Seasonal changes in depth distribution of salmon sharks (*Lamna ditropis*) in Alaskan waters: implications for foraging ecology

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**Abstract:** The salmon shark, *Lamna ditropis*, is an endothermic, apex predator in the productive waters of the Gulf of Alaska (GOA). To understand their role in these productive habitats and to identify and better understand their interactions with commercially important species and fisheries, detailed information regarding the distribution of the salmon shark is required. Archival data records from eight recovered pop-up archival transmitting (PAT) tags were analyzed to examine the geographic and vertical distribution of female salmon sharks and elucidate how their distribution changes in relation to the biotic and abiotic environment. Tagged sharks used the neritic habitats of the GOA for the duration of the PAT deployments. Sharks exhibited a diel periodicity in their dive behavior. Salmon sharks exhibited three different patterns of depth distribution (behavioral modes) that occurred during distinct oceanographic seasons, likely reflecting changes in their foraging ecology in response to seasonal changes in the distribution and availability of important prey. The distribution of salmon sharks in the GOA appears to follow consistent patterns and has a high degree of geographical and vertical overlap with commercially important prey species. This information increases our understanding of interactions between salmon sharks and commercial fisheries and may assist in fostering responsible management for this species.


[Traduit par la Rédaction]

**Introduction**

The spatiotemporal patterns of distribution of a species are fundamental to its ecology and population dynamics (Dingle and Holyoak 2001; Morales and Ellner 2002). The salmon shark (*Lamna ditropis*) (Hubbs and Follett 1947) is a wide-ranging apex predator (Nagasawa 1998; Brodeur et al. 1999) that uses neritic and oceanic habitats throughout the North Pacific Ocean (Nagasawa 1998; Hulbert et al. 2005; Weng et al. 2005). Salmon sharks have a broad depth distribution, with new electronic data tagging showing them diving to depths of up to 1864 m (A.B. Carlisle and B.A. Block, unpublished data), and thermal range, occurring at temperatures from 2 to 24 °C (Nakano and Nagasawa 1996; Nagasawa 1998; Weng et al. 2005). As an abundant, active apex predator, the salmon shark may well play an important role in North Pacific ecosystems through top-down processes (Fogarty and Murawski 1998; Pace et al. 1999; Bascompte et al. 2005). As a result, an understanding of the spatiotemporal patterns of distribution of salmon sharks is an important part of understanding their ecological role (Kareiva et al. 1990; Crist et al. 1992; Morales and Ellner 2002) and is necessary for effective...
management of this species and the ecosystems of which it is a part (Block et al. 2002; Shillinger et al. 2008).

The broad geographic distribution of salmon sharks, particularly their use of cold, productive boreal waters, is likely associated with their endothermic capacity (Bernal et al. 2005; Weng et al. 2005). All sharks in the family Lamnidae have some degree of anatomical and physiological specialization associated with a capacity for heat conservation and endothermy, but the expression of these traits is considered greatest in the genus *Lamna* (salmon shark and porbeagle shark (*Lamna nasus*)) (Carey et al. 1985). Salmon sharks possess counter-current heat exchangers (retia mirabilia) that allow them to retain the metabolic heat generated by highly aerobic tissues in the muscles, viscera, kidney, and brain (Burne 1924). This enables the sharks to maintain body temperatures that are elevated by as much as 21.2 °C above ambient water temperature (Goldman et al. 2004). In addition, salmon shark cardiac physiology is also specialized for utilizing cold habitats. Through the increased expression of SERCA2 protein in the sarcoplasmic reticulum of cardiac myocytes, salmon shark hearts are able to maintain function at low temperatures, thereby providing their active, warm tissues with enough oxygen to effectively forage in cold environments (Landeira-Fernandez et al. 2003; Weng et al. 2005). These characteristics allow *Lamna* to be highly active predators across a large geographic and depth range and likely underlie their niche expansion into the productive boreal waters of the North Pacific (Block and Finnerty 1994; Goldman et al. 2004; Weng et al. 2005).

The highly productive neritic waters of the Gulf of Alaska (GOA) support some of the largest fisheries in the world (Mundy 2005), yet much remains unknown about the role of salmon sharks in this ecosystem or how individuals use this region. Although salmon sharks are opportunistic foragers with a diverse diet (e.g., Nagasawa 1998; Hulbert et al. 2005; Goldman and Musick 2008), they are known to feed on commercially important species, including Pacific salmon (*Oncorhynchus spp.*) and walleye pollock (*Theragra chalcogramma*) (Nagasawa 1998; Goldman and Musick 2008). Predation by salmon sharks may be an important component of natural mortality for these species, especially considering the abundance and high energetic requirements of salmon sharks due to their high metabolic rate (Nagasawa 1998; Bernal et al. 2005; Weng et al. 2008).

Salmon sharks exhibit life history characteristics typical of elasmobranchs (i.e., slow growth rate, late age at first maturity, and low fecundity) (Goldman and Musick 2006); therefore, they are particularly vulnerable to overexploitation (Musick et al. 2000; Cortes 2002) and need to be managed accordingly. While there is a small directed fishery for them in Japan (Goldman and Musick 2008), there is no commercial fishery for salmon sharks in US waters. However, there is a limited sport fishery that is primarily active in Prince William Sound (PWS), Alaska (Tribuzio et al. 2008). After the 1992 ban on pelagic drift gillnetting in the North Pacific (McKinnell and Seki 1998), much of the fishing mortality, especially in the form of nontarget catch, on salmon sharks in the eastern North Pacific shifted to neritic habitats. Nontarget catch of sharks in commercial fisheries in Alaskan waters is likely high but poorly documented (Camhi 1999) and may be a source of considerable mortality for salmon sharks, especially in the GOA and PWS (Goldman and Musick 2008).

Weng et al. (2005, 2008) and Hulbert et al. (2005) described general patterns of movement and vertical distribution of salmon sharks throughout their range in the eastern North Pacific. However, detailed analyses regarding changes in vertical distribution of salmon sharks in Alaskan waters, over both short (diel) and longer (seasonal) temporal scales, have not been conducted. We use high-resolution records from recovered PAT tags to address this lack of information and examine how salmon sharks use the neritic habitats of the GOA. Specifically, we describe seasonal changes in the geographic distribution and depth distribution of salmon sharks and associate these changes with those that occur in the surrounding environments. Detailed information regarding how depth distribution changes over time in relation to changes in the biotic and abiotic environment provides important insight into the ecological role of salmon sharks and their potential interactions with commercially important species and fisheries in the GOA.

