Differential horizontal migration patterns of two male salmon sharks (*Lamna ditropis*) tagged in the Bering Sea

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Abstract

**Background:** The salmon shark (*Lamna ditropis*) is a widely distributed apex predator in the North Pacific Ocean. Many salmon sharks from the eastern North Pacific, specifically Prince William Sound, Alaska, have been satellite tagged and tracked, but due to the sexual segregation present in salmon sharks, most of these tagged sharks were female. Consequently, little information exists regarding the migration patterns of male salmon sharks. To better understand the migration and distribution of this species, information on the male component of the population as well as from sharks outside of Prince William Sound, Alaska, is needed. In this study, we deployed satellite transmitters on two mature male salmon sharks caught in the Bering Sea.

**Results:** The two mature male salmon sharks tagged in the Bering Sea exhibited distinct migration patterns. The first male, tagged in August 2017, traveled to southern California where it remained from January to April after which it traveled north along the United States’ coast and returned to the Bering Sea in August 2018. The second male, tagged in September 2019, remained in the North Pacific between 38° N and 50° N before returning to the Bering Sea in July of year one and as of its last known location in year two. The straight-line distance traveled by the 2017 and 2019 sharks during their 12 and 22 months at liberty was 18,775 km and 27,100 km, respectively.

**Conclusions:** Before this study, our understanding of salmon shark migration was limited to female salmon sharks satellite tagged in the eastern North Pacific. The 2017 male salmon shark undertook a similar, but longer, north–south migration as tagged female sharks whereas the 2019 shark showed little overlap with previously tagged females. The different migration patterns between the two male sharks suggest distinct areas exist for foraging across the North Pacific. The return of both sharks to the Bering Sea suggests some fidelity to the region. Continued tagging efforts are necessary to understand the population structure of salmon sharks in the North Pacific. This tagging study highlights the importance of opportunistic efforts for obtaining information on species and sex with limited distribution data.

**Keywords:** Lamnidae, Bering Sea, Satellite tag, Archival tag, Distribution

Background

The salmon shark (*Lamna ditropis* [1]) is a widely distributed apex predator found in the coastal and oceanic waters of the North Pacific Ocean (NPO), from the Bering Sea to the Sea of Japan in the western North Pacific (WNP) and from the Gulf of Alaska to Baja California, Mexico, in the eastern North Pacific (ENP) [2, 3]. An opportunistic predator, salmon sharks feed on various
fish and cephalopod prey [4, 5] and have been identified as a substantial consumer of Pacific salmon (Oncorhynchus spp.) [4, 6–8] with the potential to alter their demographic rates, such as age at maturity [9]. The salmon shark, like all lamnid sharks (family Lamnidae), can elevate its body temperature and inhabit cold environments that may exclude other ectothermic shark species [10, 11]. Salmon sharks can maintain their internal body temperature up to 21 °C above ambient water temperatures and can overwinter in temperatures ranging from 2 to 8 °C [12, 13]. Given their ability to withstand cold temperatures, salmon sharks are likely one of the most northerly distributed sharks in the world and have been caught as far north as 66 °N [14].

