Exxon Valdez Oil Spill
Restoration Project Final Report

Salmon Shark, *Lamna ditropis*, Movements, Diet, and Abundance in the Eastern North Pacific Ocean and Prince William Sound, Alaska

Restoration Project 02396
Final Report

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Study History: This project was initiated in 2000 as a new project (Project 00396; see Hulbert 2000). Field work is a direct component of this project, but the project also relies on samples and data gathered through cooperative efforts with the National Marine Mammal Laboratory, Alaska Department of Fish and Game, as well as data in the literature. A pilot salmon shark tagging study was carried out in July 1999 after Apex project 163A sampling objectives were completed.

Abstract: Salmon shark movement, diet, and abundance data were used to assess the role of the salmon shark, *Lamna ditropis* (Hubbs & Follett 1947), as a top predator in the trophic ecology of Prince William Sound (PWS). Based on our observations, we propose 4 modes of movement for salmon sharks in the Gulf of Alaska (GOA) and eastern North Pacific Ocean: focal foraging movements, foraging dispersals, directed migrations, and annual fidelity to PWS focal foraging areas. Salmon sharks aggregating at focal foraging areas in PWS are associated in time and space with adult Pacific salmon (*Oncorhynchus* spp.) spawning migrations. As adult salmon concentrations taper off in late summer, salmon sharks disperse from focal foraging areas in PWS; some sharks continue to forage in PWS and the northern GOA into fall and winter months, while other sharks tracked by this study underwent directed southeasterly migrations toward the west coasts of Canada and the United States. Adult Pacific salmon were the principle prey during summer months in PWS, but salmon sharks had a varied diet even when adult salmon were abundant. From systematic aerial survey counts, we estimate 2,000 salmon sharks were at the surface of Port Gravina on August 16, 2000. We estimate these 2,000 salmon sharks consumed 263,000 kg of prey during an estimated 45 day residency in Port Gravina in 2000.

Key Words: Diet, foraging, *Lamna ditropis*, movements, migration, Prince William Sound, salmon shark, tagging, residency.

Project Data: *Description of data* - Salmon shark archival and conventional tag data: geographic location coordinates, depth, temperature. Diet data. *Format* - Excel spreadsheets, Powerpoint slides. *Custodian* - Contact Lee Hulbert, 11305 Glacier Highway, Juneau Alaska 99801, work phone: (907) 789-6056, fax: (907) 789-6608, e-mail: Lee.Hulbert@noaa.gov. *Availability* - All data reside with the NOAA Fisheries Auke Bay Laboratory. Copies of specific data can be provided on a CD-rom.

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TABLE OF CONTENTS

LIST OF FIGURES

overall direction of movement between locations. Focal foraging area (blue area) was estimated using the minimum convex polygon method (MCP; Mohr 1947).

Figure 8. *Lamna ditropis*. Focal foraging area and movements of salmon shark L in Port Gravina, Prince William Sound; July 20 to September 7, 2000. Location points (green dots) are connected in chronological order; black lines with arrows indicate overall direction of movement between locations. Focal foraging area (purple area) was estimated using the minimum convex polygon method (MCP; Mohr 1947).

Figure 9. *Lamna ditropis*. Daily depth and temperature range and depth mode for salmon sharks C and D. Both sharks were tagged in Port Gravina in mid-July, 2001. The data were obtained from Wildlife Computers PAT tag transmissions to the Argos satellite system. Figure 2 shows the shark's locations at time of pop-up. Vertical black lines are daily depth range, black points are daily depth mode. Red and blue points are the maximum and minimum daily ambient temperatures encountered by the sharks, respectively.

Figure 10. *Lamna ditropis*. Daily depth and temperature range and depth mode for salmon sharks H and I. Both sharks were tagged in Port Gravina in mid-July, 2001. The data were obtained from Wildlife Computers PAT tag transmissions to the Argos satellite system. Figure 2 shows the shark's locations at time of pop-up. Vertical black lines are daily depth range, black points are daily depth mode. Red and blue points are the maximum and minimum daily ambient temperatures encountered by the sharks, respectively.

Figure 11. Stratified systematic line transects sampled during July 2000 in Port Gravina, Prince William Sound with simultaneous side-looking and down-looking Biosonics hydroacoustic systems. Squares indicate locations of salmon sharks visually spotted at the surface during the survey. Sampled transects were randomly selected and are indicated by the thick lines. Stratum A was chosen to represent an area of low shark concentration and Stratum B was chosen to represent an area of high shark concentration based upon aerial survey data.

Figure 12. Geographic location of areas where intensive strip search patterns were flown by a spotter pilot for the purpose of estimating salmon shark abundance. An estimated 500 salmon sharks were at or near the surface of region A on the morning of July 6, 2000; and 2000 salmon sharks were estimated to be at or near the surface of region B on the afternoon of August 16, 2000.

Figure 13. Schematic map of proposed salmon shark nursery grounds (after Nakano and Nagasawa 1996), and Japanese driftnet fishing grounds for flying squid, 1981-1992 (after Yatsu et al. 1993).

LIST OF TABLES

EXECUTIVE SUMMARY

Salmon sharks are the predominant apex fish predator in the boreal North Pacific, yet very little is known of their ecological role in PWS and potential affects on the recovery of spill-injured resources in the region. This research project was inspired by observations of large aggregations of salmon sharks, *Lamna ditropis* (Hubbs & Follett 1947), in bays and passages of Prince William Sound (PWS), Alaska during the mid 1990s. Prior to the 1990s, observations of large salmon shark aggregations in PWS were rare.

