymetry over the radius of extraction described above (rugosity). We included latitude and longitude in the models to account for unexplained spatial variance and as metrics of spatial segregation. We also included a random number between 1 and 100 to serve as an indicator for variables that have influence greater or less than random (Scales et al., 2017; Soykan, Eguchi, Kohin, & Dewar, 2014); only variables with influence greater than the random number were included in the final models.

## 2.3 | Boosted regression trees

We developed habitat models using a boosted regression tree (BRT) framework (Elith, Leathwick, & Hastie, 2008). BRTs have proven robust for habitat modelling applications, especially in instances where predictor datasets are incomplete, as is frequently the case with remotely sensed data. With most modelling frameworks, incomplete predictor datasets would result in valuable tracking data being lost or the removal of entire predictors from the analyses (Scales et al., 2017). Additionally, BRTs bypass issues related to data distributions (Derville, Constantine, Baker, Oremus, & Torres, 2016; Elith et al., 2008) and are relatively robust to variable model parameterization (Soykan et al., 2014). BRTs also allow for collinearity among predictor variables; as a result, SST, latitude and bathymetry could all be included in the models (Derville et al., 2016; Elith et al., 2008).

We used the “gbm” (version 2.1.1) and “dismo” (version 1.0-12) packages in R to conduct analyses (Elith et al., 2008; Ridgeway, 2006). We used a binary presence/absence framework and a Bernoulli distribution to create four seasonal models: mature males in the summer (July, August and September) and fall (October, November and December), and immature females in the summer and fall. We did not have sufficient data to create separate models for winter or spring (Table 1, Figure S1). Tracking data were used as presence data, and we randomly selected an equal number of pseudo-absence locations from a cloud of pseudo-absence points generated from the CRWs, resulting in randomly selected, unweighted pseudo-absences equal in number to presences as recommended by Barbet-Massin, Jiguet, Albert, and Thuiller (2012), and applied in Hazen et al. (2018). We ran 10 model iterations with random pseudo-absence selection to confirm the stability of the models and the influence of pseudo-absences on the influence of variables (Barbet-Massin et al. 2012), and we further limited the presence and pseudo-absence datasets to only data points that fell within the 95% utilization distribution contours for each sex-size class for each season in an effort to determine fine-scale habitat drivers. The mean and standard deviation

**TABLE 1** Blue shark satellite tracking data summary. Mean tracking duration was 124 days. Maturity of individuals is inferred from length following Nakano and Seki (2003); females were considered immature if fork length was <182.5 cm, and males were considered sexually mature if fork length was >177.5 cm. Acronyms are as follows: British Columbia (BC), California (CA), Washington (WA)

Shark ID	Fork length (cm)	Track length (d)	Start date	End date	Maturity	Sex	Tagging location
54580	137.7	39	11/7/04	12/21/04	Immature	Female	CA
54579	157.7	32	11/9/04	12/17/04	Immature	Female	CA
54583	156.8	104	11/14/04	2/24/05	Immature	Female	CA
54588	156.8	80	11/14/04	2/6/05	Immature	Female	CA
54585	163.5	25	11/14/04	12/19/04	Immature	Female	CA
54592	160.0	79	7/9/05	9/25/05	Immature	Female	CA
60989	180.1	145	7/3/06	12/19/06	Immature	Female	CA
60994	136.9	71	7/13/06	10/1/06	Immature	Female	CA
68501	145.0	75	7/20/07	10/6/07	Immature	Female	BC
68493	150.0	143	7/24/07	2/8/08	Immature	Female	BC
68498	158.0	49	7/24/07	9/15/07	Immature	Female	BC
68492	152.0	54	7/26/07	11/5/07	Immature	Female	BC
68502	160.0	149	8/1/07	1/11/08	Immature	Female	BC
52216	177.6	330	10/11/08	9/23/09	Immature	Female	WA
53791	150.2	111	11/15/08	3/5/09	Immature	Female	CA
53792	165.2	89	11/15/08	2/11/09	Immature	Female	CA
53794	153.5	80	11/19/08	2/11/09	Immature	Female	CA
52130	146.9	83	11/22/08	3/3/09	Immature	Female	CA
53793	166.8	148	12/11/08	7/17/09	Immature	Female	CA
96302	158.0	225	8/6/09	4/13/10	Immature	Female	CA
109085	160.7	53	10/31/11	1/7/12	Immature	Female	CA
109087	164.0	89	10/31/11	2/6/12	immature	female	CA
88513	169.5	136	7/14/12	12/2/12	Immature	Female	CA
37097	188.4	111	6/26/06	11/6/06	Mature	Male	CA
36895	184.3	113	6/30/06	11/12/06	Mature	Male	CA
36894	199.0	84	7/3/06	11/1/06	Mature	Male	CA
37099	186.8	100	7/8/06	11/14/06	Mature	Male	CA
37606	217.5	175	7/1/07	1/12/08	Mature	Male	CA
68507	220.0	144	7/16/07	12/11/07	Mature	Male	CA
53803	228.0	86	8/1/07	10/25/07	Mature	Male	CA
78119	250.0	284	6/16/08	4/11/09	Mature	Male	CA
96299	210.0	140	8/1/09	12/23/09	Mature	Male	CA
96294	224.0	139	8/1/09	12/17/09	Mature	Male	CA
96297	191.0	164	8/11/09	2/12/10	Mature	Male	CA
96300	219.0	108	8/11/09	11/26/09	Mature	Male	CA
87547	200.0	37	8/19/09	9/29/09	Mature	Male	CA
87555	200.0	52	8/23/09	10/19/09	Mature	Male	CA
95120	200.0	91	7/29/10	10/27/10	Mature	Male	CA
95114	202.0	74	7/29/10	10/10/10	Mature	Male	CA
95121	205.0	50	7/29/10	9/16/10	Mature	Male	CA
96370	217.0	167	7/31/10	1/12/11	Mature	Male	CA
87551	221.0	226	8/7/10	4/23/11	Mature	Male	CA
100957	260.0	614	9/19/10	9/25/12	Mature	Male	CA
109086	226.0	179	7/3/11	12/28/11	Mature	Male	CA
100947	221.0	125	6/23/12	11/21/12	Mature	Male	CA
109084	247.0	76	7/13/12	10/11/12	Mature	Male	CA
88513	241.0	136	7/14/12	12/2/12	Mature	Male	CA

**TABLE 2** Environmental variables used, the specific product and source, spatial and temporal resolution of each product

Variable	Product name and source	Spatial resolution	Temporal resolution
Sea Surface Temperature (SST)	GHRSSST L4 AVHRR Reynolds, Global (ERDDAP)	0.25°	Daily
Chlorophyll-a (chl <sub>a</sub> )	Aqua MODIS NPP, Global (ERDDAP)	4 km	8-day
Sea Level Anomaly (SLA)	AVISO Absolute Dynamic Topography (MADT-H), Global (CMEMS)	0.25°	Daily
Eddy Kinetic Energy (calculated using geostrophic surface velocities; EKE)	AVISO Absolute Dynamic Topography (MADT-UV), Global (CMEMS)	0.25°	Daily
Wind Speed (wind)	QuikSCAT/ METOP & ASCAT (ERDDAP)	0.25°	Daily
Bathymetry (bathy)	ETOPO 1 (ERDDAP)	1 arc-minute	-

of relative influence, rank, deviance explained and area under the receiving operator curve (AUC; see below) across all 10 model iterations is reported (Table 3), and consistency in results among the combinations of track and pseudo-absence data indicated the models were robust to pseudo-absence selection. The pseudo-absence set with highest explained deviance and AUC was used to conduct the remaining analyses, though analyses were also run with additional randomly chosen pseudo-absence sets to confirm stability of results. We conducted sensitivity analyses following Elith et al. (2008) to determine the appropriate model parameters (trees, learning rate, bag fraction and tree complexity) for each of the four BRT models individually (final parameters are listed in Table 3). Sensitivity analyses and model validations were conducted by comparing AUCs and explained deviance (Elith et al., 2008). Additionally, we cross-validated the models by running a training model by randomly choosing 75% of the entire dataset, then comparing model predictions against the remaining 25% of the data, while maintaining the same ratio of presences to pseudo-absences. Ten iterations using different sets of randomly removed data were run, and the mean validation statistics are reported across all ten iterations (Table 3).