Our current understanding of salmon shark migration and ecology within the NPO highlights the disparity in research between salmon sharks in the ENP and WNP. For this paper, we defined the WNP as waters west of 180° from southern Japan to the Kamchatka Peninsula including the Sea of Okhotsk, the ENP as the waters between the Gulf of Alaska to southern California, and the Bering Sea as those waters bordered by the Aleutian Islands to the south, Russia to the west, and Alaska to the east. Our knowledge of salmon shark migration in the WNP is limited to historic catches from Russian and Japanese trawl, longline, and gillnet surveys between 1980 and 1991 and a single dart tagging study with only one recapture in 1979 [7, 15]. Salmon sharks are strongly separated by sex, with female dominance in the ENP and male dominance in the WNP [7, 16], and previous satellite tagging work has only been conducted within the ENP, specifically Prince William Sound, Alaska, which almost exclusively tagged female salmon sharks [4, 17–19]. To the best of our knowledge, only one male salmon shark has been satellite tracked for just 26 days in the ENP [4]. Most satellite-tagged female sharks (at least 126 sharks) in the ENP migrate from summer foraging areas in coastal Alaska to overwintering areas within the California Current, located along the west coast of the United States [4, 17–19]. Migration in female salmon sharks is likely linked to their reproductive ecology. Female salmon sharks are believed to mate in September and, following an approximately 9-month gestation period, give birth in May or June [20] primarily in the North Pacific Transition Zone (climatologically defined between 32° N and 42° N) [21–23] but also within the California Current [16, 17]. The limited data for WNP salmon sharks suggests a northern migration towards the Bering Sea in spring and summer and a return migration south to Japan for overwintering [15, 22, 24]. Like female salmon sharks in the ENP, salmon sharks in the WNP are believed to mate in autumn and give birth from March through May [7]. The presence of small salmon sharks in northern Japan/ southern Kuril Islands and offshore waters suggests these areas may be birthing grounds [15, 22, 24]. To date, no salmon sharks outside the ENP have been satellite tagged so seasonal movement patterns, distribution, and key foraging or reproduction locales from the central and western Pacific Ocean have been inferred from limited observations or are unknown.

In addition to gaps in our understanding of salmon shark migration, the population structure of salmon sharks in the NPO is also not well understood [16]. Currently, there is no consensus on whether salmon sharks in the NPO comprise a single population or whether salmon sharks in the WNP and ENP are two separate populations [16]. The population genetic structure has not been examined as sample sizes are limited. To date, satellite-tagged salmon sharks from the ENP have not crossed the dateline in the NPO; therefore, it is unknown if or when mixing might occur in the Pacific Ocean [4, 16–19]. However, because only female sharks in the ENP have been effectively satellite tracked, it is possible that sharks outside the ENP exhibit different migrations that may be indicative of separate populations. Identifying the underlying population structure and distribution of salmon sharks is identified as a research priority by the International Union for the Conservation of Nature [25].

Here, we report results from the first satellite-tagged male salmon sharks caught in the Bering Sea. The tracking data presented are only the second and third satellite tracks available for male salmon sharks and the first tracking data for salmon sharks outside the ENP. These movement data provide new information on the distribution and migration patterns of this understudied segment of the salmon shark population.

**Results**

**Shark A**

On August 27, 2017, a mature male salmon shark [1.76 m total length (TL)/1.39 m pre-caudal length (PCL); Shark A] was tagged with a pop-up satellite archival tag (PSAT) and released east of Nunivak Island, Alaska, in the Bering Sea (59.99 °N, 169.03 °W; Table 1; Fig. 1). A year later, the tag reported to satellites from a location just north of St. Lawrence Island, Alaska, (64.05 °N, 171.28 °W) on its scheduled pop-off date of August 28, 2018 and transmitted 73% of the subsampled (30 min resolution) archived temperature, depth, and light level data. Depth, temperature, and light level data were available for 367 days, but some days had lower resolution (60 min resolution) resulting from the incomplete transmission of the archived data.

Daily estimated geolocations and corresponding error polygons derived from the Hidden Markov model (HMM, see Section “Data filtering and analysis” in
“Methods” section) revealed a direct migration from the Bering Sea to southern California and back again (Fig. 1). Immediately after tagging, Shark A swam south and exited the Bering Sea by mid-September. After leaving the Bering Sea, Shark A moved east across the NPO, arriving in offshore waters of northern Oregon by the end of October. From November through the following June, Shark A traveled southwest to offshore waters during December, headed inshore towards southern California from January through April, and turned northward towards Oregon in May. In July, Shark A initiated a directed transit to the Bering Sea where it arrived in late August. Shark A remained in the northern Bering Sea until its last known location just north of St. Lawrence Island, Alaska. Over the course of its 367-day track, Shark A’s minimum distance traveled was 18,775 km and it averaged at least 51.1 km/day.

