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# Seasonal foraging movements and migratory patterns of female *Lamna ditropis* tagged in Prince William Sound, Alaska

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Conventional and electronic tags were used to investigate social segregation, distribution, movements and migrations of salmon sharks *Lamna ditropis* in Prince William Sound, Alaska. Sixteen salmon sharks were tagged with satellite transmitters and 246 with conventional tags following capture, and were then released in Prince William Sound during summer 1999 to 2001. Most salmon sharks sexed during the study were female (95%), suggesting a high degree of sexual segregation in the region. Salmon sharks congregated at adult Pacific salmon *Oncorhynchus* spp. migration routes and in bays near Pacific salmon spawning grounds in Prince William Sound during July and August. Adult Pacific salmon were the principal prey in 51 salmon shark stomachs collected during summer months in Prince William Sound, but the fish appeared to be opportunistic predators and consumed sablefish *Anoplopoma fimbria*, gadids, Pacific herring *Clupea pallasi*, rockfish *Sebastes* spp. and squid (Teuthoidea) even when adult Pacific salmon were locally abundant. As Pacific salmon migrations declined in late summer, the salmon sharks dispersed; some continued to forage in Prince William Sound and the Gulf of Alaska into autumn and winter months, while others rapidly moved south-east thousands of kilometres toward the west coasts of Canada and the U.S. Three movement modes are proposed to explain the movement patterns observed in the Gulf of Alaska and eastern North Pacific Ocean: 'focal foraging' movements, 'foraging dispersals' and 'direct migrations'. Patterns of salmon shark movement are possibly explained by spatio-temporal changes in prey quality and density, an energetic trade-off between prey availability and water temperature, intra-specific competition for food and reproductive success. Transmissions from the electronic tags also provided data on depth and water temperatures experienced by the salmon sharks. The fish ranged from the surface to a depth of 668 m, encountered water temperatures from 4·0 to 16·8° C and generally spent the most time above 40 m depth and between 6 and 14° C (60 and 73%, respectively). 

Key words: Alaska; *Lamna ditropis*; migration; movements; salmon shark; satellite tagging.

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## INTRODUCTION

The salmon shark *Lamna ditropis* Hubbs & Follett is widely distributed in coastal and oceanic environments of the subarctic and temperate North Pacific Ocean. This species ranges across the North Pacific Ocean from the Bering Sea and the Sea of Okhotsk to the Sea of Japan in the western Pacific, and from the Gulf of Alaska to southern Baja California, Mexico, in the eastern Pacific (Hart, 1973; Tanaka, 1980; Compagno, 1984; Brodeur, 1988; Blagoderov, 1994; Nagasawa, 1998; Mecklenburg *et al.*, 2002; Goldman, 2003).

Salmon sharks belong to the family Lamnidae, together with four other species: the white shark *Carcharodon carcharias* (L.), the shortfin mako *Isurus oxyrinchus* Rafinesque, the longfin mako *Isurus paucus* Guitart Manday and the porbeagle *Lamna nasus* (Bonnaterre). The capacity to elevate body temperature (endothermy) has been documented for all lamnids (Lowe & Goldman, 2001) and salmon sharks are ranked as the most endothermic in this family (Tubbesing & Block, 2000). Whether *L. ditropis* is able to maintain high and uniform temperature values regardless of changes in ambient temperature (the home-othermy hypothesis of Lowe & Goldman, 2001), however, requires further investigation.

In the central and western North Pacific Ocean, *L. ditropis* migrates north in spring and south in autumn (Tanaka, 1980; Blagoderov, 1994; Nagasawa, 1998). In winter they concentrate in the coastal waters of Honshu, Japan, where they are thought to breed (Blagoderov, 1994). High salmon shark concentrations in more northern latitudes in spring and summer have been observed to coincide in time and space with Pacific salmon *Oncorhynchus* spp. and Japanese pilchard *Sardinops melanosticta* (Temminck & Schlegel) aggregations (Sano, 1960; Blagoderov, 1994; Nagasawa, 1998). In the eastern North Pacific, however, little is known about the migratory patterns of this apex predator. Furthermore, the degree of intermixing between salmon sharks from the eastern and western sides of the North Pacific is unknown.

Sexual and life-stage (age- or length-dependent) segregation patterns of salmon sharks have been documented for both sides of the North Pacific Ocean (Sano, 1962; Tanaka, 1980; Nagasawa, 1998; Goldman, 2003). Patterns of sexual segregation increase with increasing latitude (Sano, 1962; Nagasawa, 1998). The sex ratio is dominated by males in the western North Pacific (Sano, 1962; Nagasawa, 1998), and females apparently predominate in the eastern North Pacific (Goldman, 2003). Adult salmon sharks are distributed north of the subarctic boundary (Nakano & Nagasawa, 1996), with the largest salmon sharks in the western North Pacific found in the Sea of Okhotsk and Bering Sea (Blagoderov, 1994) and in Alaskan waters in the eastern North Pacific (Goldman, 2003). Small and medium-sized salmon sharks with a relatively balanced sex ratio predominate in the southern extent of the salmon shark range in the western North Pacific Ocean (Nagasawa, 1998). The open waters of the North Pacific Ocean adjacent to the highly productive subarctic boundary and transitional domain (Pearcy, 1991) are probably salmon shark parturition and nursery grounds (Blagoderov, 1994; Nakano & Nagasawa, 1996; Nagasawa, 1998).

The movement patterns of *L. ditropis* in the eastern North Pacific are still unknown. The species has been noted to occur in the surface waters of the Gulf of Alaska during all seasons of the year, without obvious seasonal changes in its distribution (Neave & Hanavan, 1960). Large aggregations have been observed to overlap in time and space with summer migrations of Pacific salmon in Prince William Sound, Alaska, and are suspected to disperse as Pacific salmon runs decline in autumn (L. Hulbert, pers. obs.). This suggests that seasonal foraging migrations into prey-rich waters of Alaska might be a key feature of the life-history of the salmon shark in the eastern North Pacific Ocean. Scientific information on ecological aspects of salmon shark life-history, such as residency times in Prince William Sound, foraging movement patterns, habitat preferences and large-scale migrations is required for management and conservation of the species in the eastern North Pacific Ocean.

This study investigated the movements and habitat of salmon sharks tagged in Prince William Sound as they foraged during summer. Conventional and electronic tags were used to collect information about social segregation, movement patterns, and depth and thermal preferences of *L. ditropis* in the eastern North Pacific.

## MATERIALS AND METHODS

### STUDY AREA

Salmon shark field sampling took place in south-east Prince William Sound at Port Gravina (60°39′ N; 146°22′ W), and at Hinchinbrook Entrance (60°21′ N; 146°45′ W) (Fig. 1). Port Gravina is one of many estuarine embayments in Prince William Sound where adult Pacific salmon aggregate in summer before entering their natal streams. Hinchinbrook Entrance is one of four narrow migration routes through which adult Pacific salmon must pass as they move into Prince William Sound from the Gulf of Alaska.

### DIET COMPOSITION

Twenty of 51 salmon shark stomachs were collected opportunistically from port sampling operations. They were frozen and shipped to Juneau for analysis. Stomachs were collected from 31 specimens during field sampling operations. All salmon sharks sampled for diet were caught during July and August in Prince William Sound. The contents of each stomach were identified to the highest practical taxonomic level, enumerated and weighed when possible.

### TAGGING

Purse seine and hand line gear was used to capture individual salmon sharks aboard the chartered fishing vessel F/V *Pagan* during a pilot study in July 1998, and aboard the chartered Alaska Department of Fish and Game (ADF&G) research vessel R/V *Montague* during sampling in July 1999 to 2001. The purse seine measured 200 × 20 m and had 25 mm stretched mesh. Hand lines consisted of two weighted 50 m long, 0·95 cm diameter polypropylene lines with single #3 (16/0) circle hooks attached to 2 m lengths of galvanized steel cable and baited with Pacific herring *Clupea pallasi* Valenciennes.

