



Salmon shark seasonal site fidelity demonstrates the influence of scale on identifying potential high-use areas and vulnerabilities

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ABSTRACT: Considering habitat use throughout the whole range of a highly mobile marine species is necessary to understand life history, identify vulnerabilities, and inform effective management. We used satellite tagging data from 128 adult female salmon sharks *Lamna ditropis* to identify seasonal hotspots of activity in an extended California Current region (ECCR; encompassing the California Current Large Marine Ecosystem), an area far away from their well-described primary habitat in the Alaska Downwelling Region where they have been documented, but whose utility has been poorly understood. Tag track durations had a mean of 447.7 ± 381 d, and 88 sharks (68.8%) visited the ECCR, comprising 33.6% of 28 019 total daily Argos detections. Tracking data revealed that the timing and duration of migrations to the ECCR varied, but salmon shark distribution within the ECCR displayed consistent latitudinal shifts in accordance with regional oceanographic seasons. High site fidelity across multi-year tracks to high-productivity features, such as sea banks, and previously published knowledge of salmon shark life history suggest that the ECCR provides important foraging habitat which may be linked to reproductive success. The data reveal high overlap of salmon shark distribution with cumulative fishing effort collected by Global Fishing Watch for 2012–2019, particularly around seasonal hotspots, suggesting that female salmon sharks might be at risk of fisheries encounters. Collectively, our findings emphasize the importance of the ECCR in salmon shark life history and demonstrate the influence of spatial and temporal scale on interpretation of large movement data sets and identification of critical habitat outside of well-studied regions.

KEY WORDS: Salmon shark · *Lamna ditropis* · Migration · Site fidelity · Hotspots · Fisheries interaction

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1. INTRODUCTION

Research, management, and conservation of highly mobile marine predators is challenging due to their large-scale movements through a 3-dimensional habitat. Advancements in electronic tagging technologies and increased tagging efforts have greatly improved our capacity to track marine animal movements over vast distances and depths, providing insight into dis-

tributions and complex population dynamics (Block et al. 2011, Harrison et al. 2018, Andrzejaczek et al. 2022). However, there remain significant gaps in our understanding of the spatial ecology of highly mobile species with irregular or uncoordinated migrations, defined here as migrations with variable length, periodicity, or duration among individuals. While some highly migratory sharks have been shown to have repeatable migrations, such as mature white sharks

Carcharodon carcharias in the Northeast Pacific (NEP) which predictably move from inshore foraging to offshore locations on a seasonal basis (Jorgensen et al. 2010), others have more variable patterns in their movements that are harder to categorize (Weng et al. 2005, Nasby-Lucas et al. 2019, Elliott et al. 2022). In addition, broad-scale analyses of large spatial data sets spanning 100s or 1000s of km may mask fine-scale patterns of habitat use or site fidelity. Identifying such potential areas of cryptic high-use habitat is crucial for understanding the full scope of a species' ecological niche and vulnerabilities to human interactions and other stressors, particularly for areas linked to important life history activities such as reproduction.

The salmon shark *Lamna ditropis* is one such highly mobile marine predator for which, despite some of the longest telemetry tracks recorded for marine megafauna (Weng et al. 2008, Block et al. 2011, Coffey et al. 2017), complex population dynamics and highly variable migrations have hindered understanding of life history. Salmon sharks are endothermic, with a high capacity for heat production and conservation, as well as cardiac physiology to occupy high-latitude niches (Weng et al. 2005, 2008, Goldman & Musick 2008). Their flexible diet enables salmon sharks to utilize diverse habitats as they range from sub-polar waters to subtropical seas in the North Pacific (Smith & Rhodes 1983, Weng et al. 2005, 2008, Carlisle et al. 2011). The population is highly segregated by sex and size class, with mature females primarily inhabiting the NEP, mature males primarily inhabiting the Northwestern Pacific (but also occurring in the NEP), and juveniles (in even sex ratios) found in more southerly waters, expanding northward and increasingly segregating by sex as they reach maturity (Goldman & Musick 2006, 2008, Garcia et al. 2021). However, adults of both sexes are known to mix to some extent in the highly productive Alaska Downwelling Region (ADR) where they aggregate to forage on salmonids and other prey species, particularly along the Aleutian island chain (Goldman & Musick 2008, Weng et al. 2008, Carlisle et al. 2011, Garcia et al. 2021). Weng et al. (2008) and others (Goldman & Musick 2008, Conrath et al. 2014, Carlisle et al. 2015a) have hypothesized that mating may occur in the ADR before females migrate south to give birth and forage in the North Pacific Transition Zone, North Pacific Subtropical Gyre, and the California Current Large Marine Ecosystem (CCLME). However, extensive satellite tagging efforts have shown that the timing, route, and duration of southern movements from the ADR are highly variable among female salmon sharks (Weng et al. 2008). This suggests they do not undergo regu-

lar or coordinated migrations, making it challenging to assess the importance of these southern habitats.

Examination of pregnant females by Conrath et al. (2014) in Alaska revealed that salmon sharks have a biennial reproductive cycle consisting of approximately 9 mo of gestation and a resting phase of at least 14 mo. Thus, it is possible that variability in migrations might in part be explained by mismatched synchronicity in reproductive cycles between females. Conrath et al. (2014) hypothesized that mating most likely occurs in the autumn months (September–November) in the ADR and that parturition occurs in nursery habitat in the North Pacific Transition Zone and offshore of the CCLME during late spring or early summer. Weng et al. (2008) showed that the highest density of female salmon shark activity outside of the ADR occurred in the CCLME in the spring months, demonstrating that individuals may visit the region after parturition to forage. If female salmon sharks give birth after fasting during their pelagic migrations, as hypothesized in other highly mobile shark species (Del Raye et al. 2013), then the coastal CCLME may provide critical foraging habitat before they return to the northern extent of their range.

The CCLME is a complex, highly productive region (Checkley & Barth 2009) used extensively as a foraging area, aggregation site, and migration corridor for many species of marine megafauna, including sharks, tunas, marine mammals, seabirds, and turtles (Block et al. 2011). The CCLME is also a highly productive fishing ground supporting a range of important commercial fisheries where salmon sharks and other large elasmobranchs are often caught as bycatch by a myriad of gear types, including longlines, purse seines, and trawls (Camhi 1999, Ohshimo et al. 2015, Queiroz et al. 2019, Rigby et al. 2019, White et al. 2019, Jannot et al. 2021). White et al. (2019) found that 35% of salmon shark core habitat in the NEP, including the CCLME, overlapped with industrial fishing fleets from 7 nations. This spatial overlap suggests that salmon sharks are likely vulnerable to bycatch in this region. Therefore, additional information on foraging hotspots, phenology, and fidelity of use is needed, especially if movements in the CCLME are linked to parturition or other critical life history phases.

In this study, we investigated the role of the CCLME and northern bordering region along the coast of Canada, hereafter called the extended California Current region (ECCR), in female salmon shark life history. We used a large spatial data set spanning 2002–2019 from 128 female salmon sharks satellite-tagged in Prince William Sound, AK, USA. We focused on behavior in the ECCR, aiming to characterize (1) spa-

tiotemporal patterns of distribution, (2) potential hotspots of activity, and (3) overlap of salmon shark distribution with commercial fishing effort. Our results indicate consistent seasonal patterns of distribution and use, existence of high-use focal areas, and potential interactions with fisheries. Collectively, these findings demonstrate the importance of detailed investigation of species' whole ranges to understand life history and characterize vulnerabilities.

2. METHODS

2.1. Satellite telemetry data set

We analyzed satellite tracking data from 128 salmon sharks between 2002 and 2019, of which 109 were included in Block et al. (2011) and 64 in Weng et al. (2005, 2008), with an additional 19 sharks satellite tagged between 2015 and 2019. Salmon sharks were caught by hook and line and tagged with Smart Position or Temperature Transmitting Tags (SPOT2-5; Wildlife Computers) in the months of July and August in Port Gravina, Prince William Sound, AK, USA (Fig. 1), as described in previous publications (Weng et al. 2005, 2008, Block et al. 2011, Carlisle et al. 2011).

SPOT tags use the Argos satellite system to generate a geographical location when the animal breaks the surface (www.argos-system.org) and the tag is exposed to air for long enough for uplinks to the ARGOS satellite constellation. Argos position data are estimated by Doppler and reported by location classes (LCs) ranked according to position accuracy. The highest-accuracy positions, LC 3, 2, and 1, have resolutions of <150, 150–300, and 350–1000 m, respectively. Locations classified as LC 0, A, and B have estimated resolutions ranging from 8 to 50 km (Hays et al. 2001, White & Sjöberg 2002), and LC Z has no estimate provided. In this study, we estimated movement paths for all SPOT-tagged salmon sharks at daily intervals by applying random walk continuous-time models in state-space from Jonsen et al. (2023) using the 'aniMotum' package in R version 4.2.3 (R Core Team 2020). For transmission gaps > 1 d (i.e. when the animal either did not come to the surface or the tag did not transmit), the model generated a straight path of evenly distributed daily positions between Argos locations. Transmission gaps varied among tags but lasted up to several months for some individuals. Because these segments represent periods of unknown movement and straight-line swimming is biologically unfeasible behavior, these segments were removed from the model output before analyses. All

points that occurred on land were also removed from the model output. All calculations were conducted using the R statistical environment (R Core Team 2020).

2.2. Study area

We extracted all of the Argos-modeled salmon shark positions within the ECCR using ArcGIS Pro 3 (ESRI, ArcGIS Pro 3.1.0; Fig. 1A). We opted to extend our study area north of the CCLME to the southern boundary of the Alaskan exclusive economic zone to include data occurring in waters surrounding Haida Gwaii, British Columbia, Canada, where salmon sharks frequently occur (Williams et al. 2010) but their distribution has not been well described.