A principal goal of the project was to estimate the composition and biomass of prey consumed by salmon sharks in Port Gravina, a bay in southeast PWS. To address this objective we: 1. investigated salmon shark seasonal residency in PWS by describing movements and migrations from tagging studies; 2. described salmon shark prey composition by analyzing stomach contents of sharks aggregating in PWS during summer, and; 3. estimated the abundance of aggregating salmon sharks in Port Gravina from aerial strip surveys. These basic parameters have not been described for salmon sharks in the northeast Pacific Ocean and are necessary to calculate the biomass of prey consumed by aggregating salmon sharks in Port Gravina. We used the estimates of salmon shark prey composition and biomass resulting from these analyses to evaluate salmon shark predation in PWS.

Satellite tag transmissions and conventional tag recoveries provide insights into the seasonal residency and movement patterns of salmon sharks in PWS and the eastern North Pacific Ocean. Based on our observations, we propose 4 modes of movement for salmon sharks in the Gulf of Alaska (GOA) and eastern North Pacific Ocean: focal foraging movements, foraging dispersals, directed migrations, and annual fidelity to PWS focal foraging areas. Our observations strongly suggest that salmon sharks are attracted by Pacific salmon (*Oncorhynchus spp.*) runs returning to the streams, rivers, and hatcheries in PWS. In PWS, large salmon shark aggregations are associated in time and space with peak adult Pacific salmon spawning migrations during July and August. Focal foraging movements were concentrated at an adult Pacific salmon staging area (Port Gravina) and migration corridor (Hinchinbrook Entrance). As the summer salmon runs taper off, the sharks disperse from focal foraging areas; some continue to forage in PWS and the GOA into autumn and winter months, while others undergo rapid southeasterly migrations hundreds to thousands of kilometers toward the west coasts of Canada and the United States. Overall, 50% of the sharks tracked by this study underwent large-scale migrations.

Adult Pacific salmon (pink, *Oncorhynchus gorbuscha*, chum, *Oncorhynchus keta*, and coho, *Oncorhynchus kisutch*) were the principal prey as measured by both percent number (35%) and percent weight (76%). Even when adult salmon were locally abundant, the sharks had a varied diet that included Teuthoidea squid, sablefish (*Anoplopoma fimbria*), Pacific herring (*Clupea pallasi*), rockfish (Sebastes spp.), Eulachon (*Thaleichthes pacificus*), Capelin (*Mallotus villosus*), spiny dogfish (*Squalus*

acanthias), arrowtooth flounder (Atheresthes stomas), and (codfishes (Gadidae).

From counts of salmon sharks during aerial strip surveys in Port Gravina we estimate there were at least 500 sharks at the surface within an area measuring 1.5 km^2 (333 sharks km^{-2}) on July 6, 2000, and on August 16, 2000 at least 2,000 sharks were at the surface within a 12 km^2 area (166 sharks km^{-2}). We estimate that salmon sharks consumed at least 263,000 kg of prey in Port Gravina during a 45 day period of peak salmon shark abundance in the summer of 2000. If we assume the sharks consumed equal proportions of pink and chum salmon by weight the sharks would have consumed 116,000 pink salmon and 36,000 chum salmon. From ADF&G estimates for salmon escapement and commercial harvest for Port Gravina in 2000, the sharks would have consumed 12% and 29% of the pink and chum salmon run, respectively.

While the accuracy of the consumption estimate can certainly be debated as to how conservative, the direction and significance of the consumption to the salmon run is real. Low salmon runs at a time of high salmon shark survival could be devastating until shark numbers decline or redistribute (in other words, switch prey) away from adult salmon staging areas.

A convergence of environmental and human induced changes in the northeast Pacific Ocean during the 1980s and 1990s might help explain strong anecdotal evidence of a rapid increase in salmon sharks in the PWS region. We propose the apparent increase in salmon shark abundance is likely due to: (1) the moratoria on high seas industrial driftnet fishing in 1992; (2) trophic regime shifts which resulted in sharp increases in Pacific salmon, cod, and flatfish production (salmon shark prey) during the 1980s and 1990s; (3) Pacific salmon hatchery production in PWS, Kodiak Island, and Southeast Alaska during the 1980s and 1990s, and; (4) a northward shift in range as the as the salmon shark population matures. Due to these factors and salmon sharks' longevity, we predict their abundance in PWS and the GOA will likely increase. Because salmon sharks occupy the highest trophic level in the food web of subarctic waters, and their apparent increase during the 1990s, we believe salmon sharks should be more closely monitored as a possible keystone species.

INTRODUCTION

A convergence of environmental and human induced changes to the northeast Pacific likely affected a change in the importance of salmon sharks as a top-level predator in Prince William Sound (PWS) and the Gulf of Alaska (GOA) during the 1990s. Considerable numbers of juvenile salmon sharks were taken as bycatch from 1978 to 1992 in large-scale pelagic driftnet fisheries in the North Pacific (McKinnell and Seki 1998, Nakano and Nagasawa 1996). A moratorium on these fisheries in 1992 eliminated an important source of juvenile salmon shark removals on the high seas. The apparent increase of salmon shark also follows 10-15 years after Northeast Pacific Ocean climate and trophic regime shifts characterized by warmer ocean temperatures, a rapid decline in crustaceans and capelin (Mallotus villosus), and increases in codfishes (Gadidae) and flatfish (Pleuronectidae) (Anderson and Piatt 1999; McGowan et al. 1998; Anderson et al. 1997; Bechtol 1997). Improved marine survival of Pacific salmon following the ocean climate shift and increased hatchery output resulted in overall increasing trends in north Pacific salmon production (Hilborn and Eggers 2000; Downton and Miller 1998; Francis and Hare 1994; Beamish and Bouillon 1993). Because of observed salmon shark increases in bays and passes in PWS, abundant prey, and reduced exploitation, salmon sharks might play an increasingly important role in the PWS and GOA ecosystems.