Shark B
On September 7, 2019, a mature male salmon shark (2.20 m TL/1.78 m PCL; Shark B) was tagged just south of St. Lawrence Island, Alaska, in the Bering Sea (62.01 °N, 170.95 °W; Table 1; Fig. 1) with a smart position transmitting tag (SPOT). The location data from Shark B’s SPOT tag were analyzed by year: the first was from September 7, 2019 through September 6, 2020 and the second was from September 7, 2020 through June 15, 2021. In total, Shark B’s SPOT transmitted 10,685 locations. Of these locations, 1748 (16%) were removed due to large error radii (i.e., Argos Location Classes A, B, or Z). From the remaining locations, one “Best of Day” location (see Section “Data filtering and analysis” in “Methods” section) was selected resulting in 332 days of high-quality locations, 230 days from the first year and 102 days from the second.

In its first year, Shark B initiated a direct southerly movement out of the Bering Sea shortly after tagging, similar to Shark A (Fig. 1). Unlike Shark A, however, Shark B traveled southwest towards the Emperor Seamount Chain (c 40 °N, 174 °E) where it arrived at the end of October and remained through mid-November. From mid-November through December Shark B traveled north then east from the Emperor Seamount Chain to the central NPO (c 48 °N, 155 °W), approximately 1100 km southeast of Kodiak Island, Alaska. Shark B remained in this area for approximately 4 months from January through April. Following a brief foray south in early June, Shark B redirected his travel straight north and was in the Bering Sea by early July. Shark B continued to travel north and remained in the northern Bering Sea through early September 2020. As of September 6, 2020, Shark B’s minimum distance traveled was approximately 16,607 km, averaging at least 45.5 km/day. In its first year of movement, Shark B crossed the international dateline in the NPO, the first tagged salmon shark to do so.

At the start of the second year, Shark B traveled north toward the Gulf of Anadyr and then began traveling south out of the Bering Sea in mid-September 2020 (Fig. 2). Similar to the first year, Shark B exited the Bering Sea in early October and arrived east of the Emperor Seamount Chain (c 40 °N, 174 °E) at the end of October. Shark B remained in this area until early January 2021 after which it began to move north where it arrived in the southern Bering Sea shelf in February. Shark B did not visit the surface from February 11, 2021 through March 22, 2021, and this was the longest gap in transmitted locations since it was tagged in September 2019. After resurfacing in the southern Bering Sea in late March, Shark B traveled south near the dateline (c 41 °N, 177 °E). Beginning in June, Shark B began to travel north towards the Bering Sea, similar to its first year at liberty. As of June 15, 2021, the last location available from the filtered data set, Shark B was at 49.9 °N, 179.5 °E. During its second year at liberty, Shark B’s minimum distance traveled was 10,500 km, averaging at least 37.4 km/day.

Discussion
This study documents different migration patterns exhibited by two male salmon sharks captured and tagged in the Bering Sea. The two deployments presented here provide the longest satellite telemetry data-set for male salmon sharks. Although both sharks were tagged in the Bering Sea, they undertook drastically different migrations during their time at liberty; Shark

| TL/PCL length (m) | Tag model | Start location date | Final location date | Data transmitted | Data resolution | Data days |
|-------------------|-----------|---------------------|--------------------|-----------------|---------------|-----------|
| Shark A           | 1.76/1.39 Standard rate X-tag | 27-Aug-17 | 28-Aug-18 | Temp (°C) and depth (m) dawn and dusk | 30–60 min Daily | 367       |
| Shark B           | 2.20/1.78 SPOT-257 | 7-Sep-19 | 6-Sep-20 | Location Daily | 230           |
|                   |           | 7-Sep-20 | 15-June-21 | Location Daily | 102           |

TL total length, PCL pre-caudal length
Fig. 1  HMM-derived locations from August 27, 2017 to August 28, 2018 for Shark A (top) and best daily locations transmitted by a SPOT tag carried by Shark B (bottom) from September 7, 2019 through September 6, 2020. Arrows depict swim direction.
A traveled south to southern California and associated offshore waters whereas Shark B remained in the central NPO and Bering Sea. While we can only speculate the reason for these south–north movement patterns, they likely reflect behaviors to optimize foraging success over seasonally productive regions of the NPO, as well as breeding opportunities. These movements may also function to balance the energetic cost of maintaining elevated body temperature with prey availability. The timing of both sharks’ departure from the Bering Sea in September coincides with declining average sea surface temperatures (SST) in the northern Bering Sea (ranging from 5.5 to 9.8 °C in September) [26] and with a reduced density of Pacific salmon in the region following the completion of their spawning migrations [27–30]. The distinct tracks between the two male sharks could indicate stock structure, but additional data are needed before drawing conclusions. This new information expands our current understanding of salmon shark ecology and adds much needed information about an understudied segment of the population, but it also underscores that more work is necessary to better understand salmon shark migration within the NPO.