## 2.4 | Kernel density estimations

To visualize the area used seasonally by blue sharks in our study region, kernel density estimations were made for each of the seasons modelled, resulting in four estimations across seasons and size classes as above. We used the kernel density functions in the “adehabitatHR” package, specifically the fixed kernel density (KD) estimation (Calenge, 2006; Maxwell, Conners, Sisson, & Dawson, 2016; Silverman, 1986). Bandwidth was determined using the reference bandwidth (href) for all datasets. In order to make the visualizations

comparable across all datasets, we determined the mean of the four reference bandwidths and applied that to the final kernel density models (href = 1.054). We also used the same grid intervals (number of grid intervals = 150) and determined the 50, and 95% utilization distribution (UD) across all datasets.

## 3 | RESULTS

Tracking data revealed large-scale patterns within our study area across seasons and between sex and size classes. During the summer (July-August), mature males were found largely in the southern half of the study area, with immature females found further north near tagging sites off Washington state and California; however, one immature female (ID 54592) was tagged off California in early July and moved north to the area off Washington by mid-August (Figure 1). Overlap of home ranges occurred between the two sexes in the Southern California Bight (the region south of 35°N and east of 127°W and constrained by the coast; Figure 2), with the core area home range for mature males overlapping entirely with a portion of female core area, though it should be noted that tagging occurred in this region. From the summer to the fall, female sharks typically moved south. During the fall, tracked mature males and immature females were found largely in the southern half of the study area although two immature females were still moving south from tagging locations in off British Columbia in the fall (Figure 1). The majority of locations in the fall for both groups occurred south of Monterey Bay and were concentrated in the Southern California Bight, though it should be noted that most of the mature male and some of the immature female tagging took place in this area. A broader area of the total home range overlapped in the fall than in

**TABLE 3** Boosted regression tree model summary. The parameters used in each model are listed in the first column below each model grouping. Model validation statistics (proportion deviance explained and AUC, area under the receiver operating curve) are shown for the training model as well as cross-validation (CV) where models were trained on 75% of the dataset and validated using the remaining 25%. Top predictors (above relative influence of 10) are bolded. CV was run on 10 times proportioning data differently each time; means of the 10 iterations are reported. Abbreviations are as follows: sea surface temperature (SST), surface chlorophyll-*a* (chl<sub>a</sub>), mean sea level anomaly (SLA) and its standard deviation (SLAsd), eddy kinetic energy (EKE)

Dataset	Variable	Relative influence (SD over 10 pseudo-absence groupings)	AUC (SD)	Proportion deviance explained (SD)	CV AUC (SD)	CV proportion deviance explained (SD)	
Males—Summer	<b>Latitude</b>	<b>29.66 (1.56)</b>	0.97 (0.001)	0.61 (0.004)	0.84 (0.02)	0.27 (0.04)	
	<b>SST</b>	<b>15.17 (1.15)</b>					
	No. of trees = 2,100	Chla					8.34 (0.81)
	Learning rate = 0.07	SLA					7.88 (0.67)
	Bag fraction = 0.8	Wind					7.76 (0.96)
	Tree complexity = 2	SSTsd					6.93 (0.47)
		Bathymetry					5.78 (0.61)
		Longitude					5.70 (0.42)
		EKE					4.52 (0.37)
		Rugosity					4.37 (0.44)
	SLAsd	3.90 (0.14)					
Males—Fall	<b>SST</b>	<b>21.91 (0.92)</b>	0.98 (0.002)	0.67 (0.01)	0.90 (0.01)	0.41 (0.38)	
	<b>Latitude</b>	<b>15.69 (1.66)</b>					
	No. of trees = 1,000	<b>Longitude</b>					<b>14.58 (0.88)</b>
	Learning rate = 0.05	<b>Wind</b>					<b>12.09 (1.59)</b>
	Bag fraction = 0.8	SLA					9.44 (3.10)
	Tree complexity = 2	Chla					8.15 (1.33)
		Bathymetry					7.68 (1.82)
		EKE					3.01 (0.53)
		SSTsd					2.94 (0.36)
		Rugosity					2.25 (0.34)
	SLAsd	2.22 (0.55)					
Females—Summer	<b>Latitude</b>	<b>25.76 (2.87)</b>	0.98 (0.003)	0.64 (0.02)	0.88 (0.02)	0.38 (0.51)	
	<b>SST</b>	<b>18.82 (1.46)</b>					
	No. of trees = 1,450	<b>Longitude</b>					<b>16.42 (2.17)</b>
	Learning rate = 0.03	Chla					9.25 (1.14)
	Bag fraction = 0.8	Wind					6.44 (1.07)
	Tree complexity = 2	Bathymetry					4.95 (0.89)
		SLA					4.80 (0.87)
		Rugosity					4.41 (0.89)
		EKE					3.86 (1.30)
		SSTsd					3.01 (0.67)
	SLAsd	2.29 (0.63)					
Females—Fall	<b>SST</b>	<b>26.66 (1.91)</b>	0.96 (0.003)	0.50 (0.01)	0.80 (0.02)	0.23 (0.35)	
	<b>SLA</b>	<b>12.68 (1.37)</b>					
	No. of trees = 1,100	Longitude					9.46 (1.07)
	Learning rate = 0.03	Latitude					9.05 (1.11)
	Bag fraction = 0.8	Bathymetry					8.67 (0.97)
	Tree complexity = 2	Chla					8.62 (1.01)
		EKE					5.79 (1.01)
		SSTsd					5.26 (1.08)
		Wind					5.26 (1.32)
		SLAsd					4.62 (0.62)
	Rugosity	3.94 (0.90)					

[Correction statement added on 31 May 2019 after first online publication: The “Tree complexity” grouping was missing in the third and fourth models in Table 3. This has been added in this version]