2.3. Analyses

Spatiotemporal patterns of female salmon shark distribution in the ECCR were investigated by first comparing monthly and seasonal latitude and longitude of (1) all daily positions and (2) monthly means for individual sharks. The total proportion of daily positions within the ECCR was also calculated for all individuals. We then investigated potential seasonality of use by comparing tagging data among the 3 oceanographic seasons that have been described for the CCLME. These seasons, which are categorized by distinct shifts in environmental conditions, are the Upwelling Season (UPS), Oceanic Season (OCS), and Davidson Current Season (DCS) (Skogsberg 1936, Skogsberg & Phelps 1946, Bolin & Abbott 1963, Huyer 1983). The UPS occurs as winds along the coast intensify, resulting in upwelling of cold, nutrient-rich water from March through July. The OCS, also known as the relaxation season, is characterized by slackened winds, reduced upwelling, and the weakening of the thermocline as surface waters warm between August and November. The DCS, which occurs from December through February, is characterized by minimized upwelling of the California Current, the formation of a northward coastal current, and winter storms which often increase mixing throughout the water column.

Kernel density estimates (KDEs) of all daily positions within the ECCR for each oceanographic season were used to identify distribution patterns and potential high-use areas. We used the kernel density spatial analyst tool in ArcGIS Pro 3.1.0 (ESRI), which calculates the magnitude-per-unit area of point features using a kernel function, producing a smooth density

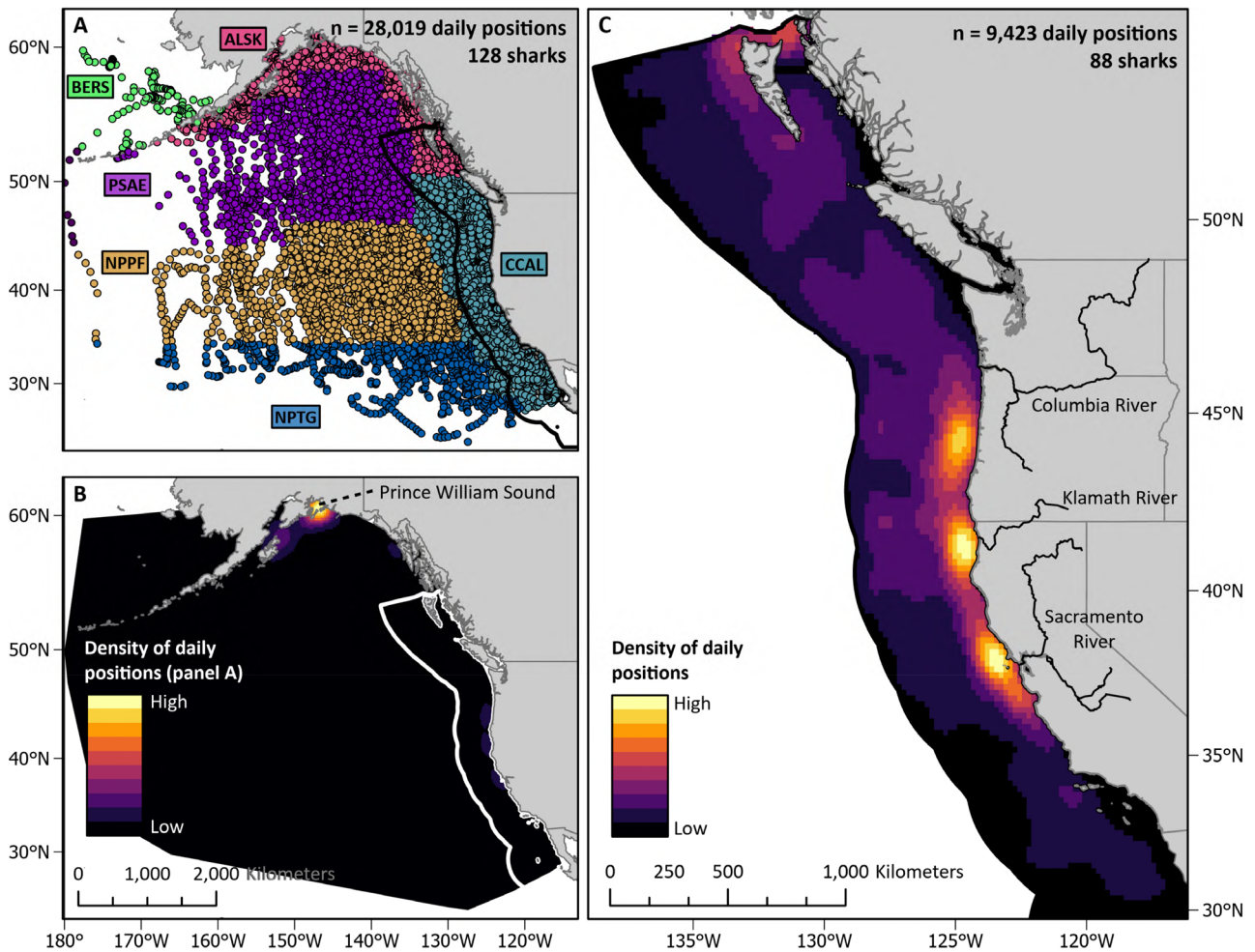


Fig. 1. Salmon shark occurrence in the Northeast Pacific between 2002 and 2019. Electronic tagging data set representing 128 female salmon sharks tagged in Prince William Sound Alaska, USA (marked in panel B). (A) Points for 28019 daily detections; point colors correspond to Longhurst Biogeographic Provinces: Alaska Coastal Downwelling Province (ALSK; pink), also known as the Alaska Downwelling Region; North Pacific Epicontinental Province (BERS; green); Pacific Subarctic Gyres Provinces East (PSAE; purple); North Pacific Polar Front Province (NPPF, yellow), also known as the N. Pacific transition Zone (NPTZ); North Pacific Tropical Gyre Province (NPTG, blue); and the California Current Province (CCAL; cyan). For additional details, see Longhurst (2007). (B) Kernel density estimates (KDEs) for all points shown in panel (A). (C) KDEs for all daily positions occurring within the extended California Current region (ECCR), outlined in all panels, comprising the California Current Large Marine Ecosystem (CCLME) and the exclusive economic zone of western Canada. In panels (B) and (C), yellow (purple) colors represent high (low) densities of detections

surface of spatial point events in 2-dimensional space. We used the default search radius, which calculates a value based on a spatial variant of Silverman's Rule of Thumb (Silverman 1986), the Geodesic method (which takes into account the curvature of earth), and used the ECCR as a boundary feature for calculations. The lowest of 10 equal-interval density classes was removed from maps to increase ease of visual interpretation.

Next, we calculated the densities of individual occurrence within the ECCR by overlaying a 50×50 km grid over the study area and quantifying the number of 'unique visitation IDs' (individual sharks) that

occurred within each cell during each season. Unique visitation IDs correspond with unique identifiers assigned to each animal for every 3-season cycle it carried a tag (i.e. 12 mo periods spanning the DCS, UPS, and OCS; for example, December 2012 to November 2013). This approach was used so that density estimates of individuals would count unique visitation events for sharks which returned to the same cell across multiple years. Note that these calculations represent the total number of sharks which occurred in each square for each season and do not account for duration of presence (i.e. 1 versus 20 d spent in a grid cell) or revisits of an animal within a

unique season (for example, if an animal moved back and forth between 2 grid cells several times during UPS 2015, it would only count as one unique visitation in each cell). We then compared mapping methods to investigate whether daily position versus unique visitation ID densities revealed the same patterns of distribution and areas of core activity.

Where high density areas overlapped for both spatial analyses, we visually examined bathymetry and potential aggregating features such as banks or marine canyons. Total shark visitation was then estimated by generating a 50 km search radius (the maximum error associated with Argos transmissions used) around focal features and quantifying the number of individuals which occurred within that boundary. We also estimated the number of sharks which revisited each feature. Revisits were defined as events where an animal returned to a feature after excursions outside of the 50 km search radius for >3 mo or >300 km away. All spatial analyses were conducted using ArcGIS Pro 3.1.0 (ESRI).

2.4. Overlap with commercial fishing effort

We investigated possible interactions between salmon sharks and fisheries by examining total apparent fishing effort data produced by Global Fishing Watch for commercial vessels in the ECCR (Kroodsma et al. 2018). This included data for all available gear types that are known to interact with salmon sharks (tuna purse seines, non-tuna purse seines, drifting longlines, trawlers, set longlines; White et al. 2019) between 2012 (the earliest data gathered) through 2019. This data set was previously produced using machine learning algorithms that identify apparent fishing activity from Automatic Identification System (AIS) vessel detections based on features such as changes in vessel speed and course (Kroodsma et al. 2018). AIS data sets capture an estimated 50–75% of offshore fishing activity, as many vessels are not outfitted with AIS devices or consistently use them (Kroodsma et al. 2018). We assessed cumulative apparent fishing effort within 0.1×0.1 degree cells throughout the whole ECCR for each oceanographic season. Monthly patterns of fishing effort were also assessed around each feature identified by mapping analyses as a potential hotspot.

3. RESULTS

Of 128 salmon sharks satellite tagged in the NEP, 88 (68.8%) visited the ECCR, comprising 9423 (33.6%)

of 28 019 daily positions (Fig. 1). Track durations (measured from tagging date to final detection) had a mean (\pm SD) of 447.7 ± 381 d and ranged from 25 to 1380 d at large for individuals. All sharks tagged were adult females, with a mean fork length of 206.2 ± 15.1 cm. All tags were deployed in July or August in Prince William Sound from 2002 to 2015. No males were tagged in the region, although coauthors witnessed sport fishers catch several males by hook and line in the same vicinity.