Shark A traversed the NPO and spent November through June in the offshore and coastal waters of the western United States before returning to the Bering Sea. Although there is uncertainty in the geolocation-based estimates derived from the HMM model, Shark A’s overall migration pattern is similar under both the 50% and 99% probability scenarios (Additional file 2: Figure S2). Shark A’s migration pattern was similar to those undertaken by female salmon sharks satellite tagged in the ENP [17, 18]. However, Shark A’s migration was longer than those of female salmon sharks from the ENP, the longest of which was 18,220 km over 640 days [13], and it may suggest that males are the more active migrants, as proposed by previous research [15]. Mating for salmon sharks in the ENP is believed to occur in September [16], and it is possible that given Shark A’s maturity status it either mated in the Bering Sea prior to initiating its migration south or migrated south to mate and then overwintered in the California Current region. The California Current is thought to be a highly productive foraging area for salmon sharks based on the long residency time exhibited by satellite-tagged female salmon sharks in this area [17]. Shark A’s return migration and residence in the Bering Sea is also likely influenced by foraging.

Fig. 2 Best daily locations transmitted by a SPOT tag carried by Shark B (bottom) from September 7, 2020 through June 15, 2021. Arrows depict swim direction.
opportunities. Interestingly, Shark A returned to the Bering Sea in August, well after most Pacific salmon (*Onchorhyncus* spp.) from that region return to their spawning streams [27–31]. Given this, Shark A’s return migration to the Bering Sea may coincide with fall aggregations of Pacific herring (*Clupea pallasi*) in the western Bering Sea [15, 31] or a return north for mating. Shark A’s PSAT provided a single year of movement information, so it is unknown whether a similar pattern would be conducted annually.

In contrast to Shark A, Shark B remained in the central NPO and Bering Sea throughout its 22 months at liberty. Interestingly, in both years Shark B moved south out of the Bering Sea in September and traveled southwest towards the Emperor Seamount Chain region, where it remained until November 2019 in the first year and through January 2021 in the second year. The Emperor Seamount Chain is known for its large aggregations of forage fish, squid, and Pacific salmon and likely provides an important foraging area for salmon sharks in the central NPO [5, 32]. Although Shark B visited the Emperor Seamount Chain during both years of available data, in the first year Shark B then traveled east and remained on the northern boundary of the North Pacific Transition Zone. This area is a known migration and foraging corridor for numerous marine predators [18, 33, 34], and also corresponds with presumed overwintering areas of Pacific salmon from the Bering Sea and NPO [27–30]. The presumed abundance of overwintering salmon and non-directed movements exhibited by Shark B during this time are likely indicative of foraging behavior. While Shark B likely used the North Pacific Transition Zone as an overwintering foraging ground, female salmon sharks tagged in the ENP have been inferred to use this region as a migratory corridor [17], possibly highlighting differences in habitat-use between sexes. In contrast to year one, after visiting the Emperor Seamount Chain region during fall of its second year, Shark B made a brief northerly foray into the southeastern Bering Sea shelf during the months of February to March. While the reasons for this observed movement pattern is speculative, the timing and location of this movement closely overlaps spatially and temporally with immature Chinook salmon from western Alaska [35], overwintering Pacific herring [31], and walleye pollock (*Theragra chalcogramma*) [36], all of which are known prey species for salmon sharks [4, 7, 8, 16]. In both years Shark B initiated a movement northward to the Bering Sea in June, which may be related to large-scale migration patterns of Pacific salmon species returning north to their spawning rivers in the Bering Sea region [27–31], or possibly a return to north to mate. Repeat migrations to the Emperor Seamount Chain and Bering Sea by Shark B may suggest fidelity to these regions. Site fidelity to regions within the ENP has been documented for some female salmon sharks tagged in the ENP [10, 11].