**Materials and methods**

**Electronic tagging**

In July and August of 2002 to 2008, female salmon sharks were caught and tagged with electronic tags in Port Gravina, PWS, Alaska (60.75°N, 146.16°W; Fig. 1), by the Census of Marine Life Tagging of Pacific Predators program (TOPP) using the techniques described in Weng et al. (2005). Sharks were tagged with a Smart Position or Temperature Transmitting Tag (SPOT) (Wildlife Computers, Redmond, Washington), a PAT tag (Wildlife Computers, Redmond, Washington), or both (double-tagged). SPOT tags use the Argos system to provide geographic positions with a high degree of resolution when the tag is not submerged. Accuracy, or location class (LC), of positions is categorized by decreasing quality from LCs 3, 2, 1, 0, A, B, to Z. LC 3 positions have the best resolution (<150 m), followed by LC 2 (150–300 m) and LC 1 (350–1000 m), as determined by the Argos system (www.argos-system.org). Resolution of Argos LCs 0, A, and B have been estimated at 8 to 50 km (Hays et al. 2001; White and Sjoberg 2002), and LC Z does not provide a position.

PAT tags archive environmental data (temperature, pressure, light) at a user-designated interval and are programmed to detach from the study animal and float to the surface. Once at the surface, PAT tags transmit summaries of the archived environmental data to the Argos system. These summaries are used to reconstruct the movements and environment that the tagged animal experienced, even if the tag is not recovered (Block et al. 1998; Arnold and Dewar 2001; Gunn and Block 2001). However, physical retrieval of the PAT tag provides the entire archived time series for study, allowing for more detailed analyses to be performed (Teo et al. 2007; Weng et al. 2007).

Eight PAT tags with a mean deployment length of 121.9 ± 82.1 days (mean ± standard deviation (SD)) have been recovered from salmon sharks that used the northern GOA, giving access to a total of 1126 days of archival data. These sharks had a mean precaudal length (PCL) of 203.9 ± 18.3 cm, and all were assumed to be mature or large subadults based on
size at maturity estimates of 164.7 cm PCL (Goldman and Musick 2006). All eight of the sharks were double-tagged with SPOT and PAT tags, providing the higher accuracy positions from SPOT tags to accompany the PAT records. Five of the recovered tags popped off on schedule and comprised the bulk of the data set (mean deployment, 205 ± 62.2 days; total data set, 1025 days) (Table 1). The other three tags were at liberty for approximately 1 to 1.5 months. Two of these sharks (nos. 119 and 097) were caught by sport fishermen. The third (no. 110) died for unknown reasons but did not exhibit abnormal behavior prior to its death and so was included in the study (Table 1). The PAT tag on shark 558 popped off ~1000 km west of Vancouver Island (45.79°N, 142.48°W) on schedule after 270 days, but we only analyzed the period of time when the shark was on the Alaskan shelf (the first 142 days). The final 23 days of 273 days of data from the PAT tag on shark 087 were corrupted, so only the first 250 days were analyzed. After removing these days from the analysis, there was a total of 975 days of data.

The PAT tags primarily recorded information during the summer, autumn, and winter. The longest PAT deployment (shark 087) lasted from the summer to the following spring (273 days) and was the only tag at liberty during the spring. During the first 3 days following tagging, shark 087 exhibited possible postrelease behavioral modification following tagging, and these days were not included in analyses (Hoohian et al. 2011). Unusual behaviors were not apparent in the other sharks following tagging.

### Data analysis

Movements were examined using Argos positions from the SPOT tags and geolocation positions from the recovered PAT tags. Argos positions from SPOT tags were filtered using a speed filter (1.5 m·s\(^{-1}\)) to remove positions that represented biologically unrealistic rates of movement (Weng et al. 2005); all positions that fell on land or of LCs A, B, or Z were removed. Positions were then summarized to one position per day; where there were multiple positions in a day, the mean position was used.

Light level data from the PAT tags were used to generate daily estimates of longitude (Hill and Braun 2001), implemented with software provided by the manufacturer (WC-TSP version 1.02.008). Daily longitude estimates and sea surface temperature (SST) data recorded by the tags were matched with remotely sensed SST measurements to estimate latitude using the method described by Teo et al. (2004). To assess the accuracy of our geolocation estimates, for each day with an Argos position, the Argos position (or “true” posi-

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**Fig. 1.** The northern Gulf of Alaska. Inset maps show Prince William Sound (PWS), with tagging location (Port Gravina) indicated, and the broader study area. Note different depth categories between map and PWS inset.

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Table 1. Female salmon sharks (*Lamna ditropis*) tagged in Port Gravina, Prince William Sound, with archival PAT records from the neritic waters of Alaska.