The number and type of tags used on salmon sharks between July 1998 and August 2002 are given in Table I. Movement and biological data collected from the tagging study varied with the type of tags used. Movement data from conventional tags were dependent on rare and opportunistic recaptures from commercial and recreational fishermen and only provided movement data to single-point locations recorded by the fishermen. In

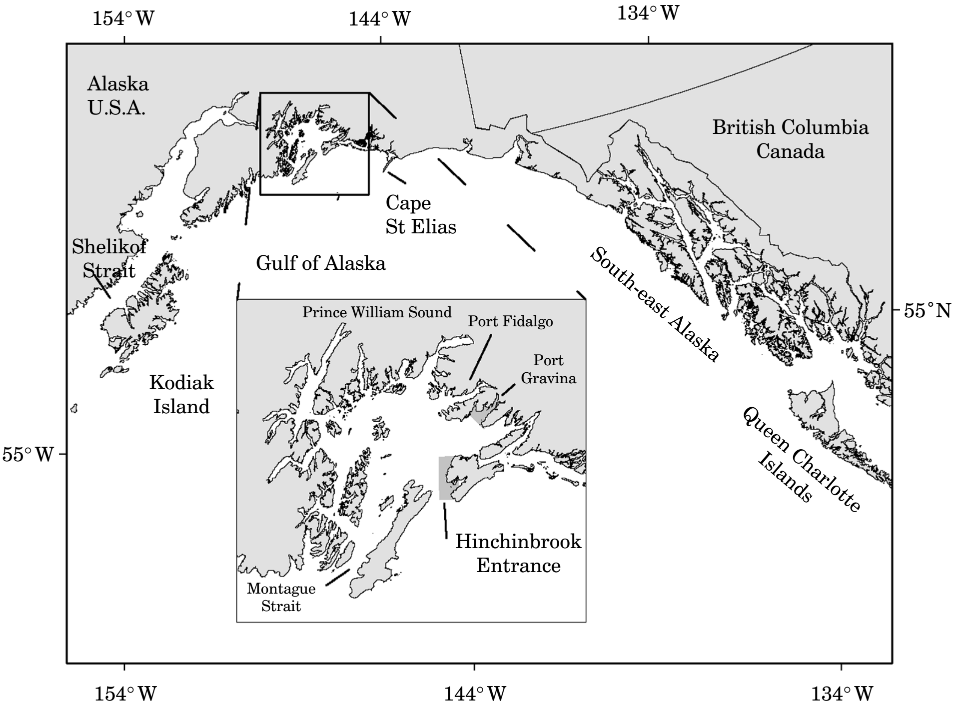


FIG. 1. Location of the salmon shark study (Port Gravina and Hinchinbrook Entrance, Prince William Sound, Alaska).

contrast, movement data from three satellite tag types provided fishery-independent final location data, variously supplemented with multiple intermediate locations and archived ambient environmental data.

## *Conventional tags*

A collaborative effort to deploy conventional tags was organized with the support of ADF&G and the Virginia Institute of Marine Science (VIMS). During the joint tagging effort from 1998 to 2002, 246 salmon sharks were tagged with either dart tags (FH69

TABLE I. Type and number of tags deployed on *Lamna ditropis* in Prince William Sound, Alaska, during 1998–2002

| Tag type | 1998 | 1999 | 2000 | 2001 | 2002 | Total |
|---|---|---|---|---|---|---|
| Conventional tags | | | | | | |
| Dart | 15 | 97 | 101 | 7 | 13 | 233 |
| Rototags | 0 | 0 | 13 | 0 | 0 | 13 |
| Satellite tags | | | | | | |
| PAT | 0 | 2 | 0 | 8 | 0 | 10 |
| KiwiSat | 0 | 0 | 3 | 0 | 0 | 3 |
| SPOT2 | 0 | 0 | 0 | 3 | 0 | 3 |

Stainless Steel Dart tags; FLOY®, Seattle, WA U.S.A.) or Rototags (double dairy tag, National Band & Tags, Newport, KY, U.S.A.). Dart tags were implanted in the back musculature near the base of the first dorsal fin, while Rototags were inserted through the first dorsal fin. During field operations conventional tags were attached after the salmon shark was lifted aboard, sexed and measured (precaudal length, $L_{Pc}$). Tags were also deployed opportunistically in the water alongside the vessel. In this case sex and measurements were collected when possible.

### *Satellite tags*

Sixteen salmon sharks were tagged with satellite transmitters during the study. Ten fish were tagged with pop-up archival transmitting (PAT) tags (Wildlife Computers, Woodinville, WA, U.S.A.), three with KiwiSat 101 position-only tags (Sirtrack, Havelock North, New Zealand) and three with Wildlife Computers SPOT2 position-only tags. All satellite tags were attached to the salmon sharks after they were lifted aboard in a cradle specifically designed for this purpose. A continuous flow of fresh salt water was circulated through the gills while the tag was deployed. Sex, $L_{Pc}$ and mass were recorded when time and circumstances permitted.

Data transmitted to the Argos Data Collection and Location System (DCLS) were used to determine geographic movements, vertical movement behaviour and temperature preferences of salmon sharks tagged with satellite tags and released at Port Gravina and Hinchinbrook Entrance. All satellite tags used by the project were programmed to transmit with a 45 s repetition rate. The Argos DCLS recorded the date and time of each signal received by the satellite and calculated a location based on Doppler shift whenever sufficient uplinks were received during a satellite overpass. For analysis and presentation of data, dates and times were converted from Greenwich Mean Time (GMT) to Alaska Standard Time by subtracting 9 h. Location records and associated data were plotted using ArcView® geographic information system (GIS) software. Large distances reported in the results were estimated using a great-circle distance calculator.

Wildlife Computers pop-up archival transmitting (PAT) tags provide fishery-independent straight-line distance travelled from release location to a single endpoint location, and depth and temperature data archived for up to a year. Depth and temperature are measured to within 0·5 m and 0·05° C resolution. While the PAT tags record and archive depth and temperature measurements each minute, this minute data are only accessible if the tag itself is recovered. The depth and temperature measurements recovered during this study were summarized data transmitted to the Argos DCLS: daily minimums and maximums, and the proportion of daily time (calibrated to Alaska Standard Time) the salmon sharks spent within 12-each user-defined depth and temperature ranges. The upper limits of time-at-depth intervals were set at 0, 2, 4, 10, 20, 40, 60, 80, 100, 200, 300 and 500 m. The upper limits of time-at-temperature intervals were set at 2, 4, 6, 8, 10, 12, 14, 16, 18, 20 and 22° C.

The PAT tags are cylindrical tags (17·5 × 2 cm) that were tethered by 12 cm long, 113 kg test monofilament to two stainless steel darts. The darts, modified from FLOY FH69 tags, were implanted in the back musculature near the base of the first dorsal fin. The tags release from the tether at a pre-programmed date and time by initiating corrosion of a stainless steel linkage. After release, it floats to the surface and begins transmitting continuously to Argos satellites for the duration of the battery life. The proportion of days of summarized environmental data actually transmitted from each PAT tag were affected by battery life, sea state, number of days of data stored and tag orientation in the water (tag transmissions are ineffective when the antennae is horizontal or the tag is dry).

The advantage of Sirtrack KiwiSat tags, and Wildlife Computers SPOT2 tags in comparison with the PAT tags is that the position-only tags can provide multiple positions over time, provided the salmon shark surfaces occasionally and long enough to transmit multiple times within one satellite pass. Hence, the position-only tags are capable of providing a more detailed picture of the geographic movements.

Position-only tags were bolted to the salmon sharks' first dorsal fin using stainless steel Allen-head socket cap screws, nylox nuts and stainless steel and rubber washers. The screw threads were sealed with polyolefin shrink tubing to prevent metal contact with the animal. When the salmon shark surfaces and the tag is exposed to air, a saltwater switch causes the tag to transmit to the Argos satellite system within 200 ms of breaking the surface.

# RESULTS

## SEX AND SIZE COMPOSITION

Within the geographic area sampled during the study (primarily south-east Prince William Sound), 123 of 130 (95%) salmon sharks sexed were female. Mean ± S.D. $L_{Pc}$ of the females was 178 ± 16 cm (range = 146 to 240 cm; $n = 79$) and the mean ± S.D. mass of 18 females was 146 ± 17 kg (range = 115 to 176 kg). Five males had a mean ± S.D. $L_{Pc}$ of 168 ± 13 cm (range = 155 to 186 cm).