Although these findings are based on small sample sizes, the data collected by these two tags provide novel information about salmon shark migration. The migration tracks presented here suggest that the Bering Sea is likely an important foraging area for male salmon sharks given that both sharks returned to this region the summer after tagging. However, the capture of a newly pregnant female salmon shark near Nunivak Island in the northern Bering Sea in September 2002 suggests that the Bering Sea might also be used for mating [20] and might explain why both sharks returned and remained in the Bering Sea in August and September. Tagging female salmon sharks in the western and central North Pacific would help assess overlap between sexes in this region and determine how important this region is to their life history. Furthermore, the distinct year-long migrations from the two salmon sharks may lead one to speculate on the presence of two salmon shark populations in the NPO, as suggested in the literature [16]. Continued investigations on the movement patterns of both sexes across the NPO will increase our understanding of the migration and distribution of salmon sharks.

**Conclusions**

As an apex predator in the NPO, understanding the migration patterns of salmon sharks is key to understanding their role in the ecosystem. Salmon sharks have been identified as substantial consumers of Pacific salmon and continuing directed studies may identify where and when salmon sharks co-occur spatially and temporally with Pacific salmon and other commercially important prey species like walleye pollock. Identifying areas and times of overlap may shed some light on the role salmon sharks play in structuring prey populations within the North Pacific. Further opportunistic satellite tagging is planned to increase our sample size for male salmon sharks. Additional deployments on male salmon sharks in general and on female salmon sharks outside of Prince William Sound, Alaska, would help address questions regarding individual and inter-annual variation in salmon shark migration. Continuing this research may also help elucidate changes in salmon shark migration and distribution as ocean temperatures continue to warm. Although this research is limited by its small sample size, the distinct migration routes undertaken by the two similarly sized male salmon sharks tagged in the same area highlights the need for further tagging efforts.
Methods

Ethics statement
All fieldwork was conducted under National Oceanic and Atmospheric Administration Scientific Research Permits #2017-8 and #2019-8.

Study area
Fieldwork for this research was conducted during annual Pacific salmon trawl surveys conducted by the National Oceanic and Atmospheric Administration and the Alaska Department of Fish and Game. These surface trawl surveys have been conducted annually in the northern Bering Sea since 2002 and occur at stations between 60 °N and 65.5 °N and from Norton Sound west to 171 °W. Surface trawls are standardized to 30 min and typically sample the upper 20 m of the water column [37–39].

Shark capture
One salmon shark was captured in each northern Bering Sea survey conducted in 2017 and 2019. Once on deck, a damp towel was placed over the shark’s eyes to reduce stress. Sex was determined by the presence or absence of claspers (present in males) and total length (TL, tip of snout to tip of the tail along the horizontal axis of the body) was measured (m). The TL of each shark was converted to pre-caudal length (PCL, tip of snout to pre-caudal pit) and compared to published length-at-maturity estimates to assess maturity [40]. Length-at-maturity estimates for male salmon sharks range from 1.25 to 1.45 m PCL [24, 41].

2017 shark tagging
In 2017, a male salmon shark (Shark A, Table 1) was tagged with a PSAT (Standard Rate X-tag, Microwave Telemetry, Columbia, Maryland, USA). The PSAT anchor was inserted into the musculature near the base of the dorsal fin using two tethers (Additional file 1: Figure S1); the first tether was attached to the base of the tag with a monofilament leader (300 lb test, 15 cm in length) attached to a stainless-steel dart. A second tether (300 lb test, 8 cm in length) was secured with a loop around the body of the tag and then anchored posterior to the primary anchor with a stainless-steel dart. The loop was loose enough to allow the tag to slip through once it detached from the tether, but kept the tag close to the shark’s body to both reduce drag and minimize tissue tearing at the tag insertion point [13, 42]. The PSAT was programmed to record and store depth, temperature, and light data every 2 min and release from the shark after a 12-month deployment. After release, the tag floated to the surface and transmitted a subset (30 min resolution) of archived temperature and depth data and daily dawn and dusk times to overhead satellites (Argos Satellite System). The pop-off location of Shark A’s PSAT (first tag transmission with Argos Location Class 1–3, error < 1.5 km) was determined by the Doppler shift in successive uplinks to satellites [43].