Salmon sharks, *Lamna ditropis* (Hubbs & Follett 1947), are highly migratory predators that occupy the highest trophic level in the food web of subarctic waters (Nagasawa 1998; Blagoderov 1993), yet their ecological role in PWS and potential affects on the recovery of spill-injured resources in the region are unknown. Salmon sharks occur in the surface waters in all of the GOA during all seasons of the year (Hart 1973, Neave and Hanavan 1960). Salmon shark seasonal and geographic movements and food habits in the eastern North Pacific Ocean have not been described. Prior to the 1990s, observations of large salmon shark aggregations in PWS were rare. Reports of large aggregations of foraging salmon sharks, sometimes numbering in the thousands in bays and passages of PWS, became common during summer months in the mid-1990s.

The goal of this final report for Restoration Project 02396 is to assess the role of the salmon shark as a top predator in the trophic ecology of PWS by estimating the composition and biomass of prey consumed by salmon sharks during their residency in Port Gravina in southeast PWS. Data archival and location transmitting satellite tags were employed to describe salmon shark movements and seasonal residency in PWS. Aerial and hydroacoustic surveys were employed to construct salmon shark abundance estimates in Port Gravina. Salmon shark stomach contents were analyzed to describe their diet during summer in PWS. These parameters are necessary to construct a prey consumption estimate for salmon sharks in Port Gravina.

OBJECTIVES

Objectives of the EVOS salmon shark project 00396 were to:

1. Estimate the annual residency time of large salmon shark aggregations in PWS using information from electronic tag transmissions and conventional tag recoveries

2. Estimate salmon shark abundance in Port Gravina with data collected from hydroacoustic and aerial surveys

3. Estimate salmon shark diet composition during summer in PWS from analysis of stomach contents

4. Estimate the biomass of prey consumed by salmon sharks in Port Gravina with parameters estimated in objectives 1-3

METHODS

Study Area

Directed salmon shark field sampling took place in southeast PWS at Port Gravina (60º 39' N 146º 22' W), and near Bear Cape at Hinchinbrook Entrance (60º 21' N 146º 45' W). Port Gravina is one of many estuarine embayments in PWS where adult salmon aggregate in summer before entering their natal streams. Hinchinbrook Entrance is one of 4 narrow passes, or migration corridors, which adult salmon must use as they migrate into PWS from the GOA (Figure 1).

Sampling Methodology

A team of 5 people collected data and tagged sharks during a pilot study in July 1999 aboard the F/V Pagan, and during directed sampling in July 2000 and 2001 aboard the R/V Montague, chartered for the project from the Alaska Department of Fish and Game (ADF&G).

In 1999 and 2000 we used purse seine gear to efficiently capture individual sharks as they swam at the surface. Because sharks were abundant, but rarely observed at the surface in 2001, fishing with purse seine gear was inefficient and we alternatively captured sharks by jigging with two 50 meter long 3/8 inch diameter polypropylene hand lines with single #3 (16/0) circle hooks attached to 24 -48 inch galvanized steel cable and baited with herring.

Most sharks (66%) were tagged in the water and were not measured or sexed. Sharks sacrificed for diet (stomach) samples were additionally weighed when possible.

Salmon shark movements and seasonal residency in PWS (Objective 1)

Salmon shark movement data were collected from conventional tag recoveries made opportunistically by recreational and commercial fishermen, and from locations derived from satellite tag transmissions. All sharks that were released were tagged with either conventional tags (Roto tags, dart tags) or satellite transmitters (PAT, KiwiSat, and SPOT2).

A collaborative salmon shark tagging effort was organized with the support of ADF&G, Virginia Institute of Marine Science (VIMS), and sport fishing charter operators. Dart tags were generally deployed by ADF&G and VIMS by approaching the sharks from a small boat and sticking them with a tag affixed to an applicator at the end of a jab stick. No sex or length data were recorded when tagged by this method. During directed field sampling by our study, sharks were normally brought aboard the vessel; sex and length data were recorded prior to tagging and released when possible.

During the NMFS-ADF&G-VIMS joint effort from 1998 to 2002, 246 salmon sharks were tagged with conventional tags and 16 sharks were tagged with satellite transmitters. Table 1 summarizes the number and type of tags deployed on salmon sharks between July 1998 and August 2002.

Movement data collected from the tagging study varied with the type of tags used. Conventional dart and Roto tag recoveries are dependent on fisheries for recaptures and provide movement data from single-point locations recorded by the fishermen at the time of recapture. Satellite transmitters provide movement data that is independent of shark recaptures. Depending on tag type, satellite tags provide single-day or multi-day locations and archival depth and/or temperature data.

Movement mode classification

We used both qualitative and quantitative methods to classify modes of salmon shark movement.