Sharks that visited the ECCR had a mean of $38.5 \pm 23.0\%$ of their daily detections occur in the region, ranging from <1 to 85.4% and 1 to 573 detections per individual. Of the sharks which visited the ECCR, 51 had tracking records >1 yr. Of these longer-duration tracks, 24 individuals (48%) made at least 2 full migrations to the ECCR from the ADR (see Fig. 1A) during the period they carried the SPOT tags. Of the remaining 27 sharks with track durations >1 yr, 9 had >50% of their detections occur in the ECCR. The phenology of occurrence (periodicity of arrival, residency, and revisitation) in the ECCR was highly variable (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m735p125_supp.pdf), with some individuals spending multiple years within the ECCR (Fig. S1A, some making recurring visits to the ECCR after spending time in the North Pacific Transition Zone (Fig. S1B), and others making repeated annual excursions from the ADR to the ECCR or only briefly passing through the ECCR during transit to destinations farther south.

3.1. Seasonal patterns of distribution in the ECCR

Monthly mean latitudes of all points (Fig. 2A) and individual shark monthly means (Fig. 2B) within the ECCR showed seasonal oscillations with lowest mean and median latitude values occurring in the UPS (March–July) and DCS (December–February) and highest values in the OCS (August–November). Mean latitudes calculated for all ECCR daily positions in each season also reflected this pattern, where the UPS had a mean of $39.5 \pm 5.5^\circ$, OCS $47.1 \pm 4.6^\circ$, and DCS $41.0 \pm 7.9^\circ$. Both all and individual monthly mean positions exhibited seasonal longitudinal patterns, with the most pronounced shift occurring eastward between the UPS and the OCS when distribution also shifted north. The OCS (44.3%) and UPS (40.0%) comprised most of the tracking record in the ECCR, with the DCS making up the remaining 16.7% of daily positions. The OCS had the highest number of individual sharks ($n = 74$) and unique visitation IDs

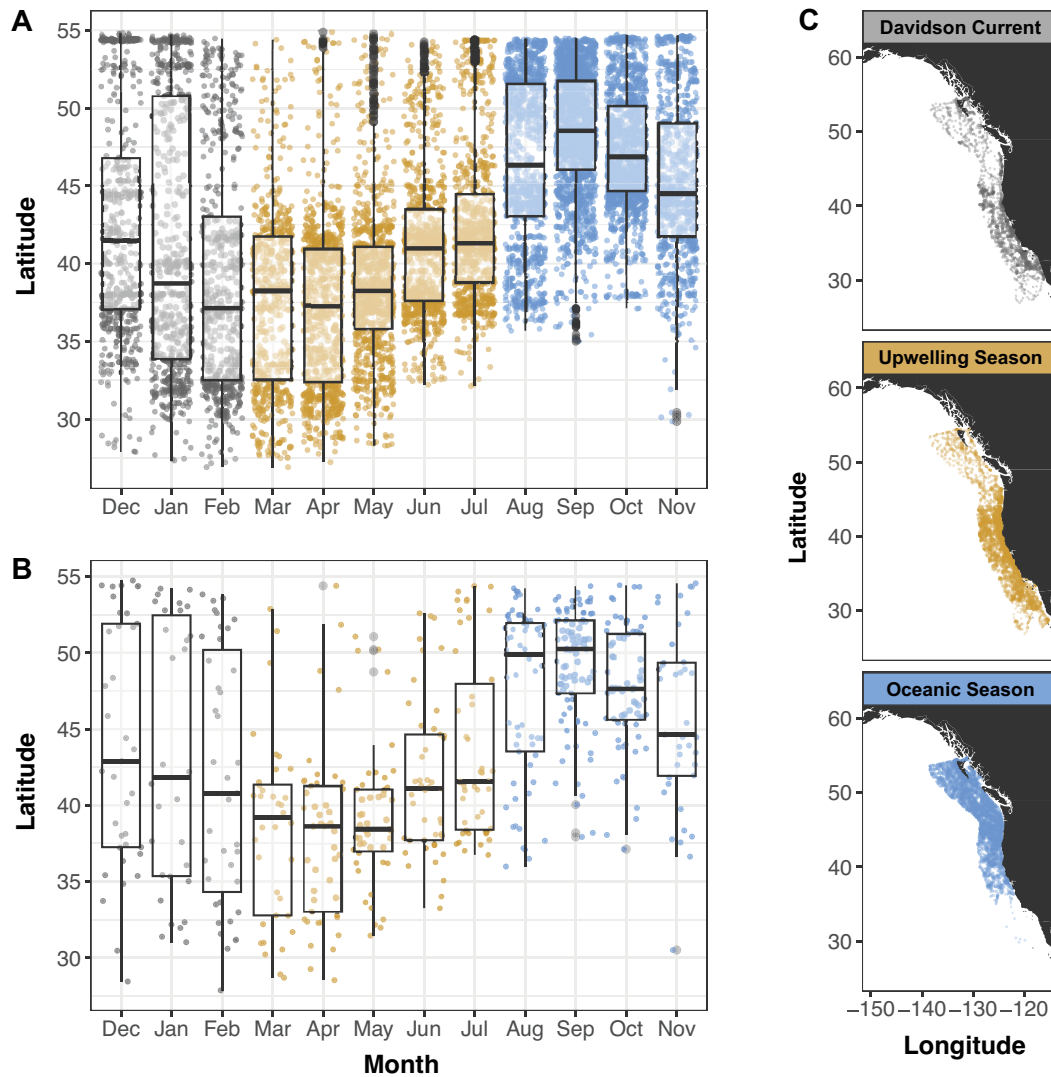


Fig. 2. Monthly latitudinal distribution of salmon sharks in the extended California Current region (ECCR) from 2002 to 2019. Points in plots represent (A) daily positions of individual sharks and (B) monthly mean values for individual sharks. Colors in (A–C) denote oceanographic season: gray, Davidson Current Season (December–February); yellow, Upwelling Season (March–July), and blue, Oceanic Season (August–November). (C) All daily positions of individual sharks within the ECCR separated by oceanographic season. Boxplots indicate monthly median values of position data with boxes representing IQR, whiskers showing minimum and maximum values $< 1.5 \times$ IQR, and large gray dots representing outlier values

($n = 109$; representing the cumulative number of visitations across all years of data), followed by the UPS (54 individuals, 73 visitation IDs) and the DCS (41 individuals, 55 visitation IDs).

3.2. Seasonal hotspots

Both mapping methods revealed high-density areas of daily positions (Fig. 3A–C) and unique visitation IDs (Fig. 3D–F) in the ECCR in the vicinity of coastal bathymetric features such as undersea banks, marine canyons, and river mouths.

3.2.1. Upwelling Season (Mar–Jul)

Salmon sharks had the most constrained and coastal distribution in the UPS compared to the other seasons. The KDE analysis showed 2 focal areas along the Central and Northern California coast centered at approximately 38.0° N, 123.4° W and 41.2° N, 124.6° W (Fig. 3B). The grid analysis showed a more diffuse distribution of high-density areas along the coast between the 2 areas identified by the KDE analysis, with the highest density of unique visitation IDs ($n = 19$) occurring near 39.0° N, 124.0° W (Fig. 3E). Among the areas where the highest density of points and shark