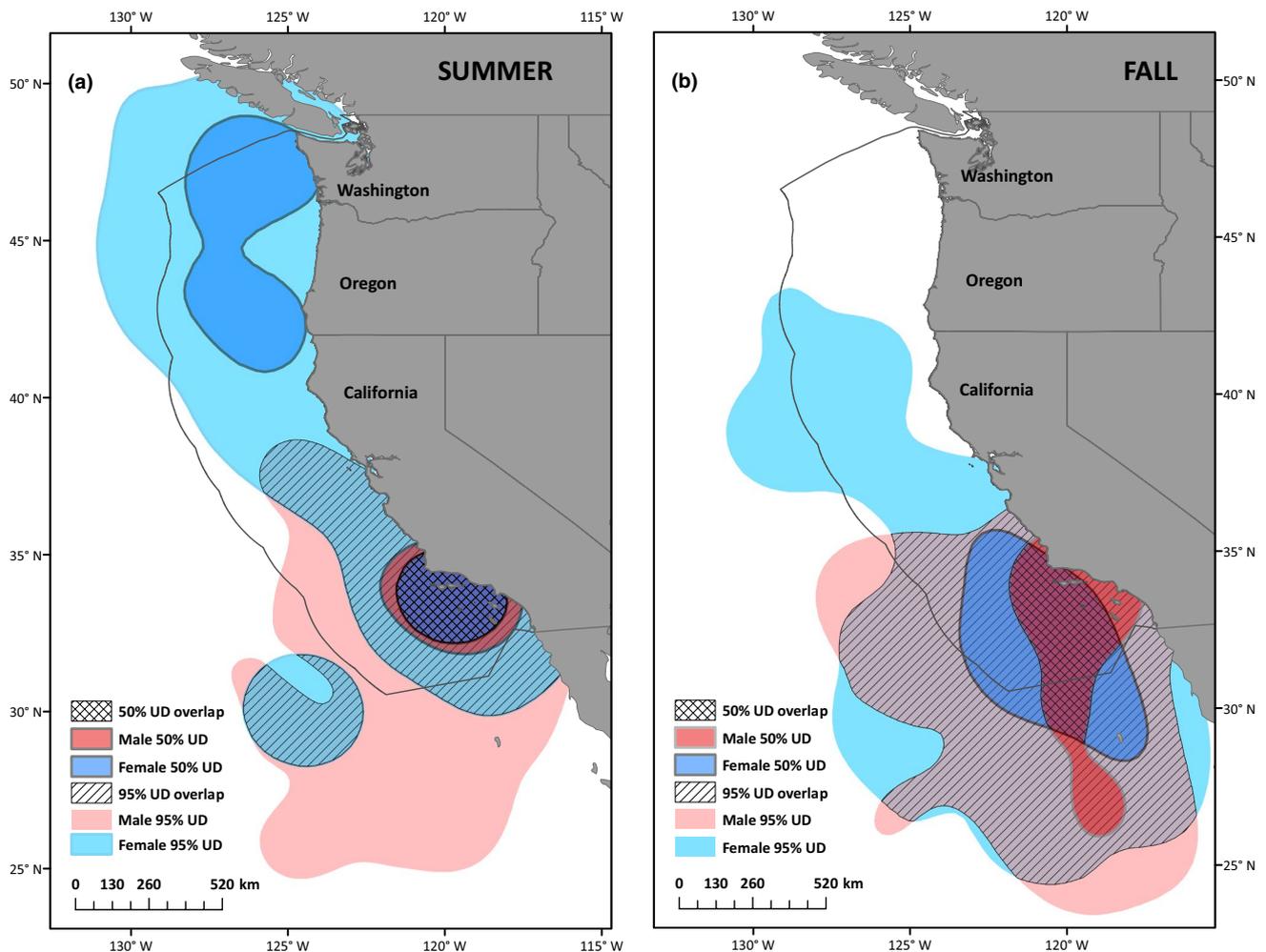
the summer, with less spatial separation between the sexes in fall months (Figure 2).

The fall mature male model explained the largest proportion of deviance (0.67) and had a relatively high predictive performance (cross-validated proportion deviance explained: 0.41), followed by the summer immature female model (0.64; predictive deviance: 0.38), the summer mature male model (0.61; predictive deviance: 0.27) and then the fall immature female model (0.50; predictive deviance: 0.23; Table 3). All models had AUC scores above 0.90, and the predictive models had AUC scores between 0.83 and 0.90, indicating relatively strong predictive performance (Table 3).

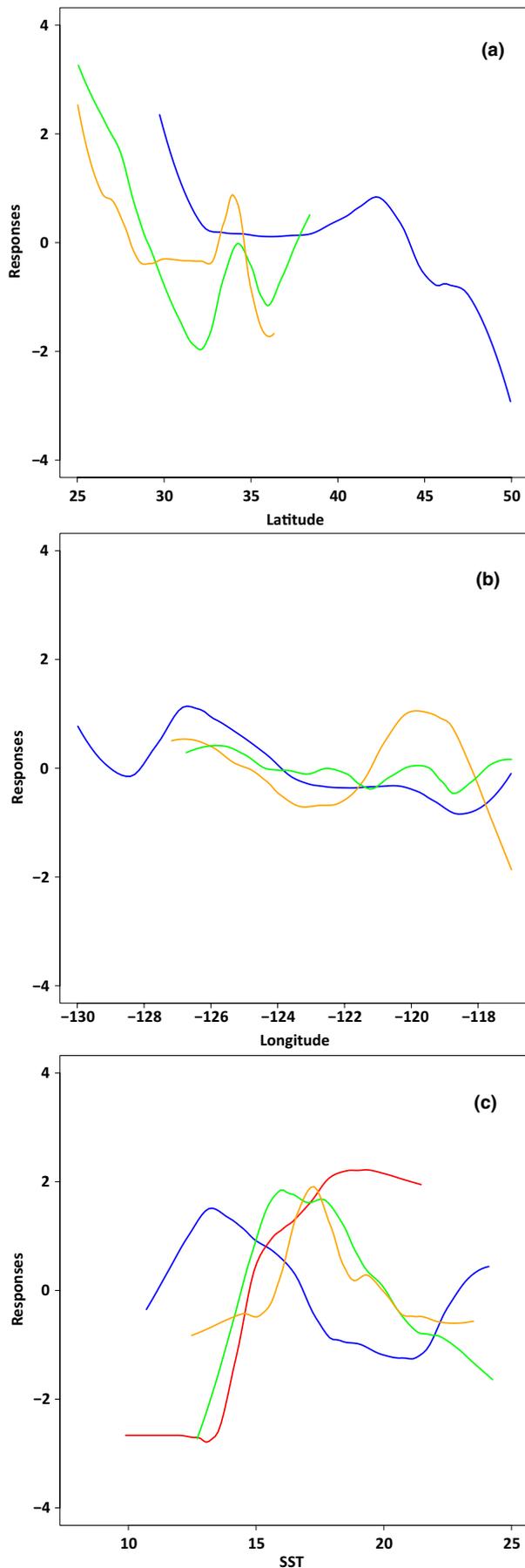
Consistent with the differences in distribution between immature females and mature males, habitat use also varied significantly (Figure 2). All variables had relative influence greater than random in all four models (Table 3). Models were robust to pseudo-absence choice, with only minor variations in the relative influence of variables with different pseudo-absence choice; changes in the order of variables of relative influence only occurred when relative influence was within 1%. Latitude was a top predictor in three of the four blue shark models: mature males in the fall (relative influence: 15.69%) and both mature males and immature females in the summer (relative

influence: males 29.66%, females 25.76%). In the summer, immature females occurred largely in the northern half of the study area, between approximately 30 and 50° N, while mature males occurred in the southern half of the study area south of 35° N. In the fall, both immature female and mature males occurred south of approximately 35° N (Figures 2 and 3).