Quantitative movement classification methods: With detailed movement data collected from position-only tags we used an ArcView® GIS application, the Animal Movement Analyst Extension site fidelity test (AMAE; Hooge et al. 2001) to test patterns of multi-day location fixes against the null hypothesis of random movement. The AMAE site fidelity test is a modification of the of the random walk test developed by Spencer et al. (1990). The simulation compares parameters from the observed movement pattern with random walks generated by a Monte Carlo simulation to determine if the observed movement pattern is random (the null hypothesis), has more site fidelity than should occur randomly, or is overly dispersed. The test uses the actual sequence of distances between successive fixes and assigns a randomly generated angle over the interval 0^o to 360^o to calculate the x,y coordinates for a random location. Taken in sequence, each set of random locations generated a random movement path. This procedure is repeated to yield 1000 random movement paths for each shark movement path, except for AMAE site fidelity tests for shark L because the highly constrained coastline in Port Gravina caused the simulation to crash repeatedly, citing "bumpbuffer" errors. Therefor, the results of the shark L site fidelity test were based upon 100 random paths.

To more realistically simulate the more constrained movements possible in coastal environments we modified the simulation to generate the random walks only at sea by using the shoreline as a constraining polygon. Using a constraining polygon for the random walks decreases power (increases the chance of a Type II error) but increases robustness (decreases the chance of a Type I error). This decrease in power is accented by not having fine-scale temporal breakdowns in movement lengths. It does this because it makes the null hypothesis of random movement (based on the random walks) less random. Because of this, we accepted a 95% probability of a Type I error ($\alpha = 0.05$) for each tail of the distribution of means generated by the random walks.

Two measures resulting from the random walks, mean squared distance (MSD), and linearity index (LI), were used to characterize site fidelity (highly constrained movement), migration (highly dispersed movement), or dispersal (random movement). Mean squared distance from the first fix measured the dispersion of use around the release location, while the linearity of the path (LI) measured shifts in the shark's movement and is a measure of directed movement. LI is the linear distance between the endpoints of an animal's path divided by the total distance traveled, where linear paths yield LI = 1 and values < 1 indicate non-linear, meandering paths. A mean and standard deviation were calculated for MSD and LI from the randomly generated paths for each animal (Table 4). If MSD or LI based on the actual movements of a shark were significantly less than the mean of these measures for the random movement paths the movements were judged to be more constrained than random, a positive test for site fidelity (focal foraging movements). If MSD or LI based on the actual movements of a shark were not significantly different than the mean of these measures for the random movement paths, an individual was judged to exhibit random movements (foraging dispersal). If MSD or LI based on the actual movements of a shark were significantly greater than the mean of these measures for the random movement paths, the movements were judged to exhibit highly dispersed (migratory) movements. We judged sharks recaptured near the release locations during summer 1 + years later as exhibiting seasonal affinity to the region.

The "shape" or symmetry of a shark's movement was measured as it's eccentricity, where ECC = 1 characterizes a symmetric movement pattern and values of ECC > 1 indicate an increasingly elongate movement.

<u>Qualitative movement classification methods</u>: We classified shark movements from two-fix location data (release location and recapture or tag pop-up location) based upon overall distance traveled, and overall direction and rate of travel. Sharks that were within 10 km of their release locations after ~ 1+ months were judged to exhibit focal foraging behavior. Sharks that moved away from release locations with an overall rate of travel < 10 km/day were judged to exhibit foraging dispersal movements. Sharks that rapidly moved >500 km to the southeast with an overall rate of travel >20 km per day were judged to exhibit migratory movements. Sharks that were recaptured in PWS 1+ years after release were judged to exhibit annual fidelity to PWS focal foraging areas.

Conventional tags

Conventional tags provide two locations (release and recapture) and overall distance and rate of travel.

<u>Dart tags</u>: Dart tags (FLOY®, Seattle, WA) are composed of a stainless steel dart head and #13 vinyl tubing on 200 lb test nylon monofilament with Shrink-lock™. The tags have a legend with return instructions printed in English. Dart tags are implanted in the back musculature near the base of the first dorsal fin.

<u>Rototags</u>: The rototag (double dairy tag, National Band & Tags, Newport, KY, USA) is a

two piece plastic cattle ear tag which is inserted through the first dorsal fin.

Satellite tags

We used the Argos Data Collection and Location System (DCLS) to determine locations, depth and temperature behavior of salmon sharks equipped with satellite transmitters at Port Gravina and Hinchinbrook Entrance.

The Argos data collection and location system recorded the date and time of each signal received by the satellite (termed an "uplink") 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, to Alaska Standard Time by subtracting 9 hours. Location records and associated data were plotted using ArcView® geographic information system (GIS) software.

We used three types of satellite tags: Pop-up Archival Transmitting (PAT) tags, Smart Position-Only Tags (SPOT2), and KiwiSat tags. All tags used by the project were programmed to transmit with a 45 second repetition rate to receivers on board polar orbiting satellites operated by Service Argos and the National Oceanic and Atmospheric Administration. A goal of the electronic tagging study was to deploy tags on male and female sharks among a range of lengths.

<u>Pop-up Archival Transmitting tags</u>: PAT tags (Wildlife Computers, Woodinville, WA, USA) provide fisheries independent straight-line distance traveled from point of tagging, and depth and thermal behavior data archived for up to a year. Depth and temperature are measured to within 0.5 m and 0.05 ºC resolution. Data are collected each minute and summarized into user-defined bins. Time- at-depth histogram ranges were set at 0-2, 2.5-4, 4.5-10, 10.5-20, 20.5-40, 40.5-60, 60.5-80, 80.5-100, 100.5-200, 200.5-300, 300.5-500, and 500.5-1000 m. Upper limits of time- at-temperature histogram limits were set at 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, and >22 ºC.