2019 shark tagging
In 2019, a male salmon shark (Shark B, Table 1) was tagged with a SPOT-257 satellite transmitter (weight = 174 g in air; Wildlife Computers, Redmond, California, USA). The SPOT-257 tag was mounted to the apex of the salmon shark’s dorsal fin by drilling four holes into the fin and attaching the tag using a combination of plastic screws, plastic and stainless-steel washers, and stainless-steel hex nuts (Additional file 1: Figure S1) [13]. The SPOT-257 was programmed to transmit locations and associated errors to overhead satellites (Argos Satellite System) with a 30 s repetition rate up to 250 times per day when the tag’s wet/dry sensors indicated the shark was finning at the surface.

Data filtering and analysis
To provide insights into the horizontal migration patterns of Shark A, its migration track was estimated by geolocation with a HMM using archived light level, depth, and temperature data [44–46]. The HMM consists of coupled movement and data likelihood models in a gridded study area. The movement model accounts for the daily movement of the animal in the study area using isotropic diffusion. The data likelihood model quantitatively describes the degree to which the archived data matches mapped geolocation variable values in each study area grid cell for each day. The model operates first with a forward filter, where the prior probability surface (which begins with all of the probability at the release location) is alternately updated by the movement model and then the data likelihood model. Once the end of the time series is reached by the recursion, backward smoothing is conducted to update the probabilities with the knowledge of the PSAT pop-up location. 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depth bin for TDP) derived from a study of Pacific spiny dogfish (*Squalus suckleyi*) in the NPO [46]. The model outputs a gridded probability surface of the study area for each day of the archived time series and provides a maximum likelihood estimate value of diffusion used for the movement model. Daily location estimates are provided by points (the weighted mean of the probability surface) and polygons that encompass the highest 50% and 99% of the probability for each day.

To provide information about the horizontal migration patterns of Shark B, the SPOT-257 tag Doppler-estimated locations were filtered to retain the best possible location estimates using the Douglas Argos-filter algorithm applied in Movebank [48, 49]. The SPOT transmits Doppler-estimated locations with an associated Argos Location Class specifying the error radius: 0 (error > 1500 m), 1 (500–1500 m), 2 (250–500 m), 3 (<250 m); A and B (no error estimate); and Z (invalid location) [50]. In the Douglas–Argos filtering process, only Argos location classes ≥0 were retained, and any locations with unrealistic movement rates, which we defined as greater than 1.75 m/s for salmon sharks [17], were removed. Filtered locations were then run through a final filter, the “Best of Day” filter in Movebank, to select one location per day that favored locations with lower error radius, higher number of messages received by the satellite, and higher quality indicator values.

The minimum horizontal distance traveled for each salmon shark was calculated by summing the straight-line distance between consecutive locations for the entire track [4, 51]. To calculate straight-line distance, the daily location estimates derived from the HMM model were used for Shark A and the daily locations derived from the filtered SPOT data were used for Shark B. This estimate is considered a minimum as it does not account for distance traveled between estimated daily locations. Estimated daily locations from both the 2017 and 2019 sharks were mapped in GIS software (ArcMap 10.6.1) with a GEBCO grid base layer [52, 53].

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**Authors’ contributions**

SG and JM participated in the fieldwork required to conduct the tagging. DO, CT and AS contributed funding for the purchase of satellite tags and Argos satellite costs. MC received and outfitted satellite tags for deployment. SG, MC, and JN performed the statistical analyses. SG drafted the manuscript and all authors edited the manuscript for submission. All authors read and approved the final manuscript.

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**Availability of data and materials**

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

**Declarations**

**Ethics approval and consent to participate**

Salmon shark tagging in 2017 and 2019 was carried out under National Oceanic and Atmospheric Administration Scientific Research Permits #2017-8 and #2019-8.

**Consent for publication**

Not applicable.

**Competing interests**

The authors declare no competing interests.

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