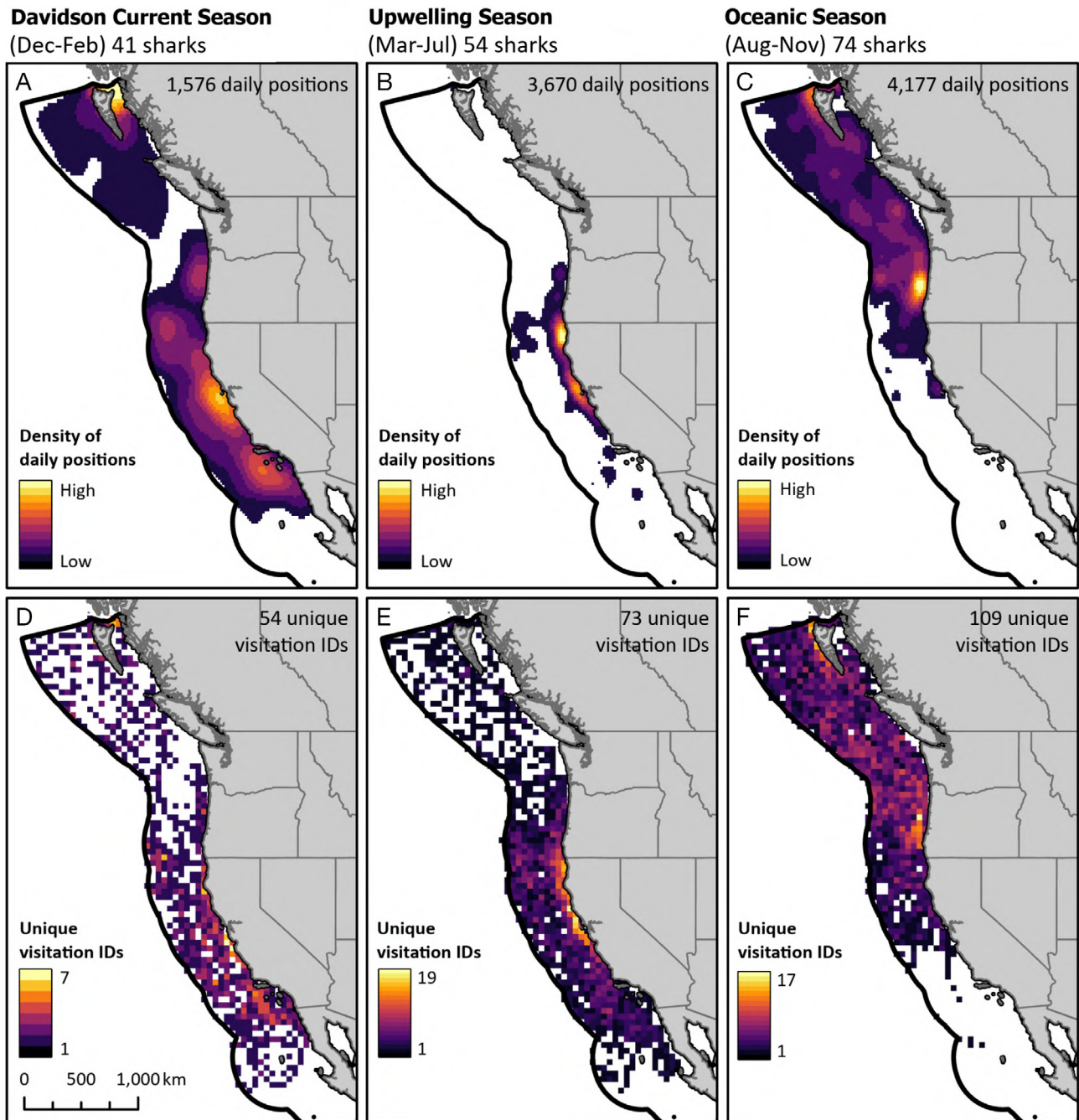


Fig. 3. Seasonal distribution of female salmon sharks in the extended California Current region (ECCR) between 2002 and 2019. (A–C) Kernel density estimates of all daily positions; yellow: areas of high density; dark purple: areas of low density, with the lowest density class removed for ease of visualization. (D–F) Grid counts of unique visitation IDs within 50×50 km squares. Unique visitation IDs correspond with unique identifiers assigned to each animal for every year it carried a tag, thus allowing quantification of repeat visitations across years. Yellow: grid cells with the highest counts; dark purple: areas with the lowest counts. Columns correspond with oceanographic season: Davidson Current Season (A,D), Upwelling Season (B,E), and Oceanic Season (C,F). The number of daily positions (A–C) and unique visitation IDs (D–F) for each season are reported in the top left of each panel

visitation ID counts (> 15 individuals) overlapped, we identified the areas surrounding Trinidad Canyon and the Klamath River mouth (Fig. 4A) and Cordell Bank (Fig. 4C) as potential aggregating features.

Search radii of 50 km revealed that 26 individual sharks visited the area surrounding Cordell Bank, a marine sanctuary, and 24 sharks visited the vicinity of Trinidad canyon, a deep > 1000 m marine canyon

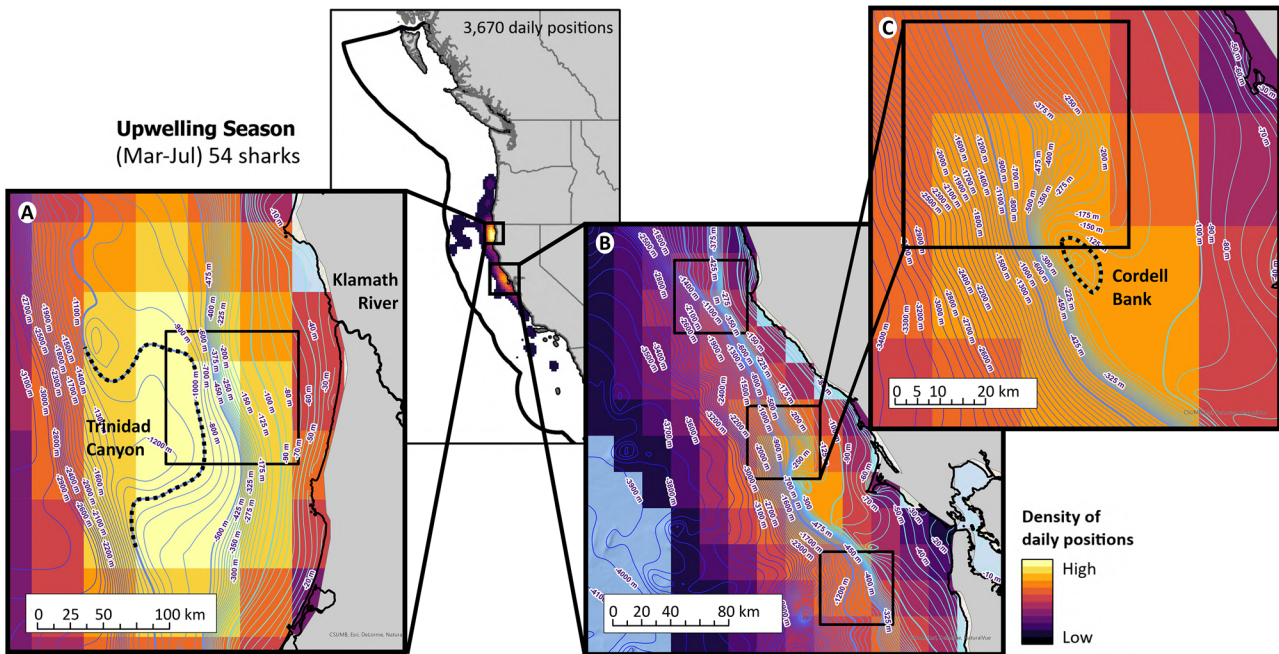


Fig. 4. High-use areas and potential aggregating features for salmon sharks during the Upwelling Season (August–November; Fig. 3B) identified by spatial analyses. Map color corresponds to results from kernel density estimates, with yellow (dark purple) showing areas of high (low) density of salmon shark daily positions. The lowest density class has been removed for ease of visualization. Black squares show the location of 50 × 50 km cells with the highest unique visitation counts from the grid analysis (Fig. 3E): 15 unique IDs in panel (A) and 19, 17, and 15 in each square moving north to south in panel (B). The dotted lines indicate the location of Trinidad Canyon in panel (A) and Cordell Bank in panel (C)

close to shore, with a maximum of 63 daily positions per individual across the whole tracking record for both sites (Table 1). Seven sharks revisited the Cordell Bank area, with 1 individual visiting 4 times during its 3 yr tracking record. Five sharks revisited Trinidad Canyon, with 1 individual visiting 4 times over its 4 yr tracking record, and 25 sharks came within 100 km and 16 within 50 km of the Klamath River mouth for a maximum of 85 and 18 daily positions, respectively (Table 1). Three sharks revisited within a 50 km dis-

tance of the Klamath River mouth for a maximum of 2 visits.

3.2.2. Oceanic Season (Aug–Nov)

Our KDE spatial analysis revealed 2 high-density areas in the OCS, one centered at approximately 44.1° N, 124.8° W and the second near the northwest corner of Haida Gwaii (Figs. 3C,F & 5). The grid

Table 1. Visitation by mature female salmon sharks to the areas surrounding potential aggregating features within the extended California Current region. Values reported include the number of individuals which came within a 50 km search radius, the maximum number of daily positions per individual within the search radius, and the number of sharks that revisited the feature after either a >3 mo or >300 km excursion outside of the 50 km radius. For the Klamath River, all values are also reported for a 100 km search radius. UPS: Upwelling Season; OCS: Oceanic Season; DCS: Davidson Current Season

Feature	Season of heightened activity	n 50 km radius	Max. n daily positions ind. ⁻¹	n revisits	n 100 km radius	Max. n daily positions ind. ⁻¹
Cordell Bank	UPS	26	63	7	—	—
Trinidad Canyon	UPS	24	63	5	—	—
Heceta Bank	OCS	24	54	9	—	—
NW Haida Gwaii	OC/DCS	18	36	4	—	—
NE Haida Gwaii	DCS	8	75	2	—	—
Klamath River	UPS	16	18	3	25	85

analysis also showed high concentrations of individuals in these areas, with the highest density of 17 unique visitation IDs occurring at the more southern site where we identified Heceta Bank and its surrounding area as a potential aggregating feature (Fig. 5B).

We found that 24 sharks came within a 50 km radius of Heceta Bank across all seasons, with a maximum of 54 daily positions per individual. Nine sharks revisited the Heceta Bank area with a maximum of 3 visits per individual over a 4 yr tracking record. For Haida Gwaii, 18 sharks visited the NW corner for a maximum of 36 daily positions per individual, and 4 sharks revisited with a maximum of 3 visits per individual (Table 1).

3.2.3. Davidson Current Season (Dec–Feb)

Sharks were more dispersed and occurred at lower densities (maximum 7 visitation IDs) during the DCS. However, both analyses showed higher densities in the area surrounding San Francisco Bay, Monterey Bay, and nearby seamounts (Guide, Gumdrop, and Pioneer; Fig. 6B), and the NE corner of Haida Gwaii (Fig. 6A), where 8 sharks visited within a 50 km radius across all seasons with an individual maximum of 75 daily positions. Two sharks revisited Haida Gwaii's

NE corner with a maximum of 2 visits per individual (Table 1).

3.3. Overlap with fishing effort

To examine the relationship between salmon shark habitat and commercial fishers, a map of cumulative apparent fishing effort across international commercial vessels between 2012 and 2019 revealed that fishing occurred throughout the ECCR but was most concentrated within 200 km of the coast across all seasons (Fig. S2). All salmon shark potential aggregating features identified in this study (Figs. 4–6) occurred within the band of high-intensity apparent fishing pressure along the coast. Cumulative fishing effort around the 2 high-activity areas identified for the UPS peaked in June for the northern site (Fig. 7D) and September for the southern site, with a secondary peak in June (Fig. 7E). Cumulative fishing effort was highest during March/April for the northern hotspot near NW Haida Gwaii identified for the OCS with a second smaller peak in September/October (Fig. 7A). The southern hotspot near Heceta Bank identified for the OCS had a peak in cumulative fishing effort in October (Fig. 7C). For the areas identified in the DCS, fishing effort peaked in September and November near NE Haida Gwaii (Fig. 7B) and August for the southern area (Fig. 7F).