Sea surface temperature was a strong predictor for all four models (relative influence between 26.66% and 15.17%) with temperature preferences above 15°C in the summer and fall for mature males and fall for immature females, and cooler temperatures in the summer for immature females, indicative of the northern portion of the study area where they were found. While males and females occupy similar habitat in the fall, immature females seem to prefer a broader range of SSTs (approximately 15–23°C) than males which had a preference for temperatures between approximately 15 and 20°C, as indicated in the curves above zero (Figure 3). SLA was a top predictor for females in the fall, indicating a potential preference for mesoscale activity (relative influence: 12.68%; Figure S2). Additionally, wind was a top predictor for males in the fall (relative influence: 12.09%; Figure S2) suggesting a preference for upwelled waters; these variables were less important predictors in the other



**FIGURE 2** Home range (50% and 95% utilization distributions, UDs) for immature females (blue shades) and mature males (red shades) in the (a) summer and (b) fall. Overlap of 50 and 95% UDs indicated via hatching. The solid black line indicates the US Exclusive Economic Zone



**FIGURE 3** Smoothed partial dependence plots for (a) latitude, (b) longitude and (c) sea surface temperature (SST) in degrees Celsius. Female immature summer model is shown in blue, the immature female fall model is shown in red (panel C only), the mature male summer model is shown in green and the mature male fall model is shown in orange

models, with relative influence <10% for each (Table 3). Longitude was a strong predictor for mature males in the fall (relative influence: 14.58%) with a preference for longitudes east of  $-123^{\circ}\text{W}$ , and immature females in the summer (relative influence: 16.42%) with a preference for longitudes west  $-124^{\circ}\text{W}$  (Figure 3). Bathy, SSTsd, SLAsd, chl $a$ , EKE and rugosity were weaker predictors (<10% relative influence) across all four models (Table 3).

## 4 | DISCUSSION

Our study found that in more coastal regions of the Northeast Pacific, there is sex and size class segregation among blue sharks and resulting differences in habitat preference. In the summer, immature females were found further north, while male habitat occurred in the southern portion of the study area (Figure 1); however, overlap does occur in the Southern California Bight for both core and overall home ranges, with core home range of males almost entirely overlapped by a portion of female core home range in that region (Figure 2). This suggests shared habitat during certain times of the year, as was found in the North Atlantic (Vandeperre, Aires-da-Silva, Fontes, et al., 2014a). Model results, however, suggest that while horizontal habitat may be similar, there may be some segregation within this habitat based on preference for specific environmental conditions. While SST had the strongest influence on model outcomes in the fall, females preferred a broader suite of SST than males (Figure 3).

Blue sharks showed a strong preference for certain SST ranges, with SST as one of the top three predictors across all four groups (relative influence between 26.66% and 15.17%; Table 3). Except for immature females in the summer, preference appeared to be greatest for SST above  $\sim 15^{\circ}\text{C}$ , similar to ranges previously found for blue sharks in the Northeast Atlantic (Howey et al., 2017; Nakano, 1994; Vandeperre et al., 2016) and off Australia (Stevens, Bradford, & West, 2010). During the summer when females are found further north off Oregon and Washington, immature females showed a stronger preference for colder temperatures (between approximately 12– $15^{\circ}\text{C}$ ), but this preference changed in the fall to temperatures  $>15^{\circ}\text{C}$  (Figure 3). While they did not partition data by season, both Howey et al. (2017) and Vandeperre, Aires-da-Silva, Fontes, et al. (2014a) also found that immature females in the North Atlantic occupied cooler temperatures than both adult and immature males. They hypothesized that the thicker skin of females may serve as protection during mating, as well as to expand their niche to cooler waters. This fits with the patterns seen in this study, and the shift to warmer waters in the fall is linked to seasonal movements south. Other studies also found that age and sex both play a role in determining distribution of

blue sharks in relation to water temperature (Nakano & Seki, 2003); however, some have suggested that colder temperatures may compromise growth rates for immature females (Carlson, Goldman, & Lowe, 2004). Additionally, Nakano and Nagasawa (1996) examined age and sex patterns in relation to SST in bycatch off the west coast of North America and found a preference for warmer temperatures by younger individuals (less than approximately 140 cm). The female individuals in this study are larger in size (mean = 157.7 cm,  $\pm 9.8$ ; Table 1) than those studied by Nakano and Nagasawa, which may reduce their dependence on warm waters for growth.

Influence of other environmental variables varied across sex and age. While SST and latitude were top drivers for all four models (except latitude for immature females in the fall), longitude was a top predictor for both males in the fall (14.58% relative influence) and females in the summer (16.42% relative influence; Table 3). Females were found further west in the summer (Figure 3), largely as a result of their distribution in higher latitudes and the North American landmass occupying the eastern longitudes further north (Figure 2). In contrast, male habitat in the fall was found in greater concentration further east. SLA was a top predictor for immature females during the fall (12.68% relative influence), indicating a preference for mesoscale features that are likely to be characterized by aggregations of prey (Figure S2); a preference for productivity fronts and areas indicative of upwelling or mixing were also found for blue sharks in the Northeast Atlantic (Queiroz et al., 2012; Vandeperre et al., 2016) and for this population using catch data (Bigelow, Boggs, & He, 1999).

#### 4.1 | Coastal movements and the N-S model

Most studies of blue shark distribution in the Pacific have focused on almost entirely pelagic habitats, movements and individuals. Pelagic habitats were the basis for the North-South (N-S) model developed by Nakano for blue sharks in the North Pacific, with the majority of data collected west of 130°W (Nakano, 1994). In the present study, animals were tagged closer to the coast and as a result we are able to provide insights into more coastal habitat preferences and highlight differences between more coastal and pelagic distributions.

Nakano's N-S model (1994) suggests that smaller juvenile sharks are found in temperate and subarctic waters north of 35°N, and that larger subadult females similar to the ones found in our study occur in the pupping area north of 35°N and into the Gulf of Alaska, where they stay from juvenile stages until maturity. While observer data from the drift gillnet fishery support the N-S model of blue shark segregation (Urbisci et al., 2013; Walsh & Teo, 2012), our tracking data and models suggest a broader distribution, particularly for immature females. During the summer, immature females were distributed between approximately 32° and 45°N as suggested by the N-S model (Figure 2). In the fall, however, there was a marked shift to the region south of 35°N with immature females occurring along Southern California and south of 35°N to the southern boundary of our study area at 25°N (Figure 2), an area

suggested to be habitat for subadult males (Nakano & Seki, 2003). Additionally, the few individual tracks that continued beyond fall ranged even further south towards hypothesized breeding grounds in the winter months. The population of immature female sharks tagged in this study are relatively large (mean 157.7 cm; Table 1) so this could be a reflection of sharks nearing maturity, and beginning to undertake larger-scale seasonal migrations as they do in both the Pacific and Atlantic (Nakano & Seki, 2003; Stevens, 1976). Subadult females are known to mate and begin these migrations even before they are able to store sperm (Nakano & Stevens, 2008), and in the North Atlantic, large juvenile females are known to undertake seasonal migrations until maturity, moving into northern waters during the warmer summer months (Vandeperre, Aires-da-Silva, Fontes, et al., 2014a; Vandeperre et al., 2016). The observed movements may be a reflection of this ontogenetic shift, or it may be a result of different oceanographic drivers in more coastal regions, and particularly the influence of mesoscale variability within the California Current system.