PAT tags are cylindrical tags that were tethered to a dart by a 12 cm long, 250 lb test monofilament. The dart was implanted in the back musculature near the base of the first dorsal fin. The tags release and float to the surface at a pre-programmed date and time by initiating corrosion of a stainless steel1inkage. After release from the shark, the PAT tag transmits continuously to ARGOS satellites. Tag location is calculated from Doppler shift by Argos satellites when it begins transmitting.

<u>Position-only tags</u>: KiwiSat tags (Sirtrack, Havelock North, NZ), and Smart Position Only Tags (SPOT2; Wildlife Computers, Woodinville, WA, USA) were bolted to the sharks first dorsal fin using stainless steel Allen head socket cap screws, nylox nuts, stainless steel and rubber washers. When the sharks surface, a saltwater switch causes the tag to transmit to the ARGOS satellite system within 200 mS of breaking the surface. Service Argos provides the locations with an accuracy as good as ±350 m, provided the

tag is at the surface long enough to transmit multiple times within one satellite pass. Location records and associated data were plotted using ArcView® geographic information system (GIS) software. The tags also collect and transmit the proportion of time spent within user-specified temperature ranges during the previous 24 hours prior to surfacing. Upper limits of time- at-temperature histogram limits were set at 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, and >22 ˚C.

Salmon shark abundance estimates (Objective 2)

Remote sensing gear was used to collect data on shark abundance below the surface along systematic stratified line transects. Visual (surface) counts were collected concurrently with the remote sensing gear. Aerial abundance survey and statistical methods followed the methodology for sea otter abundance estimates detailed in Bodkin and Udevitz (1999).

Aerial abundance surveys: We recorded aerial counts of salmon shark surface aggregations in PWS from a Bellanca Scout seaplane. Because the timing of surface aggregations is unpredictable, salmon shark counts and abundance estimates were conducted opportunistically while the pilot conducted directed salmon and sea otter aerial surveys throughout PWS during July and August 2000. Intensive strip search patterns were flown in Port Gravina when the pilot observed abundant salmon shark surface aggregations. The pilot determined strip width by using distance indicators marked on the wing struts. Strip lengths were determined by elapsed time and airspeed. Shark abundance estimates were extrapolated from shark counts and area swept to the area of a localized shark aggregation.

Acoustic surveys: We collected surface and sub-surface salmon shark abundance data from the R/V Montague using simultaneous side looking (120 m, starboard) and down looking (60 m) single beam Biosonics DT 4000, 120 kHz hydroacoustic systems, visual surface counts from the crows nest, down sounder, and side-scanning sonar. Data sampling for calculating unbiased estimates of salmon shark abundance followed a pre-determined systematic stratified line transect sampling design with a random start (Figure 11). Two strata were chosen to represent an area of low shark concentration and high shark concentration based upon aerial survey data and advice from our spotter pilot. The sampling protocol measured two variables: (a) sharks visually counted at the surface, and (b) sharks counted below the surface using Biosonics hydroacoustics, down sounder, and side-scanning sonar.

Salmon shark diet composition (Objective 3)

Diet sampling: Thirty of 51 salmon shark stomachs were collected from sport fishermen by ADF&G port samplers, and by Ken Goldman (VIMS). They were frozen and shipped to Juneau for analysis. Twenty-one sharks were sacrificed for lethal samples during field sampling operations. All sharks sampled for diet were caught during July and August in PWS. Contents of each stomach were identified to the highest practical taxonomic resolution, enumerated, and weighed when possible.

Feeding periodicity, daily ration: We deployed Data Storage Tags (DST; Star-Oddi, Reykjavik, Iceland) in the sharks' stomachs for the purpose of gathering data on salmon shark daily ration. DSTs are miniature data loggers that record and store a series of high resolution temperature and depth measurements. Because salmon sharks have body temperatures 10-14^{o}C above ambient water temperatures and eat poikilothermic (cold-blooded) prey, time and depth of prey ingestion would be noted in the tag data by a decrease in stomach temperature. The magnitude of temperature drop would be an indication of meal size. DSTs were fitted with small treble hooks, sutured into a squid, and inserted into the sharks' stomachs through a PVC tube. We configured the DSTs to record depth and temperature measurements every minute until the tags' memory was filled, for a total of 11.5 days of data each. Rototags were attached high on the first dorsal fin of all sharks released with Star -Oddi tags to increase the likelihood of sighting and recapture. Roto tags are flourescent cattle ear tags that are highly visible at a distance from both sides of the sharks' dorsal fin when above the waters surface.

RESULTS

Salmon shark capture and sampling

Table 1 summarizes the number and type of tags deployed on salmon sharks, *Lamna ditropis,* between July 1998 and August 2002. Most sharks (66%) were tagged in the water and were not measured or sexed. Within the geographic range sampled during the study (primarily southeast PWS), striking spatial segregation by sex and size prevailed; of the 91 sharks sexed, 87 (95.6%) were female; average pre-caudal length of the females was 178 cm (range = 146-200 cm; SE = 12 cm; n = 60); the average weight of 18 females was 146 kg (range = 115-176 kg; SE = 17 kg). The two males measured were 175 and 190 cm total length.

Table 1. Type and number of tags deployed on salmon sharks during 1998-2002.