## DIET

Of the 51 salmon shark stomachs analysed, adult pink salmon *Oncorhynchus gorbuscha* (Walbaum), chum salmon *Oncorhynchus keta* (Walbaum) and coho salmon *Oncorhynchus kisutch* (Walbaum) were the most important prey as measured by per cent number (35%) and per cent mass (76%; Table II). Teuthoidea squid were the second most important prey by per cent number (30%) and sablefish *Anoplopoma fimbria* (Pallas), were the second most important prey item by per cent mass (11%). Other teleost prey included Pacific herring, rockfish *Sebastes* spp., eulachon *Thaleichthys pacificus* (Richardson), capelin *Mallotus villosus* (Müller), arrowtooth flounder *Atheresthes stomias* (Jordan & Gilbert) and codfishes (Gadidae). Non-teleost prey included squid and spiny dogfish *Squalus acanthias* (L.). All salmon sharks sampled for stomach contents were captured in July and August, during the period of peak Pacific salmon spawning aggregations in the Prince William Sound region.

TABLE II. *Lamna ditropis* diet from the contents of 51 stomachs collected in Prince William Sound, Alaska, during July and August 1999 to 2001 expressed as per cent number (*N*, %) and per cent mass (*M*, %)

| Prey items | *N*, % | *M*, % |
|---|---|---|
| Pacific salmon *Oncorhynchus* spp. | 35·2 | 76·1 |
| Squid (Teuthoidea) | 29·6 | 4·0 |
| Sablefish *Anoplopoma fimbria* | 12·7 | 11·4 |
| Pacific herring *Clupea pallasi* | 8·5 | 1·1 |
| Rockfish *Sebastes* spp. | 4·2 | 4·8 |
| Eulachon *Thaleichthys pacificus* | 4·2 | 0·3 |
| Capelin *Mallotus villosus* | 1·4 | 0·1 |
| Spiny dogfish *Squalus acanthias* | 1·4 | 0·8 |
| Arrowtooth flounder *Atheresthes stomias* | 1·4 | 0·5 |
| Codfishes (Gadidae) | 1·4 | 0·8 |

## MOVEMENTS

Movement data were acquired from 17 salmon sharks: 13 of 16 (81%) satellite tags, and the recapture of four of 246 (2%) conventionally tagged salmon sharks. The recovery information and movement statistics for these 17 sharks are given in Table III. Movement data were recovered within the first 7 months after release for 14 salmon sharks, whereas the other three fish were recaptured within 50 km of their release locations in Prince William Sound by sport fishermen after 1·0, 2·9 and 3·0 years at liberty.

### *Salmon shark movements out of Prince William Sound (<7 months at liberty)*

Sharks A, B, C, D and E moved rapidly to the south-east shortly after release (Fig. 2 and Table III). Shark A provided 94 Argos satellite-derived locations and averaged 58 km day$^{-1}$ across 22 days, and travelled 1277 km during the period the tag transmitted. The salmon shark's final position on 9 August was located 120 km west of the southern tip of the Queen Charlotte Islands in British Columbia, Canada. Fish B (the only male salmon shark tagged with a satellite transmitter) provided 26 Argos satellite derived locations and averaged 30 km

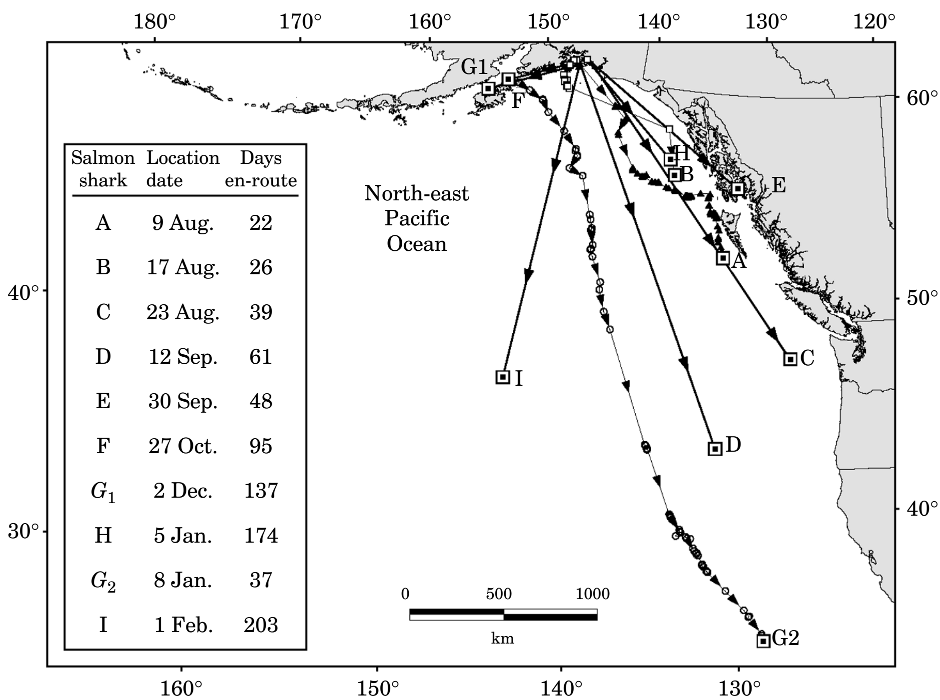


FIG. 2. Large-scale movements of salmon sharks tagged in Prince William Sound during July 1999 to 2001. Location co-ordinates are from Global Positioning System at time of release, recapture location (fish E), and Argos satellite-derived final positions (fish A, B, C, D, F, G, H and I). Multiple intermediate locations from SPOT2 tags are indicated for fish A (▲), B (□) and G (○). The G1 and G2 positions indicated are fish G locations following 137 days of meandering movements in the Gulf of Alaska, and the final location obtained from tag transmissions following 37 days of 'directed movement' to the south, respectively. →, net direction of movement.

TABLE III. Tag types, release and final dates, and movement statistics for individual *Lamna ditropis* tagged in Prince William Sound, Alaska, that (1) emigrated from Prince William Sound and were at liberty for <7 months, (2) were local to Prince William Sound and were at liberty for <4 months, or (3) were local to Prince William Sound and at liberty for >1 year. All but salmon shark B were female

| Salmon shark | $L_{PC}$ (cm) | Tag type | Release date | Final date | Straight-line distance (km) | Locations transmitted | Time elapsed (days) | Mean distance per day (km) |
|---|---|---|---|---|---|---|---|---|
| Salmon shark movements out of Prince William Sound: <7 months at liberty | | | | | | | | |
| A | 162 | SPOT2 | 18 July 2001 | 9 August 2001 | 1277 | 94 | 22 | 58 |
| B | 155 | KiwiSat | 22 July 2000 | 17 August 2000 | 769 | 26 | 26 | 30 |
| C | 150 | PAT | 15 July 2001 | 23 August 2001 | 1917 | 1 | 39 | 49 |
| D | 165 | PAT | 13 July 2001 | 12 September 2001 | 2163 | 1 | 61 | 35 |
| E | No length recorded | Dart | 26 July 1999 | 12 September 1999 | 1049 | – | 48 | 22 |
| F | 169 | PAT | 24 July 1999 | 27 October 1999 | 436 | 1 | 95 | 5 |
| $G_1$ | 240 | SPOT2 | 18 July 2001 | 2 December 2001 | 505 | 48 | 137 | 4 |
| $G_2$ | 240 | SPOT2 | 2 December 2001* | 8 January 2002 | 3271 | 73 | 37 | 88 |
| H | 187 | PAT | 15 July 2001 | 5 January 2002 | 692 | 1 | 174 | 4 |
| I | 165 | PAT | 13 July 2001 | 1 February 2002 | 1714 | 1 | 203 | 8 |
| Salmon shark movements within Prince William Sound: <4 months at liberty | | | | | | | | |
| J | 192 | SPOT2 | 17 July 2001 | 15 August 2001 | 9 | 49 | 29 | 0·24 |
| K | 185 | KiwiSat | 20 July 2000 | 23 August 2000 | 7 | 3 | 34 | 0·21 |
| **L | 170 | KiwiSat | 20 July 2000 | 17 September 2000 | 55 (6) | 51 (49) | 60 (52) | 0·98 (0·11) |
| M | 160 | PAT | 24 July 1999 | 30 September 1999 | 76 | 1 | 68 | 1·12 |
| N | 190 | PAT | 13 July 2001 | 1 November 2001 | 98 | 1 | 111 | 0·88 |
| Salmon shark recoveries in Prince William Sound: >12 months at liberty | | | | | | | | |
| O | 210 | Dart | 22 July 1999 | 6 July 2002 | 43 | – | 1080 | – |
| P | 207 | Dart | 21 July 1999 | 20 July 2002 | 46 | – | 1095 | – |
| Q | No length recorded | Dart | 29 August 2000 | 8 September 2001 | 49 | – | 375 | – |