Male shark movements and habitats were largely in keeping with the N-S model. Nakano (1994) and other studies suggest that larger adult sharks are found throughout the Pacific basin, though mainly in tropical and subtropical waters between 20° and 30°N (Nakano & Seki, 2003; Walsh & Teo, 2012). In this study, males remained primarily south of 35°N, especially in the fall (Figures 1 and 2). This southern region is hypothesized to be breeding habitat by Nakano and Seki (2003).

The differences seen in this study versus the N-S model indicate differences in habitat use between pelagic and more coastal waters. Our results may further differ from pelagic distributions as a result of localized oceanographic drivers (such as SST) and localized prey availability. More coastal movement patterns in the North Atlantic were shown to be similar to the patterns seen here, with large subadult females making latitudinal migrations on a similar scale (across ~15°) (Vandeperre, Aires-da-Silva, Fontes, et al., 2014a).

#### 4.2 | Model performance and caveats

The predictive capacity of the models varied by grouping. The models for mature males in the fall and immature females in the summer explained greater deviance (67% and 64% respectively), and also had the greater predictive performance (41% and 38% CV proportion explained deviance) than the other two models, though all models performed well (Table 2). Regardless of season, adult males seemed to be largely driven by location and SST, while females in the fall were also driven by indicators of mesoscale structure (SLA). This indicates that movement between the two groups (immature females and mature males) and across seasons is better captured when analysed separately rather than in concert. This is likely due to different drivers in habitat, such as differences in the preferred range of SST, spatial segregation between these two groups, and different drivers resulting from differing life history stages.

A number of caveats should be taken into account when interpreting this study. First, and most critically, all of the mature

males and the majority of immature females were tagged off the coast of Southern California, thereby biasing the study to individuals already distributed in this region, though two immature females (tags 68493, 68502) travelled from the British Columbia/Washington coast where they were tagged in the summer to Southern California in the fall, and one (tag 54592) travelled from Southern California where it was tagged into waters off Washington's coast; interestingly, this migration occurred in the summer months (July/August) (Figure 1). Additionally, tag durations ranged widely (from 25 to 614 days; Table 1) but the average duration was close to 4 months (124.8 days), further biasing the analyses to the tagging locations, and limiting our ability to predict long-term movements; hence, seasonal predictions were most appropriate for this dataset, and we chose seasons that overlapped with the majority of data (Figure S1). Despite this bias in our tracking data, studies using fishery observer data from the drift gillnet fishery have shown that shark bycatch spans all size classes and occurs in the same regions as our tracking data (Urbisci et al., 2013). It is possible that our tagging sample size, or location of tagging particularly for the different size classes, resulted in our inability to capture the N-S pattern as expected; however, at sea tagging is costly due to vessel time, and our tagging was semi-random as most of tag deployments occurred in association with periodic survey efforts over a broad region (Runcie et al., 2016). While the tracking data reflect similar patterns to fisheries observer studies (Urbisci et al., 2013), we cannot be certain about the degree to which our tracking data are fully reflective of the entire blue shark population given the tagging location bias. Regardless, we present data that supports an alternate hypothesis that blue shark movements have more variability across sex and size class than the N-S model predicts, especially in more coastal regions where the majority of data were collected.

Another important caveat in this analysis is the absence of vertical data on space use, which may be a segregating factor between male and female blue sharks in studies in the Atlantic (Hazin et al., 1994; Queiroz et al., 2012; Vandeperre et al., 2016). The inclusion of depth would provide additional insights into the segregation seen here, or into the habitat preferences of different size classes, and may reveal patterns of habitat segregation in regard to temperature preferences at depth.

Finally, habitat preferences are based on both presence tracks and simulated pseudo-absences. Presence-only models exist (e.g., BIOCLIM (Busby, 1991)); however, models that incorporate some form of absence data, even if simulated, have been shown to be preferable to presence-only models (Elith et al., 2006). Despite this, the choice and simulation of pseudo-absence data can influence model outcomes (Barbet-Massin et al., 2012). CRWs are regularly used for simulating pseudo-absence tracks (Briscoe et al., 2018; Hazen et al., 2016, 2018; Willis-Norton et al., 2015); however, no simulation method is capable of fully capturing where animals were not present (Aarts, MacKenzie, McConnell, Fedak, & Matthiopoulos, 2008). CRWs can result in biases, particularly

when animals conduct long-distance movements. As in Hazen et al. (2018), we attempted to reduce these biases by resampling presences and pseudo-absences and ensuring consistency in results; however, no method is entirely free from biases.

### 4.3 | Management implications

Developing stock assessments for blue sharks has been a focus of the International Scientific Committee Shark Working Group in recent years. Understanding spatial segregation and the drivers behind this segregation is critical for creating assessments that reflect the underlying structure of the population and understanding differences in fisheries mortality across the population. This study suggests that segregation exists in coastal regions and between size classes, at least in the summer, however, immature females in particular may have a broader distribution than suggested, and immature female and adult male habitat overlaps considerably in the fall along the US West Coast; this should be taken into account when considering the potential for bycatch and thus mortality in fisheries in the Northeast Pacific. Additionally, sea surface temperature was a strong predictor of blue shark habitat regardless of sex or size class. This suggests that climate change and variability could influence blue shark distribution, and thus dynamic ocean management approaches may be well suited to reducing bycatch of this species (Hazen et al., 2018; Maxwell et al., 2015). Furthermore, insights into the habitat preferences of blue sharks can be used to determine means of understanding catch rates or reducing bycatch through changes in gear configurations, time-area closures or other management techniques (Bigelow & Maunder, 2007; Carruthers, Neilson, & Smith, 2011; Dewar et al., 2011; Gilman et al., 2008). These additional insights into habitat preferences can aid managers and fishermen in determining means of reducing bycatch and managing blue sharks.

Tracking datasets have inherently under-sampled certain critical life history stages based on difficulty in sampling juveniles (Hazen et al., 2012), yet understanding ontogenetic differences in movement and habitat can be critical for conservation and management (Gianuca, Phillips, Townley, & Votier, 2017; Gonzalez Carman et al., 2012; Hays et al., 2016). Management decisions that target only adults can leave critical bottlenecks in place that hamper population recovery. For example, a population viability analysis for loggerhead sea turtles (*Carretta carretta*) showed that efforts to protect hatchlings on nesting beaches and adults nearshore were insufficient to recover the population (Crowder, Crouse, Heppell, & Martin, 1994); juveniles were one of the most sensitive life history stages and one that was not adequately addressed by conservation measures. Thus, studies like this one that look across life history stages can highlight differences in habitat preferences that are critical for protecting sensitive life history stages. Additionally, understanding differential fisheries mortality across sex and size classes is critical to target and bycatch management (Sippel et al., 2015).

## ACKNOWLEDGEMENTS

Funding for this effort was provided by Stanford University, the Center for Ocean Solutions, NOAA Bycatch Reduction and Engineering Program (NA14NMF4720312), the California Sea Grant Program (NA14OAR4170075) and by NASA Earth Science Division/Applied Sciences ROSES Program (NNH12ZDA001N-ECOF). We thank the NOAA Southwest Fishery Science Center's Fisheries Research Division, especially Suzanne Kohin, Tim Sippel and James Wraith. We also thank the satellite data providers (NASA, NOAA, AVISO) and data servers (ERDDAP) used in this study.

## DATA AVAILABILITY STATEMENT

All environmental data are freely available online via the NOAA Environmental Research Division Data Access Portal (<https://coastwatch.pfeg.noaa.gov/erddap>). Tracking data are housed within the US National Marine Fisheries Service Southwest Fisheries Science Center and freely available by contacting the authors.