<table>
<thead>
<tr>
<th>Shark no.</th>
<th>PCL (cm)</th>
<th>Tag types</th>
<th>Pop-up date</th>
<th>Pop-up location</th>
<th>Record length (days)</th>
<th>Behavior days</th>
<th>No. of days with Argos</th>
<th>Distance (km)</th>
<th>Pop-up date</th>
<th>Pop-up location</th>
<th>Behavior</th>
<th>No. of recapture location</th>
</tr>
</thead>
<tbody>
<tr>
<td>931</td>
<td>208</td>
<td>PAT1/SPOT1</td>
<td>120 July 2002</td>
<td>54.96°N, 160.51°W</td>
<td>122</td>
<td>15 July 2002</td>
<td>14 Nov. 2002</td>
<td>54.96°N, 160.51°W</td>
<td>122</td>
<td>51, 63, 8</td>
<td>32 (26%)</td>
<td>1057</td>
</tr>
<tr>
<td>110</td>
<td>218</td>
<td>PAT3/SPOT3</td>
<td>60 July 2004</td>
<td>60.69°N, 146.64°W</td>
<td>28^a</td>
<td>8 Aug. 2004</td>
<td>8 Aug. 2004</td>
<td>60.69°N, 146.64°W</td>
<td>28^a</td>
<td>27, 0, 0</td>
<td>1 (4%)</td>
<td>50</td>
</tr>
<tr>
<td>119</td>
<td>214</td>
<td>PAT3/SPOT3</td>
<td>60 July 2004</td>
<td>60.34°N, 146.64°W</td>
<td>28^a</td>
<td>9 Jan. 2005</td>
<td>28 Aug. 2004</td>
<td>60.34°N, 146.64°W</td>
<td>28^a</td>
<td>59.29°N, 146.11°W</td>
<td>180</td>
<td>46, 0, 0</td>
</tr>
<tr>
<td>111</td>
<td>224</td>
<td>PAT3/SPOT3</td>
<td>60 July 2004</td>
<td>60.34°N, 146.64°W</td>
<td>28^a</td>
<td>13 July 2004</td>
<td>22 May 2004</td>
<td>60.34°N, 146.64°W</td>
<td>28^a</td>
<td>59.72°N, 146.11°W</td>
<td>250</td>
<td>65, 81, 104</td>
</tr>
<tr>
<td>979</td>
<td>207</td>
<td>PAT3/SPOT3</td>
<td>60 July 2004</td>
<td>60.34°N, 146.64°W</td>
<td>28^a</td>
<td>13 July 2004</td>
<td>16 May 2007</td>
<td>60.34°N, 146.64°W</td>
<td>28^a</td>
<td>60.71°N, 146.11°W</td>
<td>180</td>
<td>65, 81, 104</td>
</tr>
<tr>
<td>558</td>
<td>186</td>
<td>MK10/SPOT5</td>
<td>30 Aug. 2005</td>
<td>59.71°N, 147.53°W</td>
<td>28^a</td>
<td>22 Aug. 2005</td>
<td>22 May 2006</td>
<td>59.71°N, 147.53°W</td>
<td>28^a</td>
<td>60.71°N, 146.11°W</td>
<td>142</td>
<td>46, 0, 0</td>
</tr>
<tr>
<td>571</td>
<td>168</td>
<td>MK10/SPOT5</td>
<td>30 Aug. 2005</td>
<td>59.71°N, 147.53°W</td>
<td>28^a</td>
<td>22 Aug. 2005</td>
<td>16 May 2007</td>
<td>59.71°N, 147.53°W</td>
<td>28^a</td>
<td>45.79°N, 142.48°W</td>
<td>142</td>
<td>46, 0, 0</td>
</tr>
</tbody>
</table>

Note: PCL, precaudal length; sampling interval, sampling interval of PAT tag; behavior days, numbers of days of the archival records designated as the different behavioral modes (B1, B2, B3); number of days with Argos, the number of days (percentage in parentheses) in the archival record with an associated high-resolution Argos position; distance, the distance between tagging location and pop-up or recapture location.

*Shark caught by sport fishermen.*

*Record length is 270 days, but only analyzed data for period of time when shark was in neritic region of Alaska (first 142 days, to 8 January 2007).*

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A fast Fourier transformation (FFT) with Hamming window smoothing (implemented using Matlab R2009b, The Mathworks Inc., Natick, Massachusetts) was applied to the full depth record of every tag to identify periodicities (rhythmic patterns) (Graham et al. 2006). A FFT decomposes a time series record into component sine and cosine waves of different frequencies (periodicities), and the relative magnitude of the different periodic components is indicated by the size of the spectral peak in a power spectrum (Chatfield 2004). Results allow periodicities corresponding to tidal, diel, or longer term patterns of behavior to be identified (Graham et al. 2006; Shepard et al. 2006; Meyer et al. 2007).

Ambient light levels from the PAT archival records were used to divide each 24 h period into day or night. The inflection point in the dusk and dawn light curves from the WCTSP output was used to delineate period of day. Where there were gaps in daily estimates of dusk and dawn, values were based on linear interpolation.

The thermal structure of the water column was recreated for the duration of each shark’s track. Time series of temperature, time, and depth from the tags were used to create a linearly interpolated cross section of temperature across depth and time. This was implemented in Matlab using the TriScatteredInterp function (The Mathworks Inc.).

Depth and oceanographic data were summarized for each day of data from the archival record of every shark. We calculated daily estimates of mean and modal depth during the day, night, and entire day. Isothermal layer depth (ILD), a proxy for mixed-layer depth, was calculated for each day using the depth and temperature archival record and the method described in Kara et al. (2000) with a threshold value (ΔT) of 0.8 °C. Mean daily SST was estimated using the mean temperature of all temperatures recorded at depths ≤ 5 m.

There were three general patterns or behavioral modes apparent in the depth distribution of the sharks that generally occurred during different times of the year. Sharks were generally either shallow throughout the day (summer and early autumn), exhibited a diel shift in depth distribution in which they were shallow during the night and deeper during the day (autumn and early winter), or were generally deep throughout the day relative to the other two behavioral modes (winter and spring) (see Results: Vertical and thermal habitat). Every day was objectively assigned to one of these three behavioral...
Table 2. Error in light-based longitude and SST-based latitude geolocation estimates.

<table>
<thead>
<tr>
<th></th>
<th>Error (km)</th>
<th>Error (°)</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td>291.9 (330.5)</td>
<td>2.6 (2.9)</td>
<td>4.0</td>
</tr>
<tr>
<td>Longitude</td>
<td>51.2 (75.4)</td>
<td>0.9 (1.2)</td>
<td>1.5</td>
</tr>
</tbody>
</table>

Note: Mean and standard deviation of error (in kilometres and degrees) and root mean square error (RMSE) are presented. Estimates are based on difference between high-resolution Argos positions and geolocation estimates on corresponding days.

modes according to what each day’s mean depth during the day and night was relative to the overall mean depth of that individual shark’s depth record. Overall mean depth was very similar to overall median depth (mean difference, 8 m; minimum, 1 m; maximum, 18 m), and using median and mean depths produced very similar behavioral mode assignments.