*'Release date' for $G_2$ was the date just prior to the start of a 3271 km movement to the south.
**L, Numbers in parentheses represent data for movements within Port Gravina, Prince William Sound, for the first 52 days after release.
$L_{Pc}$, precaudal length.

day$^{-1}$ (straight-line distance) across 26 days, and travelled 769 km. The fish left Port Gravina shortly after release, moved out of Prince William Sound through Montague Strait, and was located 165 km off the coast of central south-east Alaska when the last transmission was received on 17 August. Fish C traversed 1917 km in 39 days and averaged 49 km day$^{-1}$ overall, fish D traversed 2163 km in 61 days and averaged 35 km day$^{-1}$ overall, and fish E traversed 1049 km in 48 days, averaging 22 km day$^{-1}$ overall.

Fish F and H dispersed away from capture locations in Prince William Sound but were located in the Gulf of Alaska after 95 and 174 days at liberty, respectively (Fig. 2 and Table III). The final position of fish F was located near Kodiak Island in late October, 436 km south-west of its release location. After nearly 6 months, fish H was located 150 km west of central south-east Alaska, 700 km south-east of its release location in Prince William Sound. Fish I was located 1800 km off the coast of Oregon and 1714 km south of its release location in Prince William Sound on 1 February, 203 days after release.

Two phases of movement were discerned for fish G: phase one movements (designated as $G_1$) meandered between Prince William Sound and Shelikof Strait in the northern Gulf of Alaska during the first 137 days after release, and phase two movements (designated as $G_2$) followed a highly linear track to the south during the last 37 days of transmissions from the salmon shark (Table III and Figs 2 and 3). Forty-eight locations were recovered during phase one across 137

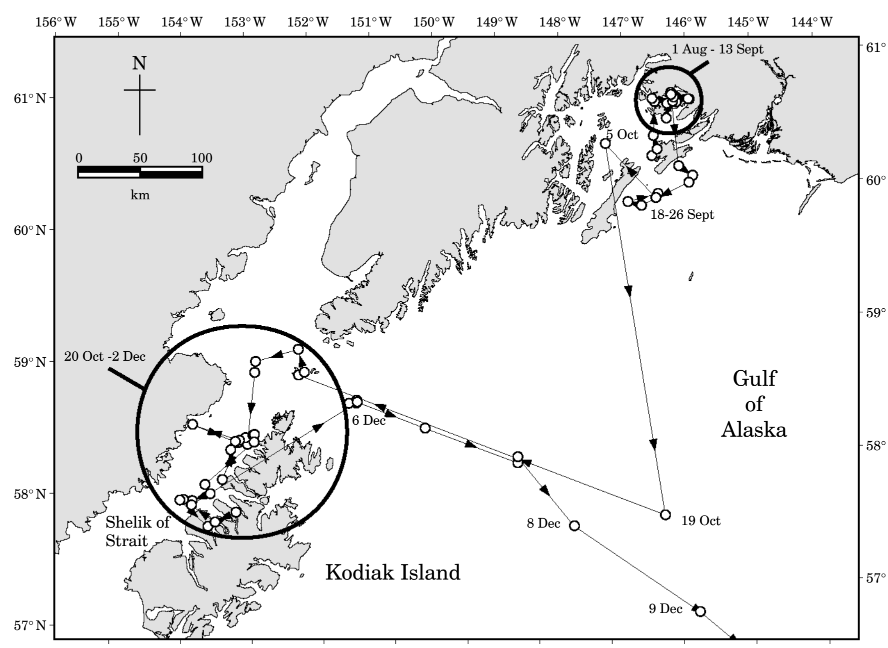


FIG. 3. Salmon shark G foraging dispersal movements. The figure shows detail of fish G movements in the northern extent of its range during autumn and winter 2001. The data are Argos satellite-derived locations from SPOT2 tag transmissions. Fish G was released at Hinchinbrook Entrance, Prince William Sound, on 18 July 2001. ○, locations (lines connect locations in chronological order).

days and 500 km from Prince William Sound south-west to Shelikof Strait (Fig. 3). Shortly after release, the salmon shark moved from Hinchinbrook Entrance to the Port Fidalgo and Port Gravina region where it spent *c.* 1·5 months. By November, the salmon shark had moved to Shelikof Strait where it spent *c.* 1 month in an area utilized by overwintering Pacific herring (M. Carls, pers. comm.,). Phase 2 began in early December when fish G left Shelikof Strait and began a 'directed movement' to the south. During this phase of movement 73 location fixes were recovered while the salmon shark traversed 3271 km in 37 days at an average rate of 88 straight-line km $day^{-1}$. When the final transmission was received on 8 January, salmon shark G was located 1000 km due west of Los Angeles, California.

*Salmon shark movements within Prince William Sound (<4 months at liberty)*

Endpoint positions of fish J, K and L were within 10 km of their release locations after 29, 34 and 52 days, respectively (Fig. 4 and Table III). 'Pop-up' positions acquired for fish M and N showed that they were located in Prince

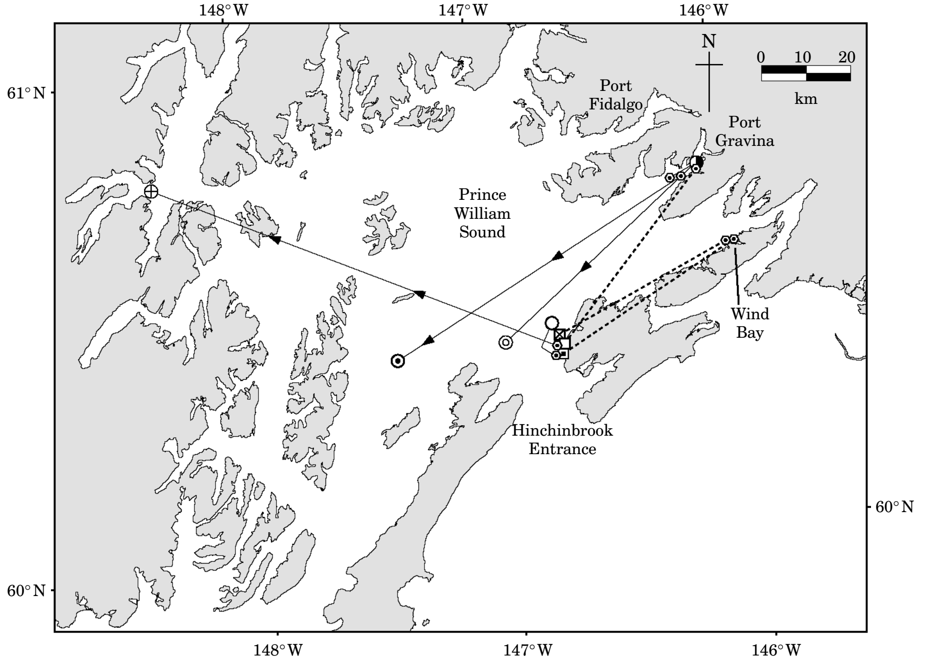


FIG. 4. Salmon shark movements from Argos satellite-derived final locations [fish J (○), K (◑), L (◎), M (⊙) and N (⊕) with 24, 34, 59, 68 and 111 days respectively, at liberty] and conventionally tagged salmon shark recapture locations [fish O (⊠), P (▣) and Q (□) with 35·5, 36·0 and 12·4 months respectively at liberty] within Prince William Sound. →, overall direction of movement of satellite-tagged salmon sharks from the release locations; .. . . . , connection between release (⊙) and recapture locations of conventionally-tagged salmon sharks.

William Sound on 30 September and 1 November, but had dispersed 76 and 98 km from release locations after 68 and 111 days, respectively.