## ORCID

Sara M. Maxwell  <https://orcid.org/0000-0002-4425-9378>

Kylie L. Scales  <https://orcid.org/0000-0003-0843-0956>

Dana K. Briscoe  <https://orcid.org/0000-0002-8891-9294>

## REFERENCES

- Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., & Matthiopoulos, J. (2008). Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, *31*, 140–160. <https://doi.org/10.1111/j.2007.0906-7590.05236.x>
- Adams, G. D., Flores, D., Flores, O. G., Aarestrup, K., & Svendsen, J. C. (2016). Spatial ecology of blue shark and shortfin mako in southern Peru: Local abundance, habitat preferences and implications for conservation. *Endangered Species Research*, *31*, 19–32. <https://doi.org/10.3354/esr00744>
- Bailey, H., Shillinger, G., Palacios, D., Bograd, S., Spotila, J., Paladino, F., & Block, B. (2008). Identifying and comparing phases of movement by leatherback turtles using state-space models. *Journal of Experimental Marine Biology and Ecology*, *356*, 128–135. <https://doi.org/10.1016/j.jembe.2007.12.020>
- Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, *3*, 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>
- Becker, E. A., Forney, K. A., Foley, D. G., Smith, R. C., Moore, T. J., & Barlow, J. (2014). Predicting seasonal density patterns of California cetaceans based on habitat models. *Endangered Species Research*, *23*, 1–22. <https://doi.org/10.3354/esr00548>
- Bigelow, K. A., Boggs, C. H., & He, X. (1999). Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. *Fisheries Oceanography*, *8*, 178–198. <https://doi.org/10.1046/j.1365-2419.1999.00105.x>
- Bigelow, K. A., & Maunder, M. N. (2007). Does habitat or depth influence catch rates of pelagic species? *Canadian Journal of Fisheries and Aquatic Sciences*, *64*, 1581–1594. <https://doi.org/10.1139/f07-115>
- Breed, G. A., Jonsen, I. D., Myers, R. A., Bowen, W. D., & Leonard, M. L. (2009). Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state-space analysis. *Ecology*, *90*, 3209–3221. <https://doi.org/10.1890/07-1483.1>
- Briscoe, D. K., Fossette, S., Scales, K., Hazen, E. L., Bograd, S. J., Maxwell, S. M., ... Lewison, R. (2018). Characterizing habitat suitability for a central-place forager in a dynamic marine environment. *Ecology and Evolution*, *8*, 2788–2801. <https://doi.org/10.1002/ece3.3827>
- Busby, J. R. (1991). *BIOCLIM—a bioclimate analysis and prediction system*. *Plant protection quarterly* (Australia).
- Calenge, C. (2006). The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*, 516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Calenge, C. (2007). Exploring habitat selection by wildlife with adehabitat. *Journal of Statistical Software*, *22*, 1–19.
- Campana, S. E., Dorey, A., Fowler, M., Joyce, W., Wang, Z., Wright, D., & Yashayev, I. (2011). Migration pathways, behavioural thermoregulation and overwintering grounds of blue sharks in the Northwest Atlantic. *PLoS ONE*, *6*, e16854. <https://doi.org/10.1371/journal.pone.0016854>
- Carlson, J. K., Goldman, K. J., & Lowe, C. G. (2004). Metabolism, energetic demand, and endothermy. In J. C. Carrier, J. A. Musick, & M. C. Heithaus (Eds.), *Biology of sharks and their relatives* (pp. 203–224). Boca Raton, FL: CRC Press LLC.
- Carruthers, E. H., Neilson, J. D., & Smith, S. C. (2011). Overlooked bycatch mitigation opportunities in pelagic longline fisheries: Soak time and temperature effects on swordfish (*Xiphias gladius*) and blue shark (*Prionace glauca*) catch. *Fisheries Research*, *108*, 112–120. <https://doi.org/10.1016/j.fishres.2010.12.008>
- Carvalho, F., Ahrens, R., Murie, D., Bigelow, K., Aires-Da-Silva, A., Maunder, M. N., & Hazin, F. (2015). Using pop-up satellite archival tags to inform selectivity in fisheries stock assessment models: A case study for the blue shark in the South Atlantic Ocean. *ICES Journal of Marine Science*, *72*, 1715–1730. <https://doi.org/10.1093/icesjms/fsv026>
- Cayula, J.-F., & Cornillon, P. (1992). Edge detection algorithm for SST images. *Journal of Atmospheric and Oceanic Technology*, *9*, 67–80. [https://doi.org/10.1175/1520-0426\(1992\)009<0067:EDAFSL>2.0.CO;2](https://doi.org/10.1175/1520-0426(1992)009<0067:EDAFSL>2.0.CO;2)
- Crowder, L. B., Crouse, D. T., Heppell, S. S., & Martin, T. (1994). Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications*, *4*, 437–445. <https://doi.org/10.2307/1941948>
- Derville, S., Constantine, R., Baker, C. S., Oremus, M., & Torres, L. G. (2016). Environmental correlates of nearshore habitat distribution by the Critically Endangered Maui dolphin. *Marine Ecology Progress Series*, *551*, 261–275.
- Dewar, H., Prince, E. D., Musyl, M. K., Brill, R. W., Sepulveda, C., Luo, J. G., ... McNaughton, L. M. (2011). Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags. *Fisheries Oceanography*, *20*, 219–241. <https://doi.org/10.1111/j.1365-2419.2011.00581.x>
- Elith, J., Graham, C. H., Anderson, R. P., Dudik, M., Ferrier, S., Guisan, A., ... Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*, 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*, 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>
- Ficetola, G. F., Pennati, R., & Manenti, R. (2013). Spatial segregation among age classes in cave salamanders: Habitat selection or social interactions? *Population Ecology*, *55*, 217–226. <https://doi.org/10.1007/s10144-012-0350-5>
- Gianuca, D., Phillips, R. A., Townley, S., & Votier, S. C. (2017). Global patterns of sex-and age-specific variation in seabird bycatch.