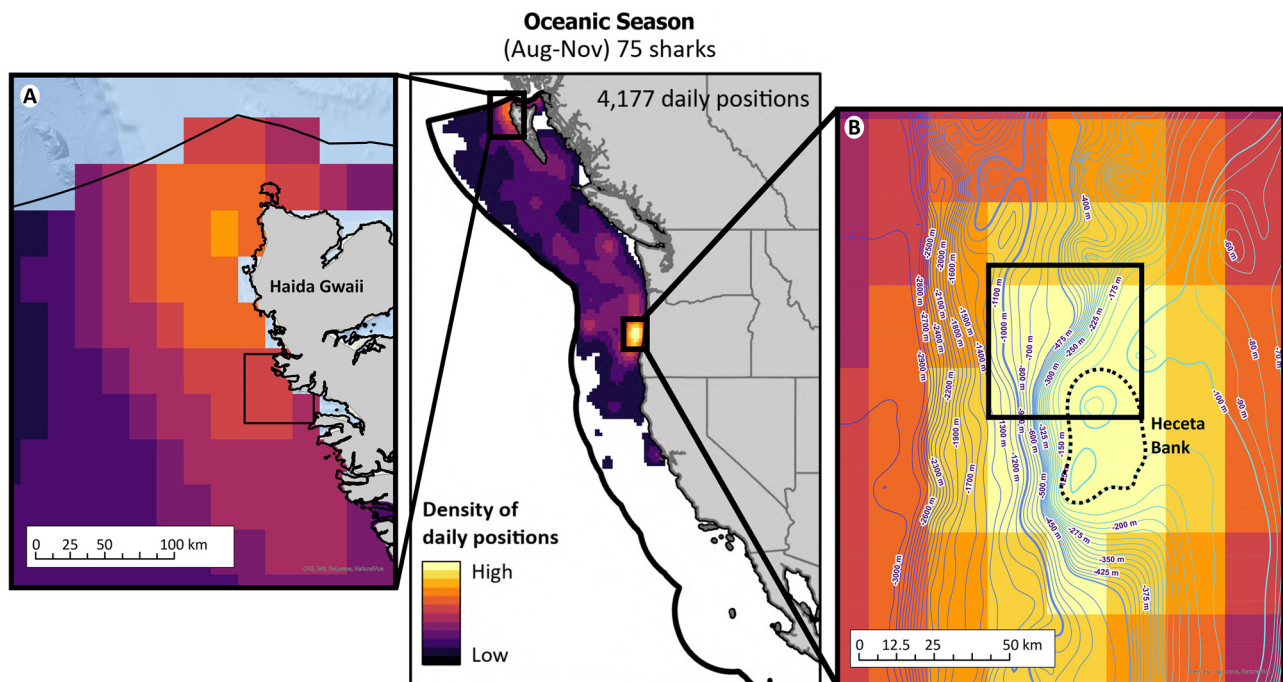


Fig. 5. As in Fig. 4, but during the Oceanic Season (August–November; Fig. 3C). Black squares show the location of 50 × 50 km cells with the highest unique visitation counts from the grid analysis (Fig. 3F): 15 in panel (A) and 17 in panel (B). The dotted line in panel (B) shows the location of Heceta Bank

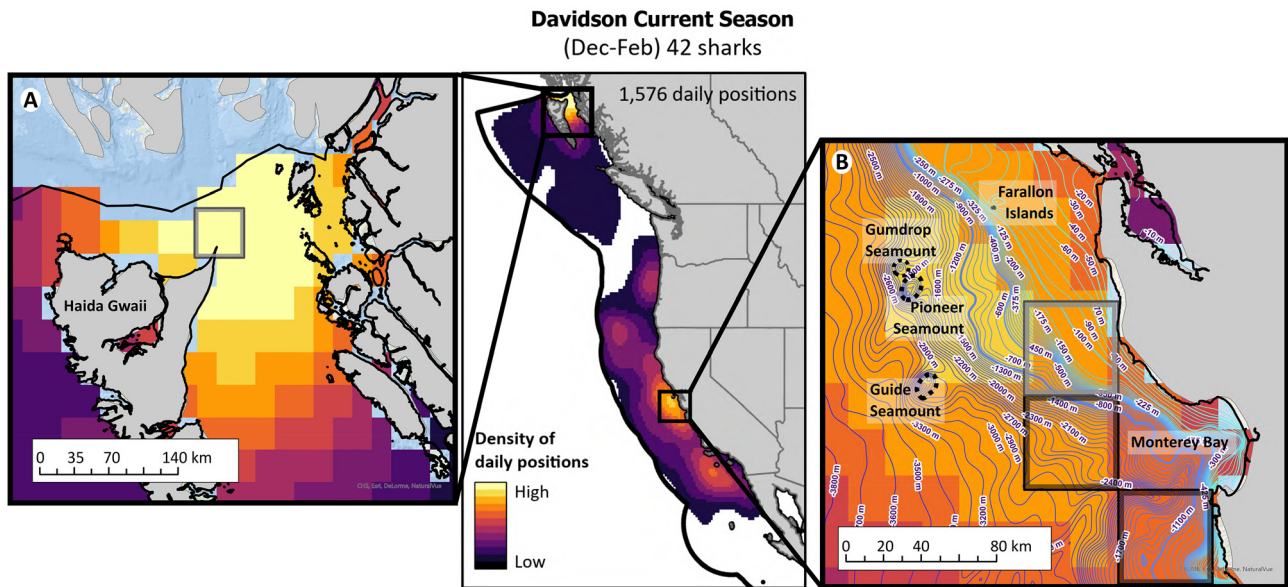


Fig. 6. As in Fig. 4, but during the Davidson Current Season (December–February; Fig. 3C) Black squares show the locations of 50×50 km cells with the highest unique visitation counts from the grid analysis (Fig. 3E): 6 in panel (A) and 7 outlined in black and 6 outlined in gray in panel (B). The dotted lines in panel (B) show the locations of Guide, Gumdrops, and Pioneer Seamounts; Monterey Bay and the Farallon Islands are also labeled

4. DISCUSSION

In this study, we utilized one of the most extensive satellite telemetry data sets from a pelagic mobile predator to examine salmon shark movement and habitat use across the ECCR. The data reveal that, despite variable migrations, female salmon sharks exhibit consistent spatiotemporal patterns of distribution within this region that are timed to specific bathymetric, river, or sea mount locations and in particular seasonal cycles. This is congruent with previous hypotheses concerning potential foraging and post-parturition behavior (Goldman & Musick 2008, Weng et al. 2008, Block et al. 2011, Conrath et al. 2014, Carlisle et al. 2015b). The high proportion of total tagged individuals and daily detections in the ECCR ($n = 88$ individuals; $38.51 \pm 23.04\%$), along with high incidence of fidelity to newly identified hotspot areas, indicate that the region plays a consistent and important role in salmon shark life history. Overlap of movement patterns in the ECCR with commercial fishing efforts of variable gear types illustrates the importance of considering the region for future management of bycatch and salmon shark population assessments. Overall, our results demonstrate the influence of spatial and temporal scale on interpretation of large-movement data sets and highlight the necessity for investigating regions of potentially important habitat outside of well-studied regions.

4.1. Seasonality of distribution

The high endothermic capacity and unique cardiac physiology of salmon sharks provides a broad thermal tolerance for this species, which is capable of occupying ambient temperatures varying as much as 25°C (Smith & Rhodes 1983, Bernal et al. 2005, Weng et al. 2005, Goldman & Musick 2008). Thus, it is unlikely that seasonal shifts in adult female salmon shark density within the ECCR are due to physiological constraints and are more likely driven by seasonal changes in prey availability and/or other life history requirements. Migrations of marine predators including sharks, tunas, whales, and pinnipeds following seasonal changes in prey distribution and productivity have previously been described in the ECCR (Block et al. 2011). For instance, shortfin mako *Isurus oxyrinchus* and white sharks, both in the family Lamnidae with salmon sharks and sharing similar endothermic physiological characteristics, exhibit seasonal movements in the ECCR associated with foraging. White sharks aggregate along the Central California coast peaking in September–February to forage on pinniped aggregations in between annual offshore migrations (Anderson et al. 2011, Block et al. 2011, Carlisle et al. 2012, Jorgensen et al. 2012, 2010). Nasby-Lucas et al. (2019) showed that mean latitudinal distribution of large (> 165 cm) and small (< 165 cm) shortfin mako sharks shifted northward in the CCLME from April to August (concurrent with the UPS) in accordance with primary