From fish J, 49 position fixes were recovered within 13 km of the release location over 29 days. Area of utilization was estimated using a modified 95% minimum convex polygon method (MCP; Morrissey & Gruber, 1993). The area utilized by fish J covered *c.* 83 $km^2$ (95% MCP) at Hinchinbrook Entrance, an adult Pacific salmon migration route (Fig. 5). From fish K, only three location 'fixes' were recovered. The final position on day 34 was in Port Gravina and was within 8 km of the release location. From fish L, 49 location fixes fell within 8 km of the release location in Port Gravina. On day 52 this salmon shark was located 6 km from its release location. Two subsequent locations on days 55 and 60 showed that the salmon shark had left Port Gravina and the final position was near Hinchinbrook Entrance, 55 km from the release location. The area utilized by fish J covered *c.* 33 $km^2$ (95% MCP) in Port Gravina, an area where adult Pacific salmon congregated (Fig. 5).

*Salmon shark recoveries in Prince William Sound (≥12 months at liberty)*

Fish O, P and Q were recaptured by sport fishermen at Hinchinbrook Entrance within 50 km of their release locations after 2·9, 3·0 and 1·0 years at liberty, respectively (Fig. 4 and Table III).

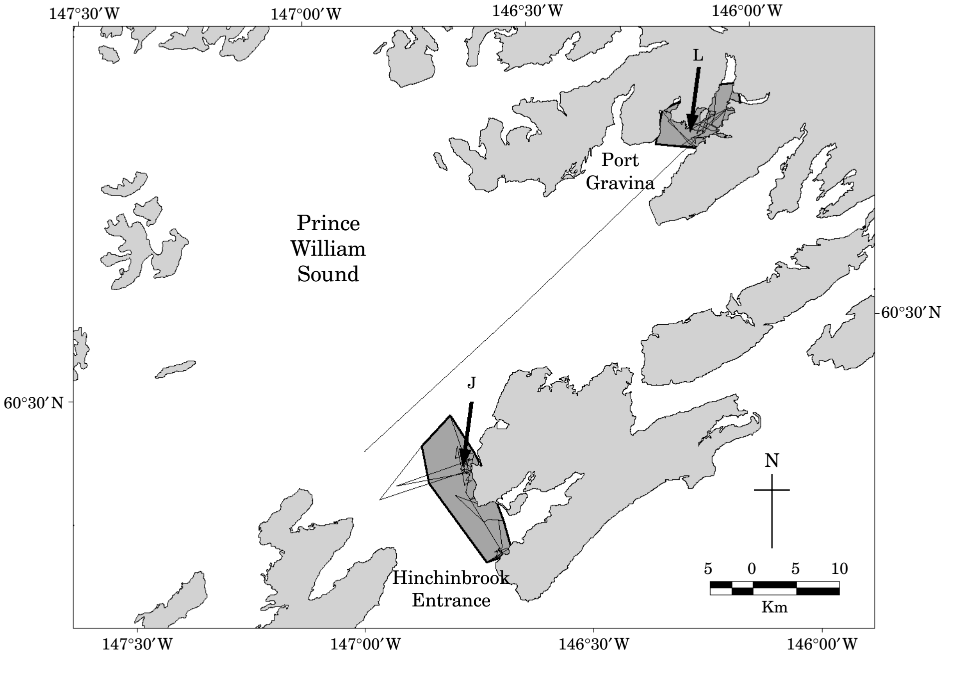


FIG. 5. 'Focal foraging' areas and movements of salmon shark J at Hinchinbrook Entrance from 17 July to 15 August 2001, and salmon shark L in Port Gravina from 20 July to 7 September 2000. Lines connect locations in chronological order, with release locations indicated by J and L. 'Focal foraging' areas (■) were estimated using a modified 95% minimum convex polygon method (Morrissey & Gruber, 1993).

## DEPTH AND TEMPERATURE

Ambient environmental data were collected for five salmon sharks that were tagged with PAT tags and released in Prince William Sound during mid-July. Fish C and D travelled large distances in relatively short periods at an average rate of 49 and 35 km day$^{-1}$, respectively (Fig. 2 and Table III). Both fish were located in the Transitional Domain of the California Current off the Oregon and Washington coast in late summer, and encountered similar well-defined thermal stratification throughout their geographic movements. The vertical movement behaviour of these salmon sharks showed some notable differences (Fig. 6).

Fish C traversed 1917 km in 39 days, after which tag pop-up occurred off the coast of Washington. This salmon shark encountered a pronounced seasonal thermocline during its course of travel, with temperature measurements averaging from 14·5° C at the surface to 7·4° C at 80 m depth (Fig. 6). During the first 10 days after release, fish C descended below the thermocline to depths >100 m on seven (70%) of these days. On the 10th day, fish C attained a maximum depth of 528 m. The salmon shark then remained in thermocline waters above 50 m on 13 of the following 16 days (81%). After this period of inhabiting shallow waters, fish C resumed its frequent incursions to depths below 100 m until tag pop-up. Overall, fish C spent 46% of the time at 0 to 2 m, 46% at 2·5 to 100 m and 8% at 100·5 to 1000 m depth. The overall thermal preferences recorded for fish C were 12·1 to 18·0° C (89%) and 4·1 to 12·0° C (11%).

Fish D traversed 2163 km in 61 days and at the time of tag pop-up was located in oceanic waters off the coast of Oregon (Fig. 2 and Table III). This salmon

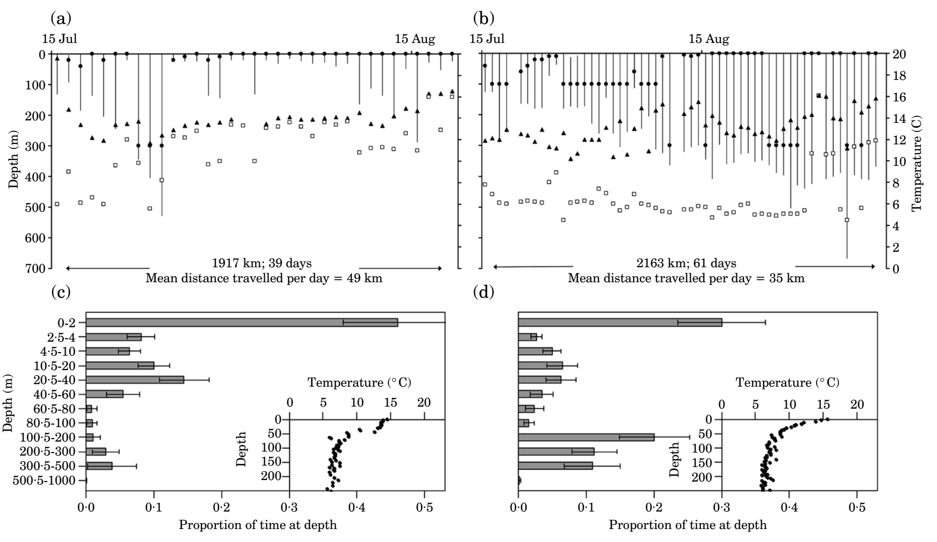


FIG. 6. Daily depth and temperatures encountered by salmon sharks (a) C and (b) D tagged with PAT tags in Port Gravina in mid-July 2001. Solid vertical lines, daily depth range; ●, daily depth mode; ▲, maximum daily temperatures recorded; □, minimum daily temperatures recorded. Histograms of proportion of time (mean ± 95% CI) at depth for fish (c) C and (d) D. Insets in (c) and (d): profiles of depth and temperature from data recorded by the PAT tags.

shark also experienced a pronounced seasonal thermocline, with temperature measurements averaging from 15·7° C at the surface to 7·0° C at 80 m. Fish D descended to depths >200 m on 40 of 61 (65%) days and attained a maximum depth of 668 m (Fig. 6). This is the maximum depth attained by a salmon shark recorded in this study. Like fish C, this salmon shark also spent a large amount of time (30%) in surface waters (0 to 2 m depth). The vertical movement behaviour of fish C and D differed in that fish D consistently crossed the thermocline throughout the period it was monitored. Fish D spent 42% of time in depths of 100 to 1000 m and only 28% in the wide epipelagic depth range of 2·5 to 100 m. This observed pattern indicated that fish D preferred to visit the mesopelagic and surface waters. Overall, the thermal preferences of this salmon shark were 12·1 to 18·0° C (40%) and 4·1 to 12·0° C (60%).