- Biological Conservation*, 205, 60–76. <https://doi.org/10.1016/j.biocon.2016.11.028>
- Gilman, E., Clarke, S., Brothers, N., Alfaro-Shigueto, J., Mandelman, J., Mangel, J., ... Werner, T. (2008). Shark interactions in pelagic long-line fisheries. *Marine Policy*, 32, 1–18. <https://doi.org/10.1016/j.marpol.2007.05.001>
- Gonzalez Carman, V., Falabella, V., Maxwell, S., Albareda, D., Campagna, C., & Mianzan, H. (2012). Revisiting the ontogenetic shift paradigm: The case of juvenile green turtles in the SW Atlantic. *Journal of Experimental Marine Biology and Ecology*, 429, 64–72. <https://doi.org/10.1016/j.jembe.2012.06.007>
- Hays, G. C., Ferreira, L. C., Sequeira, A. M. M., Meekan, M. G., Duarte, C. M., Bailey, H., ... Thums, M. (2016). Key questions in marine megafauna movement ecology. *Trends in Ecology & Evolution*, 31, 463–475. <https://doi.org/10.1016/j.tree.2016.02.015>
- Hazen, E. L., Maxwell, S. M., Bailey, H., Bograd, S. J., Hamann, M., Gaspar, P., ... Shillinger, G. L. (2012). Ontogeny in marine tagging and tracking science: Technologies and data gaps. *Marine Ecology Progress Series*, 457, 221–240. <https://doi.org/10.3354/meps09857>
- Hazen, E. L., Palacios, D. M., Forney, K. A., Howell, E. A., Becker, E., Hoover, A. L., ... Bailey, H. (2016). WhaleWatch: A dynamic management tool for predicting blue whale density in the California Current. *Journal of Applied Ecology*, 54(5), 1415–1428
- Hazen, E. L., Scales, K. L., Maxwell, S. M., Briscoe, D. K., Welch, H., Bograd, S. J., ... Lewison, R. L. (2018). A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. *Science Advances*, 4, eaar3001. <https://doi.org/10.1126/sciadv.aar3001>
- Hazin, F., Boeckman, C., Leal, E., Lessa, R., Kihara, K., & Otsuka, K. (1994). Distribution and relative abundance of the blue shark, *Prionace glauca*, in the southwestern equatorial Atlantic Ocean. *Fishery Bulletin*, 92, 474–480.
- Hobday, A. J., Hartog, J. R., Spillman, C. M., & Alves, O. (2011). Seasonal forecasting of tuna habitat for dynamic spatial management. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 898–911. <https://doi.org/10.1139/f2011-031>
- Howell, E. A., Kobayashi, D. R., Parker, D. M., Balazs, G. H., & Polovina, A. J. J. (2008). TurtleWatch: A tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic long-line fishery. *Endangered Species Research*, 5, 267–278. <https://doi.org/10.3354/esr00096>
- Howey, L. A., Wetherbee, B. M., Tolentino, E. R., & Shivji, M. S. (2017). Biogeophysical and physiological processes drive movement patterns in a marine predator. *Movement Ecology*, 5, 16. <https://doi.org/10.1186/s40462-017-0107-z>
- Jeglinski, J. W., Goetz, K. T., Werner, C., Costa, D. P., & Trillmich, F. (2013). Same size - same niche? Foraging niche separation between sympatric juvenile Galapagos sea lions and adult Galapagos fur seals. *Journal of Animal Ecology*, 82(3), 694–706. <https://doi.org/10.1111/1365-2656.12019>
- Johnson, D. S., London, J. M., Lea, M. A., & Durban, J. W. (2008). Continuous-time correlated random walk model for animal telemetry data. *Ecology*, 89, 1208–1215. <https://doi.org/10.1890/07-1032.1>
- Jonsen, I. D., Basson, M., Bestley, S., Bravington, M. V., Patterson, T. A., Pedersen, M. W., ... Wotherspoon, S. J. (2013). State-space models for bio-loggers: A methodological road map. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 88–89, 34–46. <https://doi.org/10.1016/j.dsr2.2012.07.008>
- Jonsen, I. D., Flemming, J. M., & Myers, R. A. (2005). Robust state-space modeling of animal movement data. *Ecology*, 86, 2874–2880. <https://doi.org/10.1890/04-1852>
- Kappes, M., Shaffer, S., Tremblay, Y., Foley, D. G., Palacios, D., Robinson, P. W., ... Costa, D. P. (2010). Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific. *Progress in Oceanography*, 86, 246–260. <https://doi.org/10.1016/j.pcean.2010.04.012>
- King, J., Wetklo, M., Supernault, J., Taguchi, M., Yokawa, K., Sosa-Nishizaki, O., & Withler, R. (2015). Genetic analysis of stock structure of blue shark (*Prionace glauca*) in the north Pacific ocean. *Fisheries Research*, 172, 181–189. <https://doi.org/10.1016/j.fishres.2015.06.029>
- Lewison, R., Hobday, A. J., Maxwell, S., Hazen, E., Hartog, J. R., Dunn, D. C., ... Crowder, L. B. (2015). Dynamic ocean management: Identifying the critical ingredients of dynamic approaches to ocean resource management. *BioScience*, 65, 486–498. <https://doi.org/10.1093/biosci/biv018>
- Lewison, R., Wallace, B. P., Alfaro-Shigueto, J., Mangel, J., Maxwell, S. M., & Hazen, E. L. (2013). In (J. Musick, K. Lohmann and J. Wyneken, (Ed.), *Fisheries bycatch of marine turtles: Lessons learned from decades of research and conservation* Biology of Sea Turtles, Vol. 3 (pp. 329–352). Boca Raton, FL: CRC Press/Taylor & Francis Group.
- Mannocci, L., Monestiez, P., Spitz, J., & Ridoux, V. (2015). Extrapolating cetacean densities beyond surveyed regions: Habitat-based predictions in the circumtropical belt. *Journal of Biogeography*, 7, 1267–1280. <https://doi.org/10.1111/jbi.12530>
- Maxwell, S. M., Breed, G. A., Nickel, B. A., Makanga-Bahouna, J., Pemo-Makaya, E., Parnell, R. J., ... Coyne, M. S. (2011). Using satellite tracking to optimize protection of long-lived marine species: Olive ridley sea turtle conservation in Central Africa. *PLoS ONE*, 6, e19905. <https://doi.org/10.1371/journal.pone.0019905>
- Maxwell, S. M., Conners, M. G., Sisson, N. B., & Dawson, T. M. (2016). Potential benefits and shortcomings of marine protected areas for small seabirds revealed using miniature tags. *Frontiers in Marine Science*, 3, 264. <https://doi.org/10.3389/fmars.2016.00264>
- Maxwell, S. M., Hazen, E. L., Lewison, R. L., Dunn, D. C., Bailey, H., Bograd, S. J., ... Crowder, L. B. (2015). Dynamic ocean management: Defining and conceptualizing real-time management of the ocean. *Marine Policy*, 58, 42–50. <https://doi.org/10.1016/j.marpol.2015.03.014>
- Montealegre-Quijano, S., & Vooren, C. M. (2010). Distribution and abundance of the life stages of the blue shark *Prionace glauca* in the Southwest Atlantic. *Fisheries Research*, 101, 168–179. <https://doi.org/10.1016/j.fishres.2009.10.001>
- Nakano, H. (1994). Age, reproduction and migration of blue shark in the North Pacific Ocean. *Bulletin National Research Institute of Far Seas Fisheries*, 31, 141–256.
- Nakano, H., & Nagasawa, K. (1996). Distribution of pelagic elasmobranchs caught by salmon research gillnets in the North Pacific. *Fisheries Science*, 62, 860–865. <https://doi.org/10.2331/fishsci.62.860>
- Nakano, H., & Seki, M. (2003). *Synopsis of biological data on the blue shark, Prionace glauca Linnaeus*. Bulletin-Fisheries Research Agency Japan, 18–55.
- Nakano, H., & Stevens, J. D. (2008). The biology and ecology of the blue shark, *Prionace glauca*. *Sharks of the Open Ocean: Biology, Fisheries and Conservation*, 1, 140–151.
- NOAA (2008) *Fish and invertebrate bycatch estimates for the California drift gillnet fishery targeting swordfish and thresher shark, 1990–2006*.
- Polovina, J. J., Howell, E., Parker, D. M., & Balazs, G. H. (2003). Dive-depth distribution of loggerhead (*Carretta carretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific: Might deep longline sets catch fewer turtles? *Fishery Bulletin*, 101, 189–193.
- Queiroz, N., Humphries, N. E., Noble, L. R., Santos, A. M., & Sims, D. W. (2012). Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. *PLoS ONE*, 7, e32374. <https://doi.org/10.1371/journal.pone.0032374>
- Queiroz, N., Lima, F. P., Maia, A., Ribeiro, P. A., Correia, J. P., & Santos, A. A. (2005). Movement of blue shark, *Prionace glauca*, in the north-east Atlantic based on mark - recapture data. *Journal of the Marine Biological Association of the United Kingdom*, 85, 1107–1112.