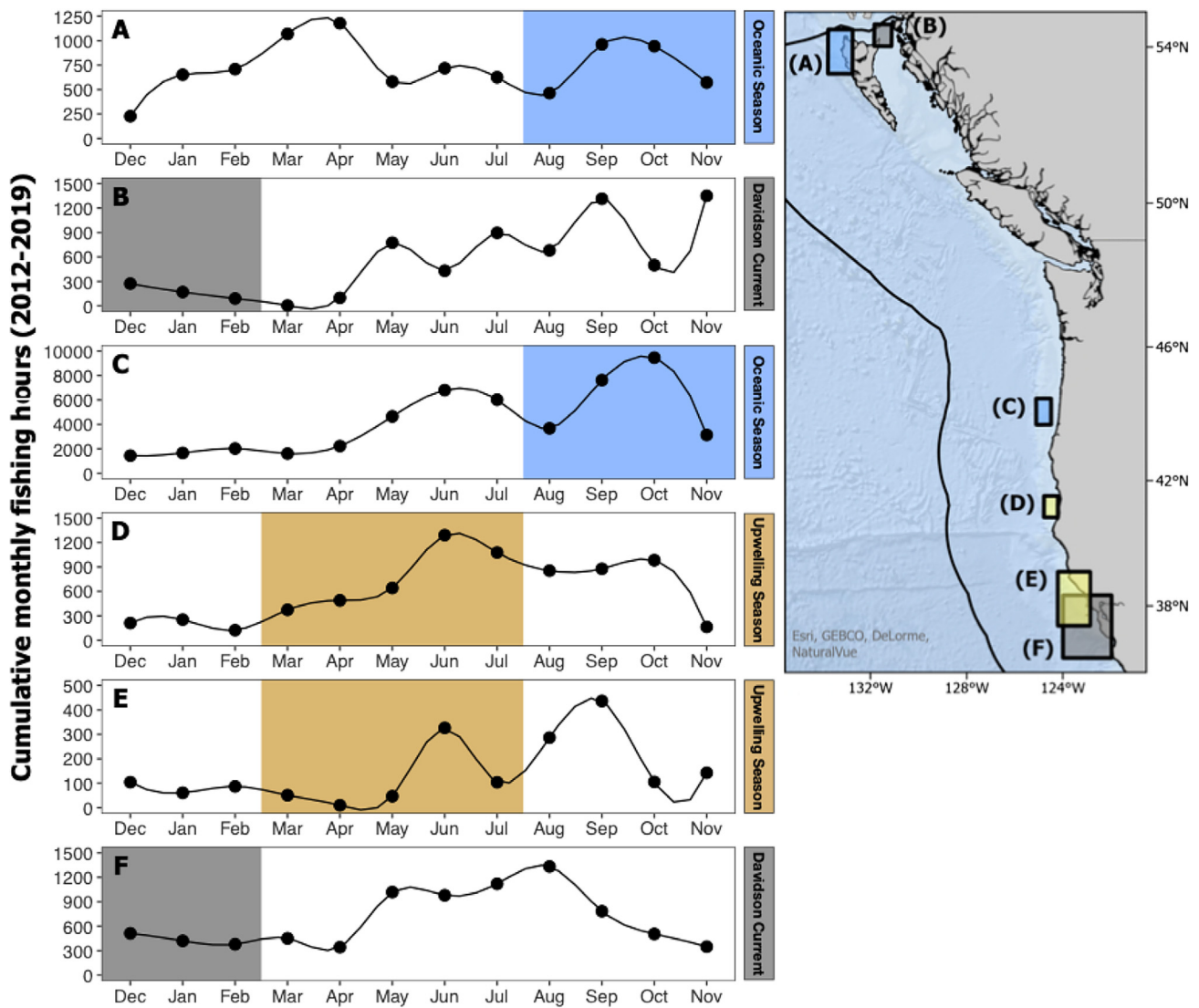


Fig. 7. Cumulative monthly apparent fishing effort within seasonal hotspots of salmon shark activity in the extended California Current region (ECCR) drawn from the Global Fishing Watch database for 2012–2019 for all gear types known to interact with salmon sharks (purse seines, longlines, trawlers). Each plot (A–F) corresponds with a labeled black rectangle on the map and shows monthly cumulative apparent fishing hours versus month. Black rectangles indicate area surrounding both the highest density of individual positions (Fig. 3A–C) and highest density of visitation IDs (Fig. 3D–F) in each area. Color labels to the right of each plot indicate the season during which it is a hotspot of salmon shark activity, and corresponding months are highlighted in the same color

production and sea surface temperature fluctuations. Phenology of the 'spring transition', marked by increased alongshore winds and upwelling along the central and northern CCLME, is variable from year to year, but generally begins in March or April, lasts for about a month, and progresses from south to north (Huyer & Smith 1977, Huyer et al. 1979, Lynn et al. 2003, Checkley & Barth 2009). Subsequently, productivity cycles peak (and end) earlier in the southern CCLME/ECCR than in the north. It is possible that our observed northward shift of salmon shark distribution is due to sharks following the progression of peak

primary productivity or northward movement of target prey species that also may be more thermally limited than salmon sharks.

Salmon shark diets within the ECCR have not been reported but are likely similar to their prey in other regions. Salmon sharks are known to be opportunistic hunters that feed on a wide array of forage species including salmonids (*Oncorhynchus* spp.), sablefish *Anoplopoma fimbria*, squid (*Teuthoidea* spp.), rockfishes (*Sebastes* spp.), Pacific herring (*Clupeidae*), and mackerel (*Scomber* spp.) (Nagasawa 1998, Hulbert et al. 2005, Goldman & Musick 2008, Carlisle et

al. 2011), all of which occur in the ECCR (Carlisle et al. 2011, Koslow & Davison 2016). Stomach content analyses of shortfin mako, blue sharks *Prionace glauca*, and thresher sharks (*Alopias* spp.) in the California Current showed high occurrence of many known salmon shark prey species, suggesting high abundance of a diverse forage base in the region (Prete et al. 2012). Studies of predator-mediated oceanographic nutrient cycling have largely focused on marine mammals, birds, and anadromous fishes (Doughty et al. 2016); however, consumption estimates by Manishin et al. (2019) suggest that salmon sharks have similar energetic requirements to piscivorous marine mammals. Thus, salmon sharks are likely an important vector of energy and nutrient transport between the ECCR and adjacent oligotrophic zones.

Previous studies of salmon shark horizontal and vertical movements corroborate salmon shark foraging behavior in the ECCR. Coffey et al. (2017) found evidence of diel vertical migrations in the region in archival satellite tracking records for adult females. Dives during daylight hours from the surface to below the thermocline to ~200–400 m suggested that they pursue vertically migrating prey when in the offshore waters within the ECCR and subtropical gyre. Weng et al. (2008) found an increase in area-restricted search behavior (often associated with foraging) by salmon sharks in the ECCR during spring months (concurrent with UPS) when chlorophyll *a* concentration peaked. However, they found a decrease in this behavior when primary production peaked in the late summer (late UPS/early OCS), a contrast to the results of this study. It is possible that our inclusion of the region surrounding Haida Gwaii and division of data by oceanographic season, which reflects the northward progression of the spring transition, may explain this discrepancy between our data and those of Weng et al. (2008). The latitudinal shift between the UPS and OCS might also be explained by niche partitioning or predator avoidance with other larger lamnid shark species, as adult white shark (Jorgensen et al. 2010) and shortfin mako shark (Nasby-Lucas et al. 2019) densities peak in Central California in the fall months, coincident with the OCS. For instance, in a region where spatial overlap among lamnid species in the NEP is assumed, there is documented evidence of predation of a tagged salmon shark (presumably by a white shark based on the stomach temperature data of 27°C from the consumed tag) (B. Block unpubl.).

It is important to note the inherent limitations associated with SPOT technology and study design which affect this data set and our interpretations. Salmon sharks likely spend extended periods at depth with-

out breaking the surface, as evidenced by transmission gaps in several tracks. These periods may correspond with important behaviors, such as extended residency around bathymetric features, which are impossible to infer with this technology, which only detects surface swimming. Further, oceanographic seasons in the ECCR affect thermal mixing, dissolved oxygen, and other conditions which impact salmon shark vertical distribution (Coffey et al. 2017), especially during the OCS when winter storm activity increases. However, Coffey et al. (2017) found that salmon sharks spent more time (45%) in the top 10 m of the water column in the ECCR compared to other regions in the NEP, and spent 80% overall between the surface and 100 m. This suggests a higher probability of detecting daily movements by surface limited technologies (such as SPOT tags) in the ECCR compared to other areas of the salmon shark range. Additional tagging efforts using technologies that capture vertical and horizontal movement, as well as deploying tags in locations other than Prince William Sound, AK, USA, would shed additional light on habitat use and behavior. It is possible that there are subpopulations elsewhere that display different movement patterns. However, there are no published records (and we are unaware) of female adult salmon sharks aggregating in numbers comparable to those observed in the ADR.

4.2. Hotspots

Seasonal hotspots of adult female salmon shark activity in the ECCR further support the hypothesized foraging function of this region. Ocean banks, seamounts, and marine canyons are highly productive and known to attract large-bodied marine predators (Morato et al. 2010, 2016, Curnick et al. 2020). These features aggregate plankton biomass and forage species (Boehlert & Genin 1987, Clark et al. 2010, Rogers 2018, Santora et al. 2018) due to localized upwelling, eddy formation, and closed circulation patterns. Heceta (Tissot et al. 2008) and Cordell (Kieckhefer 1992, Pirtle 2005) Banks support high biomass of known prey species for salmon sharks, including rockfishes. Due to high productivity and densities of forage fish species, commercial fishing effort in these areas is generally high (Morato et al. 2006, Koslow & Davison 2016, Kroodsma et al. 2018; Fig. S2).

Williams et al. (2010) observed salmon sharks near the shelf break over the heads of submarine canyons around Haida Gwaii and Queen Charlotte basin. They

hypothesized that sharks aggregate in this area to intercept salmonids returning to their natal rivers and forage on abundant prey near high productivity upwelling zones. They reported large numbers of sharks during the summer (coincident with the UPS and early OCS) but did not observe any salmon sharks during their spring surveys (early UPS). Our data corroborate these conclusions, as we found the lowest densities of salmon sharks around Haida Gwaii during the UPS. The Klamath River has historically supported populations of multiple species of salmonids (Shaw et al. 1997, National Research Council et al. 2004, Strange 2012), suggesting that salmon sharks may also target this area for foraging.