Fish H and I had a relatively slow overall rate of travel to the south, averaging 4 and 8 km day$^{-1}$ for 174 and 203 days, respectively (Fig. 2 and Table III). Although the final position of fish H was located in the Alaska Current off the coast of south-east Alaska, and fish I was located 1500 km to the south-west in the subarctic North Pacific Ocean, both salmon sharks encountered similar well-developed thermal stratification in late summer, and breakdown and collapse of thermal stratification over the course of their movements into autumn and winter months. Their vertical movement behaviour also shows similarities (Fig. 7).

Fish H traversed 700 km in 174 days and was located 150 km west of Baranof Island in south-east Alaska, when tag pop-up occurred on 5 January (Fig. 2). This salmon shark descended to depths >100 m during 81 of 174 (47%) days, attained a maximum depth of 348 m, and experienced temperatures ranging from 5·4 to 17·8° C (Fig. 7). Overall, fish H spent 41 and 53% of the time in water temperatures of 6·1 to 8·0° C and 8·1 to 18·0° C, respectively. The maximal thermal range experienced by this salmon shark in a single day was 10·8° C.

From mid-July to mid-August, fish H experienced a pronounced seasonal thermocline with temperatures averaging from 15·1° C at the surface to 6·1° C at 80 m depth. The salmon shark showed a bimodal preference for depths of 0 to 2 m and 20 to 60 m, where it spent 26 and 47% of the time, respectively; relatively little time was spent between these depths (Fig. 7). During this period, the salmon shark spent 43 and 57% of the time in temperatures of 4·1 to 12·0° C and 12·1 to 18·0° C, respectively. From mid-August to mid-October, fish H experienced the gradual collapse of the seasonal thermocline. Again, a bimodal depth distribution pattern was observed with preference for depths of 0 to 2 m (18%) and 20 to 60 m (38%). Most notably, this salmon shark extended its depth range to deeper waters, spending 25% of the time between 60 and 300 m. With respect to temperature, fish H spent 81% of the time in waters of 8·1 to 16·0° C during this period. From mid-October to early January, fish H encountered a collapsed seasonal thermocline. A bimodal pattern of depth distribution in shallow waters (<60 m depth) was still exhibited. Throughout this period, this salmon shark regularly visited mesopelagic waters (>100 m depth) and spent 12% of the time between 100 and 500 m. The overall thermal preference observed for fish H was 6·1 to 8·0° C (76%).

Fish I traversed 1714 km in 203 days and was located in oceanic waters 1800 km west of the Oregon coast on 5 February (Fig. 2). This salmon shark

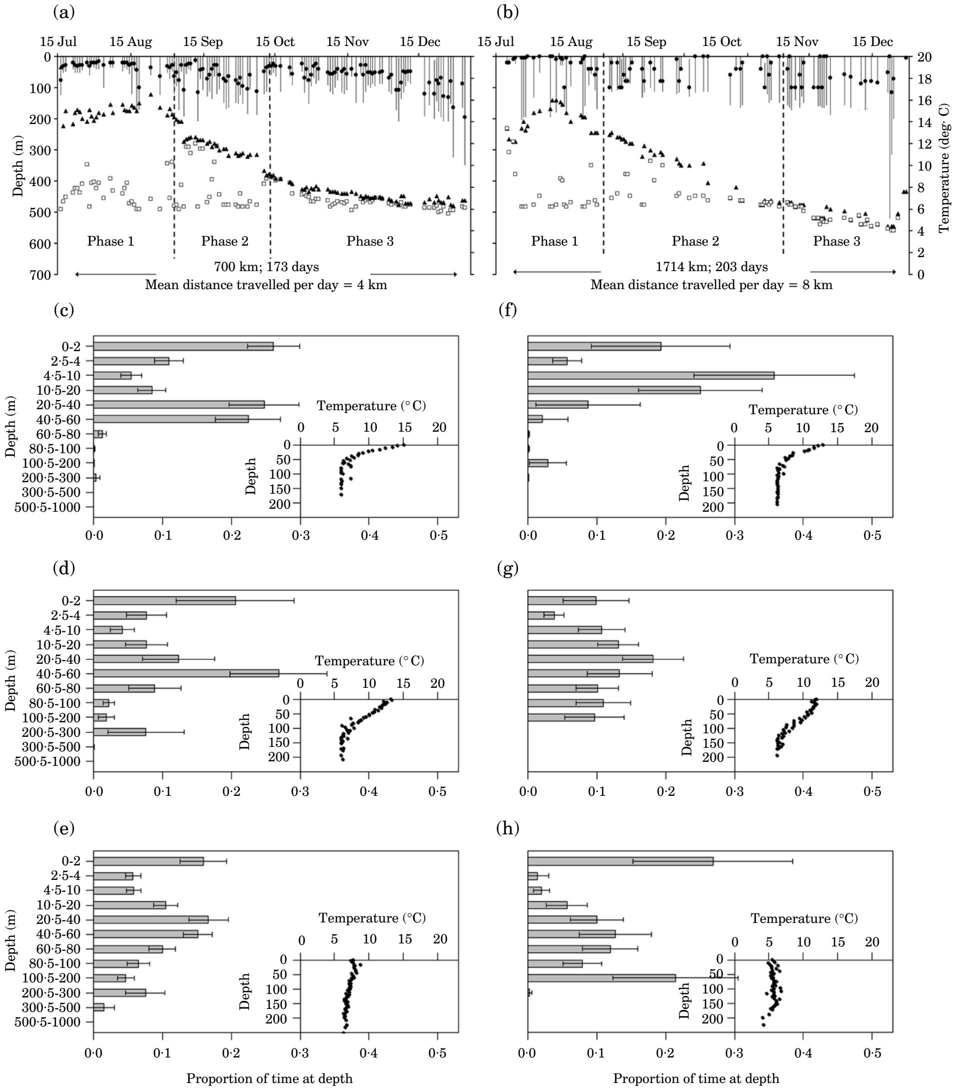


FIG. 7. Daily depth and temperatures encountered by salmon sharks (a) H and (b) I tagged with PAT tags in Port Gravina in mid-July 2001. Vertical lines daily depth range; ●, daily depth mode (upper limit of range); ▲, maximum daily temperatures; □, minimum daily temperatures. Dashed vertical lines, three seasonal ambient thermocline phases experienced by the sharks: phase 1, seasonal thermocline; phase 2, collapsing thermocline; phase 3, totally collapsed thermocline. Histograms show proportion of time (mean ± 95% CI) at depth for fish H during phases (c) 1, (d) 2 and (e) 3 and fish I during phases (f) 1, (g) 2 and (h) 3. Insets in (c)–(h): profiles of depth and temperature from data recorded by the PAT tags.

descended to depths >100 m during 56 of 87 (64%) days for which there were data, and attained a maximum depth of 520 m (Fig. 7). Temperatures ranging from 4·0 to 16·0° C were recorded; the maximum thermal range experienced by this salmon shark in a single day was 9·8° C. The overall thermal preferences observed for fish I were 4·1 to 8·0° C (42%) and 10·1 to 14·0° C (43%).

Similar to fish H, fish I exhibited a pronounced bimodal depth distribution pattern from mid-July to late August, when the thermocline was well-developed with temperature measurements averaging from 12·9° C at the surface to 6·2° C at 80 m depth. Preferred depth modes were 0 to 2 m (19%) and 4 to 20 m (61%). The salmon shark occasionally descended well below the seasonal thermocline, visiting depths from 100 to 200 m, but only spent 3% of the time in these depths. Preferred temperature modes were 10·1 to 12·0° C (55%) and 14·1 to 18·0° C (22%). Fish I experienced the beginning of the collapse of the seasonal thermocline in late-August, which was also recorded for fish H. The total collapse of the thermocline, however, was experienced by fish I in mid-November, *c.* 1 month later than the same phenomenon observed for fish H. During this collapsing phase, fish H showed a nearly uniform depth distribution down to 200 m and spent 63% of its time in waters of 10·1 to 14·0° C. From mid-November to early February when the thermocline had collapsed, fish I exhibited modal depth preferences for 0 to 2 m (27%) and 100 to 200 m (21%), and experienced a thermal environment ranging from 4·0 to 7·0° C.