A day was categorized as behavioral mode 1 (B1) when sharks were shallower than their overall mean depth during both day and night. A day was assigned to behavioral mode 2 (B2) when sharks were deeper than their overall mean depth during the day and shallower during the night. Behavioral mode 3 (B3) occurred when sharks were deeper than their overall mean during the day and night or were shallower than their overall mean during the day and deeper during the night. These two different patterns were grouped into B3 because the temporal distributions of these two patterns were not significantly different (Mann–Whitney U test, \( w = 1.19, p = 0.23 \)) as they both primarily occurred during the winter and spring, whereas B1 primarily occurred during summer and B2 primarily occurred during autumn (see Results). In addition, during only 20% of B3 days were sharks shallower than their overall mean during the day and deeper during the night, so B3 primarily represents days when mean depth was deeper than the overall mean during the day and the night. Because of the short duration of the shorter archival records (sharks 097, 110, and 119), which reflected B1 behavior, behavioral mode assignments for these sharks were made using the grand mean of all salmon sharks’ depth measurements (60.1 m) instead of the individual shark’s mean depths, resulting in all days of data for these sharks being assigned to B1.

Once a behavioral mode had been assigned to every day, daily estimates of depth (mean and modal depth during day, night, entire day) and oceanographic (ILD, SST) parameters for all the sharks were aggregated by behavioral mode and visualized using box plots. Distributions of aggregated depth and oceanographic parameters during the different behavioral modes were then compared using a Mann–Whitney U test or Kruskal–Wallis test. Due to unequal sample size, we used the Dunn–Šidák correction for multiple comparisons (Zar 1999).

To describe diel patterns of water column and thermal environment use during the behavioral modes, proportion of time spent at depth and temperature by time of day was calculated. For every shark, time at depth (TAD) and time at temperature (TAT) were calculated at 15 min increments for every 24 h period and then aggregated by behavioral mode. The TAD and TAT data for all sharks were then combined to produce a single average TAD and TAT for B1, B2, and B3. Mean vertical displacement rate by depth was calculated for each behavioral mode in the same manner for shark 571, which was the only shark that had a PAT tag with a rapid enough sampling rate (5 s) to observe behavior with relatively high temporal resolution. Vertical displacement rate was calculated by dividing the change in depth between each record by the sampling rate. This rate was then assigned to the depth or depths between which the shark moved during the sample interval.

Results

Geographic distribution

Argos positions from SPOT tags indicate that the tagged sharks remained primarily in the neritic waters of Alaska during the duration of the PAT tag deployments (Fig. 2a), although some sharks migrated south from Alaskan waters after the PAT tags popped off. We use the term neritic to describe habitats between the outer shelf slope and the coast. Of the five sharks with longer PAT deployments, four migrated south and left the neritic waters of Alaska after the PAT tags popped off. This included sharks 931 (migrated in early February), 558 (mid-January), 111 (late February), and 571 (mid-April). Shark 087 remained in Alaskan waters throughout the year and migrated during the following February, approximately 18 months after tagging.

There were large gaps in the Argos records of all the sharks (Table 1; Fig. 2b). However, based on Argos positions and longitude estimates, sharks remained primarily in central Alaska (Figs. 2a, 2b), being most concentrated in the PWS region during the summer and more dispersed during the autumn, winter, and spring. In particular, sharks used primarily the region from Kodiak Island to PWS (roughly 154°W to 144°W). Longitude estimates and Argos positions suggest that the PWS region was used throughout the year but most intensively during the summer, though this may be an artifact of tagging location. Shark use of areas to the west of PWS (regions around the Kenai Peninsula and Kodiak Island) increased later in the year, especially during the autumn.

Vertical and thermal habitat

The depth distribution of the sharks changed in a consistent manner in relation to the water column thermal structure (Fig. 3a). During summer and early autumn, the water column was highly stratified, and sharks generally remained above the thermocline in warm, shallow waters throughout the day. As the water column stratification started to break down in the autumn, sharks exhibited a diel pattern of vertical migration in which they were generally deeper during the day and shallower during the night. In the winter and spring, sharks were deeper overall, and the water column became largely well mixed and cold. Inversion layers were present during the winter and spring as well (Fig. 3a), where it was colder at the surface than at depth. During the winter and spring, salmon sharks made their deepest dives (maximum 364 m in shark 087 during April) and encountered the coldest temperatures (2.5 °C at the surface in shark 087 during January), which primarily occurred in surface inversion layers. Sharks spent considerable lengths of time in cold waters; shark 087 spent at least 170 continuous days at temperatures below 8 °C and at least 80 continuous days at temperatures below 6 °C.

Spectral analysis (FFT) of archival depth records indicated
that the dominant periodicity in salmon shark depth was a diel (24 h) cycle (Fig. 4). The depth time series of all sharks had very large peaks at 24 h regardless of record length, indicating that the diel periodicity occurred throughout the duration of the PAT deployments (late summer through winter or early spring). Most sharks had smaller sec-

Fig. 2. (a) Northern Gulf of Alaska (with inset showing Prince William Sound, PWS) showing daily Argos positions from SPOT tags (circles) and pop-up location of tags (triangles), with positions color-coded by shark. Only Argos positions that overlap temporally with the PAT record are shown. The 200 and 300 m isobaths are also shown. (b) Time series of daily estimates of longitude based on geolocation (P) and SPOT positions (S) (color-coded by longitude) for each shark. Note the large gaps in the SPOT record and the high level of concordance between SPOT longitude and geolocation longitude.
ondary peaks, most commonly at 12 h, perhaps indicative of crepuscular activity, but these were much weaker than the dominant peak.

Behavioral modes

We grouped the data into behavioral modes based on the three general patterns of vertical behavior (Fig. 5). The distribution of days assigned to the different behavioral modes showed a strong seasonal trend and reflected the observed seasonal changes in depth distribution (Fig. 3b). The temporal distributions of days assigned to the different behavioral modes were significantly different (Kruskal–Wallis test, \( H = 475.2, \text{df} = 2, p < 0.001\)). Days were generally categorized as B1 during the summer (367 B1 days; median date, 23 August; interquartile range (IQR), 2 August – 18 September). Days were typically categorized as B2 during the autumn (387 B2 days; median date, 1 November; IQR, 5 October – 27 November) and as B3 during the winter and spring (221 B3 days; median date, 6 January; IQR, 15 December – 21 February).