Tag Type	1998	1999	2000	2001	2002	Total
			Conventional tags			
Dart	15	97	101	7	13	233
Roto	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

Salmon shark movements and seasonal residency in PWS (Objective 1)

General. ---- We acquired satellite-derived movement data from 13 of 16 (81%) satellite tags and the recapture of 4 of 246 (1.6%) conventionally tagged salmon sharks (Table 2). Within 7 months of release, 64% of the sharks had moved out of PWS (Figure 2); within 4 months of release, 36% of the sharks were still in PWS (Figure 3). Three conventionally tagged sharks were recaptured in PWS within 50 km of their release locations after 1.0, 2.9, and 3.0 years at-large (Figure 3, Table 3). Based on our observations we propose 4 modes of movement for salmon sharks in the GOA and eastern North Pacific Ocean: (1) directed migrations, (2) foraging dispersals, (3) focal foraging movements, and (4) annual fidelity to PWS focal foraging areas.

Table 2. Summary of salmon shark, *Lamna ditropis*, movements in the northeast Pacific Ocean.

Shark	Tag type	Release date	Final location date	Straight-line distance traveled (km)	Time elapsed (days)	Mean straight-line distance traveled per day (km)
			Salmon shark movements out of Prince William Sound: < 7 months at-large			
A	SPOT2	July 18, 2001	August 9, 2001	1277	22	58
B	KiwiSat	July 22, 2000	August 17, 2000	769	26	30
C	PAT	July 15, 2001	August 23, 2001	1917	39	49
D	PAT	July 13, 2001	September 12, 2001	2163	61	35
E	Dart	July 26, 1999	September 12, 1999	1049	48	22
F	PAT	July 24, 1999	October 27, 1999	436	95	5
G_1	SPOT2	December 6, 2001	January 8, 2002	3271	33	99
H	PAT	July 15, 2001	January 5, 2002	692	174	4
G_2	SPOT2	July 18, 2001	December 6, 2001	505	141	4
I	PAT	July 13, 2001	February 1, 2002	1714	203	8
			Salmon shark movements within Prince William Sound: < 4 months at-large			
J	SPOT2	July 17, 2001	August 15, 2001	7	29	0.24
K	KiwiSat	July 20, 2000	August 23, 2000	7	34	0.21
**L	KiwiSat	July 20, 2000	September 17, 2000	58 (6)	59 (52)	0.98 (0.11)
M	PAT	July 24, 1999	September 30, 1999	76	68	1.12
N	PAT	July 13, 2001	November 1, 2001	98	111	0.88

* "Release date" for G_1 is the date just prior to the start of a 3,271 km movement to the south.

** Shark L moved 6 km overall in 52 days (0.11 km/day) before leaving Port Gravina between Sept 8 and Sept 11.

Table 3. Salmon shark, *Lamna ditropis*, recaptures in Prince William Sound.

Shark	Tag type	Release date	Release location	Recapture Date	Recapture location	Time-at- large (months)
O	Dart	July 22, 1999	Windy Bay	July 6, 2002	Hinchinbrook Entrance	35.5
P	Dart	July 21, 1999	Windy Bay	July 20, 2002	Hinchinbrook Entrance	36.0
Q	Dart	August 29, 2002	Port Gravina	September 8, 2001	Hinchinbrook Entrance	12.4

Table 4. Measurement of mean squared distance (MSD, $m^2 \times 10^8$), linearity index (LI), and eccentricity from actual and simulated movement patterns for sharks A, B, G, J and L. The two movement paths indicated for shark G are: movements during dispersal from release to the beginning of a directed southerly movement (G_1; Jul. 18 - Dec. 6), and movements during a directed southerly migration (G_2; Dec. 6 - Jan. 8).

Movements	MSD	LI	ECC
Shark A			
Actual	518.09	0.71	1.97
Simulated	75.64 ± 37.11	0.24 ± 0.10	1.42 ± 0.25
%	100 ††	100 ††	100 ††
n	1000	1000	1000
Shark B			
Actual	194.86	0.69	1.44
Simulated	127.04 ± 37.42	0.50 ± 0.18	1.95 ± 0.41
%	97.3 ††	82.4 ††	93.1†
n	1000	1000	1000
Shark G_1			
Actual	512.10	0.19	2.30
Simulated	637.92 ± 403.61	0.27 ± 0.12	2.13 ± 0.59
%	58.8†	73.0†	39.6†
n	1000	1000	1000
Shark G_2			
Actual	10,306.00	0.91	3.43
Simulated	1,537.34 ± 906.39	0.23 ± 0.10	1.89 ± 0.45
%	100††	100††	100††
n	1000	1000	1000
Shark J			
Actual	0.31	0.07	1.18
Simulated	0.79 ± 0.41	0.19 ± 0.09	1.44 ± 0.25
%	95.5†	90.2†	53.1††
n	1000	1000	1000
Shark L			
Actual	0.12	0.06	1.21
Simulated	0.58 ± 0.37	0.17 ± 0.08	1.75 ± 0.33
%	98†	94†	97†
n	100	100	100

n = Number of random movement paths.

† = The percentage of simulated random movement paths with HIGHER values than the actual movement path.

†† = The percentage of simulated random movement paths with LOWER values than the actual movement path.

Sharks that rapidly moved >500 km to the southeast, with an overall rate of travel >20 km per day were judged to exhibit migratory movements. Sharks that moved away from release locations with an overall rate of travel < 10 km/day were judged to exhibit foraging dispersal movements. Sharks that were recaptured in PWS 1+ years after release were judged to exhibit annual fidelity to PWS focal foraging areas.