- R Core Team (2016) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ridgeway, G. (2006) *Generalized boosted regression models*. Documentation on the R package "gbm", version 1.5-7.
- Runcie, R., Holts, D., Wraith, J., Xu, Y., Ramon, D., Rasmussen, R., & Kohin, S. (2016). A fishery-independent survey of juvenile shortfin mako (*Isurus oxyrinchus*) and blue (*Prionace glauca*) sharks in the Southern California Bight, 1994–2013. *Fisheries Research*, 183, 233–243. <https://doi.org/10.1016/j.fishres.2016.06.010>
- Scales, K. L., Hazen, E. L., Jacox, M. G., Castruccio, F., Maxwell, S. M., Lewison, R. L., & Bograd, S. J. (2018). Fisheries bycatch risk to marine megafauna is intensified in Lagrangian coherent structures. *Proceedings of the National Academy of Sciences*, 115(28), 7362–7367. <https://doi.org/10.1073/pnas.1801270115>
- Scales, K., Hazen, E., Maxwell, S. M., Dewar, H., Kohin, S., Jacox, M., ... Bograd, S. (2017). Fit to predict? Ecoinformatics for modeling dynamic habitat suitability for highly migratory marine species. *Ecological Applications*, 27, 2313–2329.
- Silverman, B. W. (1986). *Density estimation for statistics and data analysis*. Boca Raton FL: CRC Press.
- Simons, R. A. (2016). *ERDDAP*. Monterey, CA: NOAA/NMFS/SWFSC/ERD.
- Sippel, T., Paige Eveson, J., Galuardi, B., Lam, C., Hoyle, S., Maunder, M., ... Nicol, S. (2015). Using movement data from electronic tags in fisheries stock assessment: A review of models, technology and experimental design. *Fisheries Research*, 163, 152–160. <https://doi.org/10.1016/j.fishres.2014.04.006>
- Soykan, C. U., Eguchi, T., Kohin, S., & Dewar, H. (2014). Prediction of fishing effort distributions using boosted regression trees. *Ecological Applications*, 24, 71–83. <https://doi.org/10.1890/12-0826.1>
- Stevens, J. D. (1976). First results of tagging in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 56, 929–937.
- Stevens, J. D., Bradford, R. W., & West, G. J. (2010). Satellite tagging of blue sharks (*Prionace glauca*) and other pelagic sharks off eastern Australia: Depth behaviour, temperature experience and movements. *Marine Biology*, 157, 575–591. <https://doi.org/10.1007/s00227-009-1343-6>
- Torres, L. G., Read, A. J., & Halpin, P. (2008). Fine-scale habitat modeling of a top marine predator: Do prey data improve predictive capacity? *Ecological Applications*, 18, 1702–1717. <https://doi.org/10.1890/07-1455.1>
- Urbisci, L., Runcie, R., Sippel, T., Piner, K., Dewar, H., & Kohin, S. (2013). *Examining size-sex segregation among blue sharks (Prionace glauca) from the Eastern Pacific Ocean using drift gillnet fishery and satellite tagging data*. ISC Shark Working Group Paper ISC/13/SHARKWG-1/06.
- Vandeperre, F., Aires-da-Silva, A., Fontes, J., Santos, M., Santos, R. S., & Afonso, P. (2014a). Movements of blue sharks (*Prionace glauca*) across their life history. *PLoS ONE*, 9, e103538. <https://doi.org/10.1371/journal.pone.0103538>
- Vandeperre, F., Aires-da-Silva, A., Lennert-Cody, C., Serrão Santos, R., & Afonso, P. (2016). Essential pelagic habitat of juvenile blue shark (*Prionace glauca*) inferred from telemetry data. *Limnology and Oceanography*, 61, 1605–1625.
- Vandeperre, F., Aires-da-Silva, A., Santos, M., Ferreira, R., Bolten, A. B., Santos, R. S., & Afonso, P. (2014b). Demography and ecology of blue shark (*Prionace glauca*) in the central North Atlantic. *Fisheries Research*, 153, 89–102. <https://doi.org/10.1016/j.fishres.2014.01.006>
- Walsh, W., & Kleiber, P. (2001). Generalized additive model and regression tree analyses of blue shark (*Prionace glauca*) catch rates by the Hawaii-based commercial longline fishery. *Fisheries Research*, 53, 115–131. [https://doi.org/10.1016/S0165-7836\(00\)00306-4](https://doi.org/10.1016/S0165-7836(00)00306-4)
- Walsh, W. A., & Teo, S. L. H. (2012). *Catch Statistics, Length Data and Standardized CPUE for blue shark Prionace glauca taken by longline fisheries based in Hawaii and California*. ISC Shark Working Group Paper ISC/12/SHARKWG-1/02.
- Whitlock, R. E., Hazen, E. L., Walli, A., Farwell, C., Bograd, S. J., Foley, D. G., ... Block, B. A. (2015). Direct quantification of energy intake in an apex marine predator suggests physiology is a key driver of migrations. *Science Advances*, 1, e1400270. <https://doi.org/10.1126/sciadv.1400270>
- Willis-Norton, E., Hazen, E. L., Fossette, S., Shillinger, G., Rykaczewski, R. R., Foley, D. G., ... Bograd, S. J. (2015). Climate change impacts on leatherback turtle pelagic habitat in the Southeast Pacific. *Deep Sea Research Part II: Topical Studies in Oceanography*, 113, 260–267. <https://doi.org/10.1016/j.dsr2.2013.12.019>
- Wingfield, D. K., Peckham, S. H., Foley, D. G., Palacios, D. M., Lavaniegos, B. E., Durazo, R., ... Bograd, S. J. (2011). The making of a productivity hotspot in the Coastal Ocean. *PLoS ONE*, 6, e27874. <https://doi.org/10.1371/journal.pone.0027874>

#### BIOSKETCH

**Dr. Sara Maxwell** is Assistant Professor at University of Washington's Bothell Campus in the School of Interdisciplinary Arts and Sciences. Dr. Maxwell heads the Marine Sustainability Ecology Lab, which focuses on science-based solutions to issues of marine sustainability as they pertain to large marine species such as sea turtles, cetaceans, sharks and seabirds. Projects focus on the use of marine protected areas, spatial planning, dynamic ocean management and integration of social science to create more sustainable oceans around the world.

**Author contributions:** S.M.M., K.L.S, S.J.B, D.K.B., H.D., E.L.H, R.L.L and L.B.C. designed the study; H.D. collected the data; S.M.M., K.L.S., D.K.B., H.D. E.L.H. and H.W. analysed the data; and all authors contributed to the writing of the manuscript.

#### SUPPORTING INFORMATION

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

**How to cite this article:** Maxwell SM, Scales KL, Bograd SJ, et al. Seasonal spatial segregation in blue sharks (*Prionace glauca*) by sex and size class in the Northeast Pacific Ocean. *Divers Distrib*. 2019;25:1304–1317. <https://doi.org/10.1111/ddi.12941>