# DISCUSSION

## SOCIAL SEGREGATION

The life-history of salmon sharks in the eastern North Pacific Ocean appears to include concentrations of large females in nearshore regions of the Gulf of Alaska during summer. The high proportion of female salmon sharks (95%), and relatively narrow size classes found in the study (range = 145–240 cm $L_{Pc}$) supports Goldman's (2003) documentation of salmon sharks in Prince William Sound representing a life-stage segregated population dominated by large females during summer. This contrasts with salmon shark social segregation patterns in the north-western Pacific Ocean, which is dominated by large males north of 52° N (Nagasawa, 1998).

## MOVEMENT PATTERNS

The horizontal and vertical movement patterns of the salmon sharks tagged in Prince William Sound corroborates the complex segregation patterns inferred for *L. ditropis* from catch records in the eastern North Pacific (Nakano & Nagasawa, 1996; Nagasawa, 1998; Goldman, 2003). Three movement modes are proposed to explain the movement patterns observed in the Gulf of Alaska and eastern North Pacific Ocean. Two of these modes are related to foraging: 'focal foraging' movements and 'foraging dispersals'. The third observed movement mode consisted of 'directed migrations'.

### *Foraging movements*

At least three tagged salmon sharks (J, K and L) remained within 10 km of their release locations in Prince William Sound after *c.* ≥1 month and were classified as 'focal foraging' phases of movement (Figs 4 and 5). 'Focal foraging' movements were constrained to relatively small geographic regions: a Pacific salmon migration 'corridor' through which adult pacific salmon converge as they migrate into Prince William Sound from the Gulf of Alaska (Hinchinbrook Entrance), and an area where adult Pacific salmon congregate before returning to their natal streams in summer (Port Gravina). Segments of the first phase of fish G ($G_1$) movements also appear to qualify as 'focal foraging' movements, as shortly after release the salmon shark moved from Hinchinbrook Entrance to the Port Fidalgo and Port Gravina region where it spent *c.* 1·5 months (Fig. 3). Thus, the salmon sharks in this study seemed to exhibit a high degree of site fidelity during summer within habitats that concentrate adult Pacific salmon.

It appears that principal large salmon shark aggregations during summer in Prince William Sound coincide in time and space with adult Pacific salmon spawning migrations during July and August. The salmon sharks appear to begin aggregating in late June as early chum salmon runs move into Prince William Sound. Nearly continuous pulses of chum, pink and coho salmon concentrate and attract large numbers of foraging salmon sharks as late as September.

Analysis of the stomach contents of 51 salmon sharks confirms that adult Pacific salmon are the principal prey of salmon sharks in Prince William Sound during July and August. This is not surprising, given that the importance of salmonids in the diet of salmon sharks has been previously documented (Nagasawa, 1998).

At least six of 17 (35%) salmon sharks (F, $G_1$, H, I, M and N) had left 'focal foraging' areas but were still located in Prince William Sound or the Gulf of Alaska after $\geq$2 months following release, after the majority of Pacific salmon spawning runs were over (Figs 2, 3 and 4). The movements of these salmon sharks were classified as 'foraging dispersals'. Among the six salmon sharks, the average net distance travelled was 587 km and the average time at liberty was 131 days.

Detailed movements exhibited by fish G from July to December are classified as 'foraging dispersal'. Although segments of this phase of fish G's movement appear to qualify as 'focal foraging' movements, the overall behaviour of fish G during the first 141 days after release was classified as a foraging dispersal. Fish G was observed to move between 'focal foraging' areas in Prince William Sound during the autumn (Fig. 3). By October, this salmon shark had moved >500 km from Prince William Sound to Shelikof Strait, where it spent >1 month before beginning a 'directed southerly movement' in early December. The tracked movements of fish G in Shelikof Strait overlap with overwintering Pacific herring aggregations (M. Carls, pers. comm.).

Considering the final positions of fish F, H, M and N in Prince William Sound or the Gulf of Alaska, it is possible that these salmon sharks were also in foraging dispersal modes of movement. Fish F had dispersed south-west across >400 km from Prince William Sound and was near Kodiak Island in late October. By 5 January, fish H had moved 700 km south of Prince William Sound and was located 150 km west of central south-east Alaska. Fish M and N were in Prince William Sound after 68 and 111 days, respectively.

Depth and temperature data also strongly suggest a foraging dispersal phase of movement for fish I until December, when the salmon shark moved into a colder water mass. Temperatures below the thermocline experienced by fish I from July to mid-December are consistent with those found in the Alaska

Coastal Current (ACC; Schumacher & Reed, 1980), which extends from near Cape St Elias through the head of the Gulf of Alaska and down Shelikof Strait (Stabeno *et al.*, 2004). Similar temperatures were observed for fish G during its foraging dispersal phase of movement. Fish G then experienced a shift in water mass in mid-December as it moved from the ACC offshore through the Alaskan Gyre where temperatures near the 100 m depth are generally colder than those found in the ACC (Favorite *et al.*, 1976). Because fish I also experienced similar temporal changes in water temperatures near the 100 m depth, it appears that this salmon shark also exhibited a foraging dispersal phase of movement in the ACC until December, followed by offshore movement.

The vertical distribution data collected by the PAT tags revealed some aspects of depth preference possibly related to foraging behaviour. In particular, a bimodal distribution of depth preference by the salmon sharks was distinct in summer months and was characterized by a large proportion of time spent at the surface (0 to 2 m depth) and a second preferential depth mode in thermocline waters above 60 m depth. The salmon sharks spent little daily time between depth modes, suggesting that this pattern may be related to foraging behaviour involving fast ascending movements into surface waters where adult Pacific salmon are vulnerable. Observations of salmon sharks exhibiting breaching and active foraging behaviour within Pacific salmon aggregations were common during summer in Prince William Sound (pers. obs.). Similar foraging behaviours are well documented for white sharks (Klimley *et al.*, 1996).

The PAT tag depth data collected for fish H (Fig. 7) is a good example of a bimodal depth distribution pattern in shallow waters during the summer when Pacific salmon are abundant, and demonstrates how this pattern changes going into autumn and winter months. From late August to mid-October, fish H extended its depth range and by late autumn, when the thermocline had collapsed, fish H was almost uniformly visiting depths down to 300 to 500 m. Increased exploration of the water column may represent prey-searching behaviour (Carey & Scharold, 1990; Boustany *et al.*, 2002; Sims *et al.*, 2003). This is reasonable because salmon sharks are opportunistic predators and were observed to consume sablefish, gadids, Pacific herring, rockfish and squid even when adult Pacific salmon were locally abundant. Nearly 24% of the prey biomass found in salmon shark stomachs from Prince William Sound consisted of species other than Pacific salmon.

*'Direct migrations'*

Six female (A, C, D, E, $G_2$ and I) and one male (B) salmon shark exhibited 'direct migratory phases' of movement to southern latitudes (Fig. 2). These southward migrants rapidly traversed hundreds to thousands of kilometres, and the movements were often highly linear as shown by detailed movements for fish A, B and $G_2$ (Fig. 2). Based on overall distance travelled and overall rates of travel, it appears that fish A, B, C, D and E began 'direct migrations' shortly after release. Fish G delayed the start of its migratory movement until December, following foraging dispersal movements in the northern Gulf of Alaska. Based on temperature data for fish I that suggests a movement from Alaska Coastal Current waters in December, this salmon shark also may have delayed the start of migratory movements. Among the six migrating salmon sharks, the average net distance travelled was 1737 km, the average time en-route was 42 days, and the net average straight-line distance travelled per day was 44 km.

Salmon shark migratory behaviour may be in part linked to large spatial separation of optimal foraging habitat (*i.e.* Pacific salmon and Pacific herring aggregations in the Gulf of Alaska) from optimal thermal habitat (warmer temperatures at lower latitudes). The physiological adaptation of endothermy (Tubbesing & Block, 2000; Anderson & Goldman, 2001) probably underlies *L. ditropis* choosing habitat with a consistent source of concentrated prey over the energetic demands of remaining in cold waters into winter months in the Gulf of Alaska. The energetic advantages of remaining in the northern Gulf of Alaska, however, may diminish as spatio-temporal declines in prey density and surface water temperatures occur into autumn and winter months. Under this situation, energy conservation measures would entail large geographic movements to warmer temperatures in more southern latitudes due to the lack of optimal prey density and quality.