1. *Focal foraging movements*: We generally characterize focal foraging movements as constrained movement paths within distinct focal foraging areas in PWS. Sharks J, K and L were within 7 km of their release locations after 29, 34 and 52 days, respectively and were judged to exhibit focal foraging behavior (Figure 5; Table 2).

AMAE site fidelity analyses of detailed movement paths for sharks J and L showed the actual MSDs were less than 95% of the simulated values for each shark (Table 4). Since under the null hypothesis of random movement the actual movement paths should deviate from only 5% of the random movements by chance, these results are significant . Thus, actual space utilized was more constrained (actual MSD significantly less than simulated MSD) than random movement and therefor the movements for sharks J and L constitute site fidelity. Significant results for constrained movement for sharks J and L establish that sharks J and L established focal foraging areas; shark J at Hinchinbrook Entrance (a migration corridor); and shark L at Port Gravina (an adult salmon staging area) (Figures 7 and 8). Shark L occupied an area approximately 34 km^2 at the head of Port Gravina for at least 52 days after release; shark J occupied an area approximately 142 km^2 at Hinchinbrook Entrance (an adult salmon migration corridor) for at least 29 days after release.

The actual movement paths of sharks J and L were less linear than 90% and 94% of random movement paths, respectively, but were not significantly less linear than the simulated LI values. The home range shape (ECC) for shark J was indistinguishable from that resulting from random movement, but the home range shape for shark L was significantly less elongate than the simulated values. ECC did not explain why more variation existed for home range shape than for site fidelity but home range shape was probably was more influenced by the constraining effects of the coastline.

We did not receive enough location fixes to test shark K for site fidelity. However, based on the overall distance, direction, and rate of movement we judged that shark K movements exhibited focal foraging movements as well. Shark K was still within Port Gravina 34 days after release and averaged 0.21 km/day overall.

2. *Foraging dispersals.* We characterize foraging dispersals as wanderings away from tagging sites at focal foraging areas in PWS, but lingering in PWS or GOA to forage (Figures 2, 5, and 6, Table 2). Sharks F, G_1 (from July 18 -December 2), H, I, M and N dispersed away from capture locations at Port Gravina and Hinchinbrook Entrance PWS but remained in PWS or the GOA for 2+ months after release (95, 141, 174 and 203*, 68 and 111 days, respectively). Overall movements of sharks F, H, I, M and N were derived from two-point locations and were therefor unsuitable for AMAE site fidelity

analyses. However, based on the overall distance traveled, rate and/or direction of travel, we classified their movements as foraging dispersals (Figures 2, 5, and 6, Table 2). Shark F moved to the southwest and was near Kodiak Island in late October; shark H took almost 6 months to move approximately 700 km to waters 150 km west of Baranof Island. While shark I eventually moved a considerable distance to the south (1,714 km), it's overall rate of travel was 8 km/day and we surmise that much of the 203 days since release were spent in the GOA. The final locations acquired for sharks M and N showed they had dispersed more than 50 km from their release locations at focal foraging areas in Port Gravina and at Hinchinbrook Entrance, but were still in PWS when final tag locations were recovered (Figure 5, Table 2). Note that shark L eventually began moving away from Port Gravina, but at least 52 of 59 days the shark was tracked were spent within Port Gravina.

Results of the AMAE site fidelity for the first 141 days of detailed movements for shark G (G_1) were not significant (P = 60; Table 4); thus, we fail to reject H_o: the observed movement is random. We received 48 Argos satellite derived locations from the tag during the 141 day random dispersal period of shark G's movement (Figure 6). Segments of the dispersal phase of shark G's movement track appear to qualify as focal foraging movements; after release at Hinchinbrook Entrance shark G spent 1.5 months at Port Gravina and eventually moved to Shelikof Strait, where it spent approximately one month in an area utilized by overwintering herring (Clupea pallasi) before beginning a deliberate migration to the south in early December (Figure 6). Overall, however, shark G's movements for the first 141 days qualified as a foraging dispersal as the pattern was random and the shark remained in PWS and the GOA and averaged only 4 km/day.

The linearity (LI) and eccentricity (ECC) of the shark G_1 movement path were not significantly different than those resulting from random movement.

3. *Directed migrations:* In this context, we characterize migrations as rapid, highly dispersed and highly linear movements across hundreds to thousands of kilometers to the southeast. Six of nine sharks (67%) that left PWS (sharks A, B, C, D, E, and G1) exhibited directed migratory behavior (Figures 2, 3 and 4; Tables 2 and 4).

AMAE site fidelity analyses of detailed movement paths for sharks A, B, and G_2 showed the actual MSDs were greater than 95% of the simulated values for each shark (Table 4). Since under the null hypothesis of random movement the actual movement paths should deviate from only 5% of the random movements by chance, these results are highly significant. Thus, actual space was more dispersed (actual MSD significantly greater than simulated MSD) than random movement.

The movement paths of sharks A and G_2 were significantly more linear and eccentric than those of random movement paths. The movement path of shark B was not significantly more eccentric or linear from those resulting from random movement. However, the movement path of shark B was more linear that 82.4% of the random movement paths and more eccentric than 93.1% of the random movement paths.

Shark A left PWS shortly after it's release, and in 22 days was off the southern coast of Queen Charlotte Island in British Columbia, Canada (Figure 3). The shark averaged 58 km /day (straight-line distance), and traveled at least 1,800 km while traversing 1,278 km. The shark surfaced long and often enough to provide 94 Argos satellite derived locations during the 22 days we received transmissions from the tag.