Although they were tagged over the course of 6 years, tagged salmon sharks exhibited consistent patterns in depth and temperature distribution during the different behavioral modes (Fig. 6). During B1 (summer), the depth range at
which sharks spent the most time (focal depths) was in the warm, uppermost part of the water column (<10–15 m, 14–16 °C). Generally sharks spent little time below 50 m, though deeper dives generally occurred during the day. However, because of the high degree of stratification of the water column, sharks experienced a wide range of water temperatures (as cold as 4 °C) throughout the day, despite rarely going below 50 m. During B2 (autumn), sharks exhibited a strong diel periodicity, with a deeper daytime mode (median of daily modal depths during B1, 5 m; B2, 10.0 m; B3, 70 m; Kruskal–Wallis test, df = 2,  H = 219.9, p < 0.001). The modal daytime and nighttime depths were significantly different during B1 (Mann–Whitney U test, w = 34.8, p < 0.001) and B2 (median of daytime depths, 5 m; nighttime depths, 90 m; Mann–Whitney U test, w = 357.9, p < 0.001; Fig. 7a, b), although as opposed to mean depth, B3 was also significantly different (median daytime depths, 85 m; nighttime depths, 50 m; Mann–Whitney U test, w = 18.58, p < 0.001; Fig. 7b). The diel periodicity in depth identified using mean and modal depths is supported by the results of the spectral analysis, which indicated that there was a clear diel periodicity throughout the duration of the tracks. Modal depth appears to better reflect the diel pattern exhibited during B3 (Fig. 6), with sharks being deeper overall but still slightly shallower during the night than during the day overall. This highlights the importance of selecting the appropriate depth metric when examining depth distribution and how spectral analysis can inform your data analysis and interpretation.

The oceanographic conditions during the different behavioral modes also showed a clear change reflecting the seasonal nature of the behavioral modes (Figs. 7c, 7d). Sea surface temperature differed significantly between all of the behavioral modes (Kruskal–Wallis test,  H = 544.6, df = 2,  p < 0.001), with SST being the warmest during B1 (median of mean daily SST, 14.9 °C) and the coldest during B3 (median, 5.6 °C) (Fig. 7c). Isothermal layer depth decreased significantly from B1 (median, 13.2 m) to B2 (median, 55.8 m) (Kruskal–Wallis test,  H = 339.5, df = 2,  p < 0.001), but not from B2 to B3 (median, 94.7 m) (Fig. 7d). As the ILD deepened over the course of the year, the number of days with water columns categorized as isothermal (no bottom of the ILD was identified up to the maximum depth that the shark occupied) increased, as did the number of days during which an inversion layer was present. During B1, the water column was isothermal on 14.4% of the days and had an inversion layer on 4.4% of the days. During B2, 35.8% of the days were isothermal and 10.7% had an inversion layer. During B3, 92.2% of the days had isothermal water columns and 72.6% had an inversion layer. Many of the days during B1 and B2 were categorized as isothermal due to sharks remaining very shallow (above the ILD) rather than indicating a deep ILD as was the case during B3. The lack of a significant difference in ILD between B2 and B3 was due to so many days during B3 being categorized as isothermal.

As the isothermal layer deepened over the course of the year, residency time within the isothermal layer also generally increased. During B1, median percentage of time spent within the ILD was 70.5% (IQR 42.3%–96.8%) during the day and 90.7% (IQR 63.3%–99.7%) during the night. During B2, median percentage of time spent in the ILD decreased to 48.2% (IQR 22.3%–99.8%) during the day but increased to 99.8% (IQR 96.8%–100%) during the night. Sharks spent nearly 100% of their time in the ILD during both the day.
and night during B3 because of the lack of thermal stratification in the water column.

Shark 571 generally exhibited more rapid vertical movements during the day and at the bottom of its depth distribution during each behavioral mode (Fig. 8). During B1, the shark’s vertical movements were faster during the day than...
at night (day: mean, 0.13 ± 0.13 m·s$^{-1}$; maximum, 1.70 m·s$^{-1}$; night: mean, 0.09 ± 0.05 m·s$^{-1}$; maximum, 0.50 m·s$^{-1}$), and in general, most of the rapid dives occurred below about 50 m and vertical displacement rate was generally low near the surface. There was a similar pattern during B2 in which the shark again exhibited more rapid vertical movements during the day and at the bottom of its depth distribution (day: mean, 0.10 ± 0.13 m·s$^{-1}$; maximum, 1.53 m·s$^{-1}$; night: mean, 0.08 ± 0.05 m·s$^{-1}$; maximum, 0.65 m·s$^{-1}$). Most of the rapid vertical daytime movements occurred above and below focal depths. During B3, the vertical displacement rate of the shark was more consistent across depths and time (day: mean, 0.10 ± 0.07 m·s$^{-1}$; maximum, 1.35 m·s$^{-1}$; night: mean, 0.07 ± 0.04 m·s$^{-1}$; maximum, 0.7 m·s$^{-1}$). However, the shark still exhibited the highest vertical displacement rates during the day and at the bottom of its depth distribution, and the highest vertical displacement rates were at depths just above daytime focal depths.

**Discussion**

The results of this study indicate that some female salmon sharks reside in the coastal Alaskan waters of PWS and adjacent neritic habitats throughout the winter and that their movements and behaviors shift with seasonally changing oceanographic conditions. Furthermore, the vertical distribution of the salmon sharks tagged in this study changed in a predictable and consistent manner, information that may be useful in reducing fisheries interactions with this important predator in neritic habitats. Changes in the depth distribution of salmon sharks likely represent shifts in their foraging ecology and, thus, possible interactions with commercially important species such as Pacific salmon, walleye pollock, and Pacific herring (*Clupea pallasi*).

Changes in the depth distribution of salmon sharks were associated with seasonal oceanographic conditions. Specifically, we identified three distinct behavioral modes that represent shark behavior during the summer–early autumn (B1), autumn (B2), and winter–spring (B3). Oceanographic conditions during the different behavioral modes were distinct, suggesting that salmon sharks distribute themselves vertically according to three different oceanographic seasons. Oceanographic conditions recorded by PAT tags closely matched seasonal oceanographic changes reported in the literature for the northern GOA (Wang et al. 2001; Royer 2005; Sarkar et al. 2005). The shifts between behavioral modes are most
likely a response to changes in prey distribution and availability during distinct oceanographic periods.