4.3. Reproduction and potential vulnerabilities

It is possible that female salmon sharks use the ECCR as a critical foraging area following an extended gestation period and reproductive migration. In this scenario, it is likely that the energetic stores of female salmon sharks are depleted and require rapid replenishment after heavy investment into provisioning embryos, large-scale migration, and parturition. Similar behavior has been observed, for example, in female sand tiger sharks *Carcharias taurus*, which rapidly increase foraging after parturition to replenish hepatic lipid stores depleted during gestation (Willson & Smith 2017, Wyffels et al. 2020). Our finding of high salmon shark density in the southern ECCR during the UPS is consistent with the hypothesis that females give birth in the North Pacific Transition Zone or pelagic ECCR in early spring, then move to the ECCR to forage (Goldman & Musick 2008, Weng et al. 2008, Conrath et al. 2014, Carlisle et al. 2015b). However, some females entered the ECCR from northern coastal routes or spent several consecutive years in the region (Fig. S1). It is possible that these females entered the ECCR post-mating or in a reproductive resting phase. The ECCR may therefore provide important foraging habitat in complex multi-year reproductive cycles. Further, Carlisle et al. (2015a) found that the occurrence and distribution of juvenile (primarily neonatal and young of the year) salmon sharks strandings in the ECCR occurred with the same seasonal and temporal patterns as adult female distribution found in the study. This suggests that the ECCR may also provide nursery and foraging habitats for juveniles.

We found that female salmon shark distribution in the ECCR overlapped with commercial fishing effort distribution from 2012–2019, highlighting the poten-

tial for interactions in the region. This was particularly pronounced by the coincidence of peak seasonal cumulative fishing effort near hotspot regions in the UPS (Fig. 7D,E) and OCS (Fig. 7A,C), with peak occurrence of salmon sharks in those areas. Salmon sharks have historically been caught as target and non-target bycatch in commercial and small-scale pelagic longline, purse seine, gillnet, trammel net, and trawl fisheries, as well as by rod and reel (Camhi et al. 2008, Goldman & Musick 2008, White et al. 2019). In the past decade, approximately 50–75% of offshore fishing activity is now trackable via AIS detections. As such, our results should be taken as minimum estimates of fishery overlap, since it is possible that additional hotspots of overlap exist that are not reflected in our available data sets. Further, since apparent fishing effort data sets were produced using algorithms that are >95% accurate, it is also possible that some algorithm misclassification occurred in some regions. Finally, the spatiotemporal overlap of salmon sharks and commercial fisheries may not necessarily equate to patterns of catch, as factors such as catchability may differ across regions, gear types, and time periods.

Population trend data for salmon sharks in the whole NEP have not been available since the 1990s, although anecdotal information from fishers in Alaska indicates declines in interactions in recent years (Rigby et al. 2019). A 2018 stock assessment by NOAA recommended no changes to the acceptable biological catch and overfishing levels for salmon sharks based on historical catch data from the period 1997–2007, from which their model deemed overfishing had not occurred in the region (Tribuzio et al. 2018). However, this assessment only focused on the Gulf of Alaska and did not account for potential fisheries interactions in the ECCR. As such, future population assessments should take possible vulnerabilities within the ECCR into account. Cortés (2002) found that juvenile survivorship was the primary determinate of population mean elasticity of a salmon shark congener, the porbeagle shark *Lamna nasus*. As reproductive success and parturition are directly linked to juvenile survivorship, further investigation of where and when core use areas for both adult female and juvenile salmon sharks occur and potentially overlap with negative interactions is critical.

4.4. Conclusions

In light of ubiquitous declines in shark populations (Heithaus et al. 2008, Pacoureau et al. 2021, Worm et

al. 2024) and predicted changes in migrations and phenology induced by climate change and other anthropogenic stressors (Anderson et al. 2013, Poloczanska et al. 2013, Sydeman et al. 2015), identifying areas of potential critical habitat throughout whole ranges of highly mobile species is essential for successful management and conservation (Jorgensen et al. 2022). In this study, we found consistent spatio-temporal distribution and previously unknown hotspots of female salmon shark activity within the ECCR. We found that these patterns occur in accordance with the unique oceanographic seasons of the region, demonstrating the importance of considering localized drivers to understand habitat use and the influence of spatial and temporal scale on the interpretation of large spatial data sets. We conclude that the ECCR provides important foraging habitat for female adult salmon sharks. Overlap of female salmon shark activity and hotspot areas in the ECCR with high fishing effort within both the exclusive economic zones of both the USA and Canada emphasizes the necessity of understanding fine-scale space use and vulnerabilities for effective management and conservation of this wide-ranging species.

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LITERATURE CITED

- Anderson SD, Chapple TK, Jorgensen SJ, Klimley AP, Block BA (2011) Long-term individual identification and site fidelity of white sharks, *Carcharodon carcharias*, off California using dorsal fins. *Mar Biol* 158:1233–1237
- Anderson JJ, Gurarie E, Bracis C, Burke BJ, Laidre KL (2013) Modeling climate change impacts on phenology and population dynamics of migratory marine species. *Ecol Model* 264:83–97
- Andrzejczek S, Lucas TCD, Goodman MC, Hussey NE and others (2022) Diving into the vertical dimension of elasmobranch movement ecology. *Sci Adv* 8:eabo1754
- Bernal D, Donley JM, Shadwick RE, Syme DA (2005) Mammal-like muscles power swimming in a cold-water shark. *Nature* 437:1349–1352
- Block BA, Jonsen ID, Jorgensen SJ, Winship AJ and others (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* 475:86–90
- Boehlert GW, Genin A (1987) A review of the effects of seamounts on biological processes. In: Keating BH, Fryer P, Batiza R, Boehlert GW (eds) Seamounts, islands, and atolls. *Geophys Monogr Ser* 43. American Geophysical Union, Washington, DC, p 319–334
- Bolin RL, Abbott DP (1963) Studies on the marine climate and phytoplankton of the central coastal area of California, 1954–1960. *Calif Coop Ocean Fish Invest Rep* 9:23–45
- Camhi M (1999) Sharks on the line. II. An analysis of Pacific state shark fisheries. National Audubon Society, Islip, NY
- Camhi MD, Pikitch EK, Babcock EA (eds) (2008) *Sharks of the open ocean: biology, fisheries and conservation*. Wiley-Blackwell, Ames, IA
- Carlisle AB, Perle CR, Goldman KJ, Block BA (2011) Seasonal changes in depth distribution of salmon sharks (*Lamna ditropis*) in Alaskan waters: implications for foraging ecology. *Can J Fish Aquat Sci* 68:1905–1921
- Carlisle AB, Kim SL, Semmens BX, Madigan DJ and others (2012) Using stable isotope analysis to understand the migration and trophic ecology of northeastern Pacific white sharks (*Carcharodon carcharias*). *PLOS ONE* 7:e30492
- Carlisle AB, Litvin SY, Hazen EL, Madigan DJ, Goldman KJ, Lea RN, Block BA (2015a) Reconstructing habitat use by juvenile salmon sharks links upwelling to strandings in the California Current. *Mar Ecol Prog Ser* 525:217–228
- Carlisle AB, Goldman KJ, Litvin SY, Madigan DJ and others (2015b) Stable isotope analysis of vertebrae reveals ontogenetic changes in habitat in an endothermic pelagic shark. *Proc R Soc B* 282:20141446
- Checkley DM, Barth JA (2009) Patterns and processes in the California Current System. *Prog Oceanogr* 83:49–64
- Clark MR, Rowden AA, Schlacher T, Williams A and others (2010) The ecology of seamounts: structure, function, and human impacts. *Annu Rev Mar Sci* 2:253–278
- Coffey DM, Carlisle AB, Hazen EL, Block BA (2017) Oceanographic drivers of the vertical distribution of a highly migratory, endothermic shark. *Sci Rep* 7:10434
- Conrath CL, Tribuzio CA, Goldman KJ (2014) Notes on the reproductive biology of female salmon sharks in the eastern North Pacific Ocean. *Trans Am Fish Soc* 143:363–368
- Cortés E (2002) Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conserv Biol* 16:1048–1062
- Curnick DJ, Andrzejczek S, Jacoby DMP, Coffey DM and others (2020) Behavior and ecology of silky sharks around the Chagos Archipelago and evidence of Indian Ocean wide movement. *Front Mar Sci* 7:596619
- Del Raye G, Jorgensen SJ, Krumhansl K, Ezcurra JM, Block BA (2013) Travelling light: white sharks (*Carcharodon carcharias*) rely on body lipid stores to power ocean-basin scale migration. *Proc R Soc B* 280:20130836
- Doughty CE, Roman J, Faurby S, Wolf A and others (2016) Global nutrient transport in a world of giants. *Proc Natl Acad Sci USA* 113:868–873