As Gulf of Alaska Pacific salmon runs decline in late summer, southerly salmon shark movements might also coincide with the progressively later Pacific salmon spawning runs in British Columbia, Canada, and the U.S. Pacific Northwest. In theory, a foraging salmon shark feeding in a patch should leave before foraging becomes unprofitable because there may be significant travel time (energy expenditure) until the next profitable habitat is encountered (Valone, 1992). Increased intra-specific competition at Pacific salmon concentration areas may also serve as an indirect indicator of foraging quality, and may induce some individuals to leave in search of alternative prey or warmer temperatures.

Salmon shark foraging movements and large-scale migrations described in this study might also be explained by habitat selection strategies that optimize reproductive success. A sex- and life-stage segregated population dominated by large females was observed among the salmon sharks sampled while foraging on adult Pacific salmon in Prince William Sound during summer. Large-scale salmon shark movements also seem to be driven by social (age- or length-dependent) latitudinal segregation patterns.

Spatial patterns of social segregation among female salmon sharks are apparent in the data. Two groups of females can be identified based upon the movement modes described above. The first group consists of salmon sharks exhibiting either 'focal foraging movements' or 'foraging dispersals' (fish F, $G_1$, H, I, J, K, L, M and N; Figs 2 and 4). Seven of nine (78%) females in the foraging group were >165 cm $L_{Pc}$ and some should have been mature, based on information in Goldman (2003) (median length-at-maturity for females = 165 cm $L_{Pc}$). The second group is represented by salmon sharks exhibiting direct migratory movements (fish A, C, D, E, $G_2$ and I; Fig. 2). Four of five (80%) females in the migrating group were $\leq$165 cm. According to Goldman's (2003) maturity ogive for females, these specimens were probably immature or, at most, experiencing their first year of sexual maturity. These salmon sharks were considered subadults, given the immediacy of their sexual maturity.

The described segregation patterns of female salmon sharks also appear to have a seasonal component. Movements of all adult salmon sharks tagged in the study were classified under the foraging group and the salmon sharks lingered in Prince William Sound or the Gulf of Alaska for periods ranging from 29 to 174 days after release. The subadult salmon sharks in the migrating group tended to move rapidly south after release. Adult fish G and subadult fish I, however, appear to have exhibited foraging dispersal movements until December, followed by 'direct migratory movements'. Subadult fish M was also an exception and remained in Prince William Sound until November.

The southward migrations exhibited by the subadult females overlap with the nursery grounds documented for *L. ditropis* in the eastern North Pacific region. Nakano & Nagasawa (1996) suggested the existence of a pupping and nursery ground along the transitional domain, the southern boundary of the subarctic region (Pearcy, 1991). The biologically productive waters in this area, lying approximately between the Queen Charlotte Islands and northern California (Nakano & Nagasawa, 1996), depending on longitude and season, may provide greater survival probabilities for young salmon sharks. Goldman (2003) suggests a second pupping and nursery ground from south-east Alaska to the northern end of Baja California in Mexico. The final positions of all of the smallest specimens were located within these nursery areas (fish A, C, D and I).

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## References

Anderson, S. D. & Goldman, K. J. (2001). Temperature measurements from salmon sharks, *Lamna ditropis*, in Alaska waters. *Copeia* **2001,** 794–796.

Blagoderov, A. I. (1994). Seasonal distribution and some notes on the biology of salmon shark (*Lamna ditropis*) in the northwestern Pacific Ocean. *Journal of Ichthyology* **34,** 115–121.

Brodeur, R. D. (1988). Zoogeography and trophic ecology of the dominant epipelagic fishes in the northern North Pacific. In *Bulletin, Ocean Research Institute, University of Tokyo* **26**, 1–28.

Boustany, A. M., Davis S. F., Pyle, P., Anderson, S. D., Le Boeuf, B. J. & Block, B. A. (2002). Satellite tagging: Expanded niche for white sharks. *Nature* **412,** 35–36.

Carey, F. G. & Scharold, J. V. (1990). Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology* **106,** 329–342.

Compagno, L. J. V. (1984). Sharks of the world. *FAO Fisheries Synopsis* **4** (No. 125).

Favorite, F., Dodimead, A. J. & Nasu, K. (1976). Oceanography of the subarctic Pacific Region, 1960–1971. *International North Pacific Fisheries Commission Bulletin* **33**.

Goldman, K. J. (2003). Aspects of age, growth, demographics and thermal biology of two Lamniform shark species. PhD dissertation, College of William and Mary, School of Marine Science, Virginia Institute of Marine Science.

Hart, J. L. (1973). Pacific fishes of Canada. *Bulletin of the Fisheries Research Board of Canada* **180,** 1–740.

Klimley, A. P., Pyle, P. & Anderson, S. D. (1996). The behavior of white sharks and their pinniped prey during predatory attacks. In *Great White Sharks: The Biology of* Carcharodon carcharias (Klimley, A. P. & Ainley, D. G., eds), pp. 175–191. New York: Academic Press.

Lowe, C. G. & Goldman, K. J. (2001). Thermal and bioenergetics of elasmobranches: bridging the gap. *Environmental Biology of Fishes* **60,** 251–266.

Mecklenburg, C. W., Mecklenburg, T. A. & Thorsteinson, L. K. (2002). *Fishes of Alaska*. Bethesda, MD: American Fisheries Society.

Morrissey, J. F. & Gruber, S. H. (1993). Home range of juvenile Lemon sharks, *Negaprion brevirostris*. *Copeia* **1993**, 425–434.

Nagasawa, K. (1998). Predation by salmon sharks (*Lamna ditropis*) on Pacific salmon (*Onchorynchus* spp) in the north Pacific Ocean. *Bulletin of the North Pacific Anadromous Fish Commission* **1,** 419–433.

Nakano, H. & Nagasawa, K. (1996). Distribution of pelagic elasmobranchs caught by salmon research gillnets in the North Pacific. *Fisheries Science* **62,** 860–865.

Neave, F. & Hanavan, H. G. (1960). Seasonal distribution of some epipelagic fishes in the Gulf of Alaska region. *Journal Fisheries Research Board of Canada* **17,** 221–222.

Pearcy, W. G. (1991). Biology of the transition region. *NOAA Technical Report NMFS* **105,** 39–56.

Sano, O. (1960). The investigation of salmon shark as a predator on salmon in the North Pacific, 1959. *Bulletin of the Hokkaido Regional Fisheries Research Laboratory* **22,** 68–82.

Sano, O. (1962). The investigation of salmon shark as a predator on salmon in the North Pacific, 1960. *Bulletin of the Hokkaido Regional Fisheries Research Laboratory* **24,** 148–162.

Schumacher, J. D. & Reed, R. K. (1980). Coastal flow in the northwest Gulf of Alaska: the Kenai Current. *Journal of Geophysical Research* **85,** 6680–6688.

Sims, D. W., Southall, E. J., Richardson, A. J., Reid, P. C. & Metcalfe, J. D. (2003). Seasonal movements and behaviour of basking sharks from archival tagging: No evidence of winter hibernation. *Marine Ecology Progress Series* **248,** 187–196.

Stabeno, P. J., Bond, N. A., Hermann, A. J., Kachel, N. B., Mordy, C. W. & Overland, J. E. (2004). Meteorology and oceanography of the Northern Gulf of Alaska. *Continental Shelf Research* **24,** 859–897.

Tanaka, S. (1980). Biological survey of salmon shark *Lamna ditropis* in the northwestern North Pacific Ocean. In *Report of the New Shark Resource Exploitation Survey in the Fiscal Year 1979 (North Pacific Ocean)*, pp. 59–84. Tokyo: Japan Marine Fisheries Resource Centre (in Japanese with English abstract).

Tubbesing, V. A. & Block, B. A. (2000). Orbital rete and red muscle vein anatomy indicate a high degree of endothermy in the brain and eye of the salmon shark. *Acta Zoologica* **81,** 49–56.

Valone, T. J. (1992). Patch estimation via memory windows and the effect of travel time. *Journal of Theoretical Biology* **157,** 243–251.