Due to the specialized anatomical and physiological traits possessed by *Lamna* that allow them to maintain elevated body temperatures and essentially function as homeotherms (Goldman et al. 2004), the influence of water temperature on their movements and behaviors is likely moderated (Weng et al. 2008). Salinity reaches its lowest levels in the top 20–30 m of the water column (25 ppt at the surface to 29.5 ppt at 30 m) in the northern GOA during late summer and autumn (Royer 2005) when salmon sharks use these depths extensively, indicating they are not greatly impacted by reduced salinity. Therefore, it is likely that the influence of oceanographic conditions on the distribution of salmon sharks in the northern GOA is primarily mediated through its impact on the abundance and distribution of important prey species such as Pacific salmon, walleye pollock, and squid (Teuthida), which are ectothermic and may be more directly affected by oceanographic conditions such as temperature. This suggests that seasonal shifts in salmon shark depth distribution primarily represent changes in foraging behavior.

The region used by tagged sharks, which encompassed primarily areas of the continental shelf from east of PWS (including PWS itself) to west of Kodiak Island (approximately 144°W to 156°W), corresponds with areas used by salmon sharks identified by Weng et al. (2005) and Hulbert et al. (2005). This region has been reported to be highly productive (Feder and Jewett 1986; Sambrotto and Lorenzen 1986; Mueter and Norcross 2002), supporting a diversity and abundance of potential prey items (Mueter and Norcross 2002; Mundy and Hollowed 2005; Jorgensen 2007). Overall, the western GOA is characterized as having relatively higher productivity supporting a high biomass and lower diversity of fishes, and the eastern GOA is characterized as being relatively less productive, with a lower biomass and higher diversity of fishes (Mueter and Norcross 2002; Mundy and Hollowed 2005).

Several species known to be important salmon shark prey (Nagasawa 1998; Hulbert et al. 2005; Goldman and Musick 2008) such as Pacific salmon (Groot and Margolis 1991; Myers et al. 2000), walleye pollock, and Pacific herring (Hay and McCarter 1997; Mundy and Hollowed 2005) are abundant in the neritic habitats of central Alaska used by tagged salmon sharks. In particular, walleye pollock, which are one of the most abundant species of fish in the GOA and very important ecologically and economically (walleye pollock support the largest single-species commercial fishery in the world) (Springer 1992; Yang and Nelson 2000; Mueter and Norcross 2002), are generally found at their highest densities in the GOA in inner shelf habitats (100–200 m deep, within 20–40 nm of land), between 147°W and 154°W (though they are abundant to 170°W) (Brodeur and Wilson 1996b; Kendall et al. 1996; Shima et al. 2002). The distribution of cephalopods in the GOA has not been described, but they are the largest component of nontarget catch in the pollock fishery in the western and central GOA (Ormseth and Gaichas 2009) and are believed to be abundant in pelagic waters surrounding the outer continental shelf and slope (Sinclair et al. 1999).
The increased productivity and the diverse and abundant food web that coastal GOA and adjacent waters support likely underlie the extensive use of this region by salmon sharks. This region also corresponds to the area of the GOA in which the greatest numbers of salmon sharks are caught as nontarget catch in commercial fisheries. The region spanning from Kodiak to PWS saw an estimated 380.8 tonnes of salmon sharks (55% of total estimated catch in GOA) caught as reported, nontarget catch in commercial fisheries between 1997 and 2008, with the area between Kodiak and the Shumagin Islands having the next highest level of bycatch (164.4 tonnes or 24% of the catch) (Tribuzio et al. 2008).

**Seasonal shifts in depth distribution: behavioral mode 1**

The vertical distribution of the tagged sharks provides further information about foraging behavior and how this shifts over time in a dynamic and changing ocean. Caution is always warranted when drawing conclusions from a small sample size. However, the consistency of the patterns that we describe across individuals and the 6 years of tagging suggest that our results are representative.

The geographic and vertical distribution of tagged salmon sharks during the summer and early autumn (B1) likely reflects the distribution of Pacific salmon and represents foraging on salmonids. Salmon sharks have been reported to use PWS extensively during the summer and early autumn and to form large aggregations in some of its bays and fjords to feed on the aggregations of Pacific salmon that gather near the mouths of their natal rivers in PWS prior to making their upstream spawning migrations (Paust and Smith 1989; Hulbert et al. 2005; Weng et al. 2005). The major component of salmon shark diet in PWS during the summer is pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*), and coho (*Oncorhynchus kisutch*) salmon (Hulbert et al. 2005), although sharks still consumed a variety of other prey (squid and teleosts such as sablefish (*Anoplopoma fimbria*) and Pacific herring) despite high local densities of salmon (Hulbert et al. 2005).

Our results indicate that in summer months, salmon sharks likely forage primarily on salmon in shallow surface waters throughout the diel cycle. The shallow distribution of salmon sharks and slight diel shift in depth during B1 closely matches what has been reported for salmon. Many studies have documented diel vertical migration in Pacific salmon (Manzer 1964; Walker et al. 2006, 2007). Walker et al. (2006) reported that pink, coho, and chum salmon primarily remained in the upper 20 m of the water column (with occasional deeper excursions) and that their average depth was slightly deeper during the day (12–20 m) than during the night (4–8 m).

However, salmon sharks also forage on nonsalmonid prey (squid, demersal or benthic teleosts) during this period (Hulbert et al. 2005; K.J. Goldman, unpublished data), and it is likely that this occurs during the day. Sharks were slightly deeper during the day and made the deepest dives during the day, and the vertical displacement rate was highest during the day at depths below 50 m, suggesting that sharks may be more actively foraging in deeper waters during their brief daytime vertical excursions from shallow waters. Chum salmon have also been reported to move faster during dives below the thermocline, possibly while in pursuit of more active fish prey distributed below the thermocline (Tanaka et al. 2005). These deeper daytime dives may represent foraging on benthic or demersal prey as these dives are deeper than the depths typically used by salmon (Manzer 1964; Walker et al. 2006; Walker et al. 2007). That the vertical displacement rate was very low at the depths at which the shark was most concentrated (<50 m) suggests that any increased activity was in the horizontal dimension, and indeed salmon sharks are frequently observed rapidly pursuing salmon in shallow surface waters (authors, personal observations).

The behavioral shift from B1 to B2 during autumn coincides temporally with the end of the salmon runs. This suggests that the foraging ecology of the tagged salmon sharks shifted from one focused primarily on aggregating salmon to one that capitalizes on other abundant prey items or a wider variety of prey. It is important to note that these results for B1 are primarily applicable to sharks that aggregate in PWS or other bays during the summer months to feed on salmon.