- Elliott RG, Montgomery JC, Della Penna A, Radford CA (2022) Satellite tags describe movement and diving behaviour of blue sharks *Prionace glauca* in the southwest Pacific. *Mar Ecol Prog Ser* 689:77–94
- Garcia S, Tribuzio CA, Seitz AC, Courtney MB, Nielsen JK, Murphy JM, Oxman DS (2021) Differential horizontal migration patterns of two male salmon sharks (*Lamna ditropis*) tagged in the Bering Sea. *Anim Biotelem* 9:38
- Goldman KJ, Musick JA (2006) Growth and maturity of salmon sharks (*Lamna ditropis*) in the eastern and western North Pacific, and comments on back-calculation methods. *Fish Bull* 104:278–292
- Goldman KJ, Musick JA (2008) The biology and ecology of the salmon shark, *Lamna ditropis*. In: Camhi MD, Pikitch EK, Babcock EA (eds) *Sharks of the open ocean: biology, fisheries and conservation*. Wiley-Blackwell, Ames, IA, p 95–104
- Harrison AL, Costa DP, Winship AJ, Benson SR, Bograd SJ and others (2018) The political biogeography of migratory marine predators. *Nat Ecol Evol* 2:1571–1578
- Hays GC, Åkesson S, Godley BJ, Luschi P, Santidrian P (2001) The implications of location accuracy for the interpretation of satellite-tracking data. *Anim Behav* 61: 1035–1040
- Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. *Trends Ecol Evol* 23:202–210
- Hulbert LB, Aires-da-Silva AM, Gallucci VF, Rice JS (2005) Seasonal foraging movements and migratory patterns of female *Lamna ditropis* tagged in Prince William Sound, Alaska. *J Fish Biol* 67:490–509
- Huyer A (1983) Coastal upwelling in the California current system. *Prog Oceanogr* 12:259–284
- Huyer A, Smith RL (1977) Physical characteristics of Pacific northwestern coastal waters. In: Krauss RW (ed) *The marine plant biomass of the Pacific Northwest coast*. Oregon State University Press, Corvallis, OR, p 37–55
- Huyer A, Sobey EJC, Smith RL (1979) The spring transition in currents over the Oregon Continental Shelf. *J Geophys Res* 84:6995–7011
- Jannot JE, Bjorkland R, Somers KA, Mitchell T, Tuttle VJ, McVeigh J (2021) Elasmobranch bycatch in US West Coast groundfish fisheries. *Endang Species Res* 45:109–126
- Jonsen ID, Grecian WJ, Phillips L, Carroll G and others (2023) AniMotum, an R package for animal movement data: rapid quality control, behavioural estimation and simulation. *Methods Ecol Evol* 14:806–816
- Jorgensen SJ, Reeb CA, Chapple TK, Anderson S, Perle C and others (2010) Philopatry and migration of Pacific white sharks. *Proc R Soc B* 277:679–688
- Jorgensen SJ, Arnoldi NS, Estess EE, Chapple TK, Rückert M, Anderson SD, Block BA (2012) Eating or meeting? Cluster analysis reveals intricacies of white shark (*Carcharodon carcharias*) migration and offshore behavior. *PLOS ONE* 7:e47819
- Jorgensen SJ, Micheli F, White TD, Van Houtan KS and others (2022) Emergent research and priorities for shark and ray conservation. *Endang Species Res* 47:171–203
- Kieckhefer TR (1992) Feeding ecology of humpback whales in continental shelf waters near Cordell Bank, California. MSc dissertation, San Jose State University, San Jose, CA
- Koslow JA, Davison PC (2016) Productivity and biomass of fishes in the California Current Large Marine Ecosystem: comparison of fishery-dependent and -independent time series. *Environ Dev* 17:23–32
- Kroodsma DA, Mayorga J, Hochberg T, Miller NA and others (2018) Tracking the global footprint of fisheries. *Science* 359:904–908
- Longhurst AR (2007) *Ecological geography of the sea*, 2nd edn. Academic Press, San Diego, CA
- Lynn RJ, Bograd SJ, Chereskin TK, Huyer A (2003) Seasonal renewal of the California Current: the spring transition off California. *J Geophys Res Oceans* 108:3279
- Manishin KA, Goldman KJ, Short M, Cunningham CJ, Westley PAH, Seitz AC (2019) Prey consumption estimates for salmon sharks. *Mar Freshw Res* 70:824–833
- Morato T, Cheung WWL, Pitcher TJ (2006) Vulnerability of seamount fish to fishing: fuzzy analysis of life-history attributes. *J Fish Biol* 68:209–221
- Morato T, Hoyle SD, Allain V, Nicol SJ (2010) Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proc Natl Acad Sci USA* 107:9707–9711
- Morato T, Miller PI, Dunn DC, Nicol SJ, Bowcott J, Halpin PN (2016) A perspective on the importance of oceanic fronts in promoting aggregation of visitors to seamounts. *Fish Fish* 17:1227–1233
- Nagasawa K (1998) Predation by salmon sharks (*Lamna ditropis*) on Pacific salmon (*Oncorhynchus* spp.). *Bull North Pac Anadromous Fish Comm* 1:419–433
- Nasby-Lucas N, Dewar H, Sosa-Nishizaki O, Wilson C and others (2019) Movements of electronically tagged shortfin mako sharks (*Isurus oxyrinchus*) in the eastern North Pacific Ocean. *Anim Biotelem* 7:12
- National Research Council Division on Earth and Life Studies, Board on Environmental Studies and Toxicology, and Committee on Endangered and Threatened Fishes in the Klamath River Basin (2004) *Endangered and threatened fishes in the Klamath River basin: causes of decline and strategies for recovery*. National Academies Press, Washington, DC
- Ohshimo S, Shiozaki K, Yokawa K (2015) Size and standardized CPUE of two pelagic sharks in the North Pacific based on salmon driftnet surveys. National Research Institute of Far Seas Fisheries, Fishery Research Agency, Shizuoka
- Pacoureau N, Rigby CL, Kyne PM, Sherley RB and others (2021) Half a century of global decline in oceanic sharks and rays. *Nature* 589:567–571
- Pirtle JL (2005) Habitat-based assessment of structure-forming megafaunal invertebrates and fishes on Cordell bank, California. PhD dissertation, Washington State University, Seattle, WA
- Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W and others (2013) Global imprint of climate change on marine life. *Nat Clim Change* 3:919–925
- Preti A, Soykan CU, Dewar H, Wells RJD, Spear N, Kohin S (2012) Comparative feeding ecology of shortfin mako, blue and thresher sharks in the California Current. *Environ Biol Fishes* 95:127–146
- Queiroz N, Humphries NE, Couto A, Vedor M and others (2019) Global spatial risk assessment of sharks under the footprint of fisheries. *Nature* 572:461–466
- R Core Team (2020) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Rigby CL, Barreto R, Carlson J, Fernando D and others (2019) Salmon shark *Lamna ditropis*. The IUCN Red List of Threatened Species: e.T39342A124402990. <https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39342A124402990.en>

- Rogers AD (2018) The biology of seamounts: 25 years on. *Adv Mar Biol* 79:137–224
- Santora JA, Zeno R, Dorman JG, Sydeman WJ (2018) Submarine canyons represent an essential habitat network for krill hotspots in a Large Marine Ecosystem. *Sci Rep* 8: 7579
- Shaw TA, Jackson C, Nehler D, Marshall M (1997) Klamath River (Iron Gate Dam to Seiad Creek) life stage periodicity for chinook, coho and steelhead. US Fish and Wildlife Service, Coastal California Fish and Wildlife Office, Arcata, CA
- Silverman BW (1986) Density estimation for statistics and data analysis. CRC Press, Boca Raton, FL
- Skogsberg T (1936) Hydrography of Monterey Bay, California. Thermal conditions, 1929–1933. *Trans Am Philos Soc* 29:1–152
- Skogsberg T, Phelps A (1946) Hydrography of Monterey Bay, California. Thermal conditions, Part II (1934–1937). *Proc Am Philos Soc* 90:350–386
- Smith RL, Rhodes D (1983) Body temperature of the salmon shark, *Lamna ditropis*. *J Mar Biol Assoc UK* 63:243–244
- Strange JS (2012) Migration strategies of adult Chinook salmon runs in response to diverse environmental conditions in the Klamath River Basin. *Trans Am Fish Soc* 141:1622–1636
- Sydeman WJ, Poloczanska E, Reed TE, Thompson SA (2015) Climate change and marine vertebrates. *Science* 350: 772–777
- Tissot BN, Wakefield WW, Hixon MA, Clemons JER (2008) Twenty years of fish-habitat studies on Heceta Bank, Oregon. Reynolds JR, Greene HG (eds) Marine habitat mapping technology for Alaska. Alaska Sea Grant College Program, University of Alaska Fairbanks, Fairbanks, AK, p 203–218
- Tribuzio CA, Rodgveller C, Echave K, Hulson PJ (2018) Assessment of the shark stock complex in the Gulf of Alaska. <https://apps-afsc.fisheries.noaa.gov/REFM/Docs/2018/GOA/GOAshark.pdf>
- Weng KC, Castilho PC, Morrisette JM, Landeira-Fernandez AM and others (2005) Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science* 310:104–106
- Weng KC, Foley DG, Ganong JE, Perle C, Shillinger GL, Block BA (2008) Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. *Mar Ecol Prog Ser* 372:253–264
- White NA, Sjöberg M (2002) Accuracy of satellite positions from free-ranging grey seals using ARGOS. *Polar Biol* 25: 629–631
- White TD, Ferretti F, Kroodsmas DA, Hazen EL and others (2019) Predicted hotspots of overlap between highly migratory fishes and industrial fishing fleets in the north-east Pacific. *Sci Adv* 5:eaau3761
- Williams R, Okey TA, Wallace SS, Gallucci VF (2010) Shark aggregation in coastal waters of British Columbia. *Mar Ecol Prog Ser* 414:249–256
- Willson K, Smith M (2017) Reproduction of the sand tiger shark, *Carcharias taurus* (Rafinesque, 1810), at Under Water World SEA LIFE Mooloolaba from 1992–2012. In: Smith M, Warmolts D, Thoney D, Hueter R, Murray M, Excurra J (eds) The elasmobranch husbandry manual II: Recent advances in the care of sharks, rays and their relatives. Special Publication. Ohio Biological Survey, Columbus, OH, p 391–401
- Worm B, Orofino S, Burns ES, D'Costa NG and others (2024) Global shark fishing mortality still rising despite widespread regulatory change. *Science* 383:225–230
- Wyffels J, Coco C, Schreiber C, Palmer D and others (2020) Natural environmental conditions and collaborative efforts provide the secret to success for sand tiger shark *Carcharias taurus* reproduction in aquaria. *Zoo Biol* 39: 355–363

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