**Seasonal shifts in depth distribution: behavioral mode 2**

After the salmon runs end, the salmon shark aggregations disperse and tagged sharks spent more time in the neritic habitats between Kodiak Island and PWS as water temperatures cooled and the water column became less stratified. Their behavior shifted from being surface-oriented to having a strongly diel pattern during B2 (autumn) that is typical of diel vertical migration (DVM). This shift in salmon shark behavior suggests that sharks started foraging on prey items that exhibit diel vertical migration, which is common to a large number of marine organisms (Roper and Young 1975; Neilson and Perry 1990; Hays 1996). Diel vertical migration has been observed in a number of elasmobranchs, including the salmon shark’s congener, the porbeagle (Pade et al. 2009), and has typically been associated with the tracking of prey (Weng and Block 2004; Graham et al. 2006; Shepard et al. 2006). Hulbert et al. (2005) and Weng et al. (2005) showed a general bimodal depth distribution in salmon sharks during the autumn and winter. Although these patterns were not specifically addressed there, they likely reflect the diel pattern that we have described.

Although the diet of salmon sharks in coastal Alaska outside of the period of the summer salmon runs has not been described, there are a variety of organisms known to be consumed by salmon sharks that also exhibit DVM, including Pacific herring (Hay and McCarter 1997; Mackinson 1999), capelin (*Mallotus villosus*) (Mowbray 2002; Wilson et al. 2003), pollock (*Brodeur and Wilson 1996a; Adams et al. 2007; Adams et al. 2009), salmon (Walker et al. 2007), and squid (*Teuthoidea*) (Roper and Young 1975; Watanabe et al. 2006). Salmon exhibit DVM; however, the extent of their vertical movements is much more limited and primarily restricted to the upper 20–40 m (Walker et al. 2006), suggesting that this behavior is not primarily related to salmon. In addition, salmon (especially pink, chum, and sockeye) generally move offshore during the autumn to more oligotrophic waters where they remain before moving back inshore during the spring (Nagasawa 2000; Quinn 2005), so their geographic distribution may overlap with salmon sharks in neritic habitats less during the autumn and winter.

Walleye pollock exhibit DVM and are likely an important forage species for salmon sharks in neritic habitats through-
out the year, especially during the autumn, winter, and spring (B2 and B3). Pollock are known to vertically migrate from deeper diurnal depths to shallow nocturnal depths to forage (Brodeur and Wilson 1996a; Wilson et al. 2003; Adams et al. 2009). In the GOA, juvenile pollock rise in the water column at night to form diffuse layers concentrated at shallow depths (10–40 m) to forage (Brodeur and Wilson 1996a; Adams et al. 2007) and descend to deeper depths (around 90–150 m) in the daytime where they form tight ball-like aggregations (Brodeur and Wilson 1996a; Wilson et al. 2003), likely as an antipredation tactic (Brodeur and Wilson 1996b). Although adults vertically migrate at times (Miyashita et al. 2004; Adams et al. 2007, 2009), it is believed that they are primarily found in loose demersal aggregations throughout the day (Wilson et al. 2003). Both adults and juveniles generally remain within 30 m of the bottom during the day, though juveniles typically are shallower than the adults (Brodeur and Wilson 1996a; Wilson et al. 2003). These patterns of depth distribution are remarkably similar to those observed in the tagged salmon sharks.

The likely importance of pollock to salmon sharks throughout the year is supported by the fact that most of the reported nontarget catch of salmon sharks is in the commercial pollock fishery (Tribuzio et al. 2008). Approximately 73% of the total reported nontarget catch of salmon sharks in the GOA between 1997 and 2008 was in the pollock fishery (yearly average, 78%; minimum, 65%; maximum, 98%). An estimated 357.2 tonnes of salmon sharks were caught between 1997 and 2008 in pelagic pollock trawls, accounting for 57% of the total reported salmon shark catch in commercial fisheries during that period (yearly average, 59%; minimum, 12%; maximum, 98%). Bottom pollock trawls caught an estimated 102.4 tonnes of salmon sharks between 1997 and 2008, or 16% of the total reported catch (yearly average, 19%; minimum, 0%; maximum, 66%) (Tribuzio et al. 2008).

Further evidence that salmon sharks forage on pollock is that their daytime focal depths during B2 and B3 were similar to the depth of trawls that caught salmon sharks as nontarget catch in commercial fisheries (primarily the pollock fishery). Based on National Marine Fisheries Service (NMFS) Alaska groundfish observer data from the GOA, the average fishing depth of commercial pelagic trawls (aggregated by NMFS area and quarter and weighted by number of hauls) between 1993 and 2009 in which salmon sharks were caught was 135 m (minimum, 52 m; maximum, 249 m), whereas the average depth of bottom trawls in which salmon sharks were caught was 137 m (minimum, 65 m; maximum, 241 m) (Ren Narita, Fisheries Monitoring and Analysis Division, NOAA-NMFS, Alaska Fisheries Science Center, 7600 Sand Point Way N.E., Building 4, Seattle, WA 98115, USA, personal communication, 2009). In addition, a female shark (197 cm FL) tagged during this project was recaptured together with a male salmon shark (186 cm FL) in Shelikof Strait in March 2008 by the NOAA ship OScAR DsYSON in a research pollock trawl (Abigail McCarthy, Resource Assessment and Conservation Engineering Division, NOAA-NMFS, Alaska Fisheries Science Center, 7600 Sand Point Way N.E., Building 4, Seattle, WA 98115, USA, personal communication, 2008). The depth of this trawl (150 m in 4.3 °C water) was similar to the depths at which salmon sharks concentrated during the day during B2 and B3.

Other potential prey species that exhibit DVM and are known to be fed upon by salmon sharks include Pacific herring. Salmon sharks forage extensively on Pacific herring at times (Blagoderov 1994; Hulbert et al. 2005) and are in fact known as “herring sharks” in Russia (Blagoderov 1993). Indeed, the tag on shark 571 popped off inside Yakutat Bay in mid-February in the middle of one of the largest herring aggregations in recent memory (Geoff Widdows, Sea Raven Charters, P.O. Box 342, Yakutat, AK 99968, USA, personal communication, 2008). Pacific herring also exhibit DVM (Hay and McCarter 1997; Mackinson 1999; Nilsson et al. 2003). Capelin follow a similar vertical migration pattern as juvenile pollock and often are mixed together with dispersed layers of pollock (Brown 2002; Wilson et al. 2003). Cephalopods are well known vertical migrants (Roper and Young 1975; Watanabe et al. 2006), and salmon sharks are known to forage intensively on them in oceanic (Kubodera et al. 2007) and coastal (Hulbert et al. 2005) habitats. Stomach contents of salmon sharks caught in spring and early summer as they come into PWS from the GOA were dominated by squid (K.J. Goldman, unpublished data).

Shark 571 did not exhibit rapid vertical movements at its daytime focal depths but exhibited an increased vertical displacement rate above and below its focal depths. It is possible that this reflects foraging behavior such as pursuit of demersal prey up into the water column or down to the bottom. Alternatively, the increased vertical displacement rate above daytime focal depths may reflect active searching of the water column, and rapid movements during deep dives could represent dives to consume benthic prey.

Whether or not salmon sharks are following particular vertically migrating prey, following the vertically migrating assemblage, or accessing different prey at different times of the day is unclear and impossible to ascertain from tag data alone. It is likely that they forage on a diversity of prey organisms, although some prey such as pollock, herring, and squid are likely of increased importance. The frequency with which salmon sharks and squid are caught as nontarget catch in the pollock fishery indicates that these three species often co-occur, further evidence that squid and pollock are likely important prey species for salmon sharks during B2 and B3.

Seasonal shifts in depth distribution: behavioral mode 3

During B3 (winter and spring), tagged salmon sharks still primarily occurred in neritic habitats of central Alaska in a largely unstratified, very cold ocean that often had temperature inversions. During B3, sharks spent the least amount of time at very shallow depths relative to B1 and B2 (hence the lack of Argos detections during winter and spring), and sharks used the widest range of depths at night. The shift in salmon shark depth distribution during B3 may be attributable to physiological limitations in the shark and (or) a shift in the distribution of prey.

The coldest temperatures (as low as 2.5 °C) experienced by salmon sharks were primarily in the surface inversion layer during the winter and spring, when salmon sharks used shallow habitats the least and overall occupied deeper depths, suggesting that thermal physiological limitations may become a factor during this period. Shallow waters (<50 m) reach their lowest temperatures (<5 °C) from January–April, when temperatures could be as much as ~1–2 °C colder than those...
that occur at deeper depths (Royer 2005). Thus the increased use of deeper depths during the period of temperature inversions suggests that warmer waters at depth may provide a limited thermal refuge for salmon sharks (or their prey) during this period. Paust and Smith (1989) suggested that salmon sharks may be found along with other epipelagic organisms in thermal refuges beneath cold surface waters during the winter.

In addition to possible physiological limitations, the spatial and vertical distribution of prey likely changes during B3 in response to changing oceanographic conditions as ectothermic species would be more sensitive to temperature changes than salmon sharks. Although pollock exhibit some degree of DVM throughout the year (Adams et al. 2007, 2009), the degree of DVM appears to be reduced during the winter and spring as pollock remain closer to the bottom throughout the day and are generally found in deeper waters (Brodeur and Wilson 1996a). Overall, the nearshore demersal fish assemblage moves to deeper waters during the winter (Mundy and Hollowed 2005).

Despite the increase in nighttime depth distribution, shark 571 moved at a relatively steady vertical rate through the water column, although depth distribution and vertical displacement rate during the day generally followed a similar pattern as in B2. This may indicate foraging on a prey field that is more dispersed throughout the water column during the night. This might occur following a reduction in vertical migration in prey such as occurs in pollock. During the day, salmon sharks would still have access to demersal aggregations of prey.

Why some female salmon sharks overwinter in Alaska and do not migrate to southern regions is unclear. It has been suggested that female salmon sharks migrate to lower latitudes to give birth (Nagawasa 1998; Weng et al. 2008). If this is the case, it is possible that female sharks that remain at high latitudes throughout the year (e.g., shark 087) do not migrate because they are nonreproductive (immature, in a reproductive resting stage, or have been unsuccessful in mating). One would expect sharks that are not bound by reproductive (i.e., the need to migrate to pup and (or) mate) or physiological (i.e., need to leave high latitudes because of cold temperatures) constraints to utilize regions that provide them with high-quality resources.

The fact that some salmon sharks exploit the highly productive cold waters of the North Pacific throughout the year indicates that the amount of energy available to them in productive boreal waters compensates for the increased metabolic cost associated with using these cold habitats during the winter and spring. By being able to take advantage of locally available and abundant prey such as salmon, pollock, and squid, the sharks are able to successfully exploit a seasonally shifting prey field across a range of oceanographic conditions. This opportunistic foraging strategy, coupled with their endothermic capacity and cardiac physiology, allows salmon sharks to successfully exploit boreal waters throughout the year. Their unique anatomy and physiology is likely a great advantage when foraging on ectothermic prey and competing with other ectothermic predators in cold temperatures, and indeed, the endothermic capability of salmon sharks is believed to underlie their evolutionary expansion into boreal waters (Block and Finnerty 1994; Goldman et al. 2004; Weng et al. 2005). Their ability to use boreal waters gives them access to an abundance of prey and may also free them of competitive constraints that they may experience at lower latitudes from other large predatory fishes and elasmobranchs that are unable to so efficiently use these cold habitats because of their lack of endothermic capacity.

The spatial and vertical distribution of salmon sharks in the GOA overlap with a number of commercially important species, and as a result, the species is commonly caught as nontarget catch in a number of commercial fisheries (Camhi 1999; Goldman and Musick 2008). Although the impact of this removal on their population is unclear, it may be an important source of mortality. Our results suggest that given the consistent seasonal patterns of geographic and vertical distribution of salmon sharks in the GOA, measures taken to reduce gear interaction may be effective at limiting the number of sharks caught as nontarget catch and reduce the impact of commercial fishing on salmon shark populations.

Given the susceptibility of sharks to overexploitation (Musick et al. 2000) and the important ecological role that salmon sharks likely play in North Pacific ecosystems as the largest apex predator in these systems (Goldman and Musick 2008), they need to be managed responsibly. Furthermore, their possible role as important sources of natural mortality to a variety of commercially important species should be assessed and accounted for in stock assessments and management plans.

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