Shortly after December 2, after spending 141 days in the northern GOA, Shark G (G_2) began a deliberate movement from near Kodiak Island to off southern California (Figure 3). The shark averaged 99 straight-line kilometers per day for 33 days, and traversed 3,270 km (straight line distance) by January 8. The track length during this directed movement was 3,790 km, across which we collected 73 location fixes.

Shark B immediately left Port Gravina after release and moved through Montague Strait, out of PWS (Figure 4). Within 5 days the shark had moved 260 km where it spent several days near the continental shelf break south of PWS. By August 12 shark B had moved another 540 km east to the shelf break 95 km southwest of Cape Spencer. Five days later, on August 17, it had moved another 260 km to 170 km southeast of Cape Ommaney on Baranof Island. Overall, shark B traveled more than 1000 km in 26 days and averaged 30 km/day. Shark B was the only male shark tagged with a satellite transmitter. We received 26 Argos satellite derived locations during the 26 days we received transmissions from the tag.

Overall movements of sharks C, D, and E were derived from two-point locations and were therefor unsuitable for AMAE site fidelity analyses. However, based on the overall distance, direction, and rate of movement we judged their movements to exhibit migratory behavior as well. All three sharks moved rapidly to the southeast after release. Shark C traveled 1,917 km in 39 days and averaged 49 km/day overall; shark D traveled 2,163 km in 61 days and averaged 35 km/day overall; and shark E traveled 1,049 km in 48 days and averaged 22 km/day overall.

4. *Annual fidelity to PWS focal foraging areas*. Recaptures 1 + years later near release locations in PWS suggest some sharks might have annual fidelity to focal foraging areas in PWS. Sharks 0, P, and Q were recaptured at Hinchinbrook Entrance within 50 km of their release locations after 1.0, 2.9, and 3.0 years at-large, respectively (Figure 5, Table 3).

Depth and ambient temperature distribution

Archival depth and temperature data transmitted by PAT tags describe daily depth range and mode and temperature range of two sharks that moved rapidly south (sharks C and D; Figure 9), and two sharks that appear to have dispersed from PWS but lingered in the northern GOA before moving south (sharks H and I; Figure 10). All four sharks were tagged with PAT tags and released in Port Gravina during mid-July. Sharks C and D traveled large distances in relatively short periods of time at an average rate of 49 and 35 km per day, respectively. However, the vertical movement behavior of these sharks were quite dissimilar. While traversing 1,917 km in 39 days, shark C dove to depths greater than 100 m during 19 of 39 (48%) days and attained a maximum depth of 528 m. Shark C had a bimodal depth distribution at 0-2 m (46%) and 10-40 m (24%). Shark D traversed 2,163 km in 61 days, dove to depths greater than 100 m during 58 of 61 (95%) days and attained a maximum depth of 668 m. Shark D had a bimodal depth distribution at 0-2 m (36%) and 100-500 m (39%). Maximum and minimum ambient temperatures experienced by both sharks during the entire tracking periods show they remained in therma1ly stratified water and regularly dove through the thermocline. In contrast, sharks H and I had a slower overall rate of travel to the south, averaging 4 and 8 km per day, respectively. Their vertical movement behavior was also quite similar. While traversing 700 km in 173 days, shark H dove to depths greater than 100 m during 81 of 173 (47%) days and attained a maximum depth of 348 m. Shark H had a bimodal depth distribution at 0-2 m (18%) and 20-60 m (37%). The bimodal distribution was particularly pronounced during July and August (25% at 0-2 m and 47% at 20-60 m). Shark I traversed 1,714 km in 203 days, dove to depths greater than 100 m during 53 of 71 (75%) days for which there is data. Shark I attained a maximum depth of 520 m. Shark I also had a bimodal depth distribution at 0-2 m (16%) and 20-60 m (29%). Maximum and minimum ambient temperatures experienced by sharks H and I show they remained in thermally stratified water until mid October when the seasonal thermocline collapsed.

Salmon shark abundance estimates (Objective 2)

Aerial Surveys: From surface shark counts made along strip transects by our spotter pilot we estimated there were 500 salmon sharks at the surface in Beartrap Bay (region B) at the head of Port Gravina on July 6, and 2000 salmon sharks at the surface northeast of Parshas Bay (region A) on August 16,2000 (Figure 12). The shark aggregations covered 12 km^2 in Region A and 1.5 km^2 in region B.

Acoustic and Vessel Surveys: We sampled 30 km of pre-determined transects within two strata in Port Gravina (Figure 11). The sharks were not frequenting surface waters on the two days we ran the systematic transects, although we observed 10 sharks breaching near the vessel. Locations of the breaching sharks are indicated by squares along transects. Analysis of the hydroacoustic echo data with SonarData Echoview software revealed no discernable shark targets. Analysis of the sonar data also did not reveal clearly discernable shark targets. Therefore, statistical analysis of the data and shark abundance estimates from the data were not possible.

Salmon shark diet composition (Objective 3)

Of the 51 salmon shark stomachs analyzed, adult Pacific salmon (pink salmon, *Oncorhynchus gorbuscha,* chum salmon, *Oncorhynchus keta*, and coho salmon, *Oncorhynchus kisutch*) were the most important prey as measured by percent number

(35%) and percent weight (76%; Table 5). Teuthoidea squid was the second most important prey by percent number (30%) and sablefish, *Anoplopoma fimbria,* was the second most important prey item by percent weight (11.4%). Other teleost prey included Pacific herring *(Clupeapallasi),* rockfish *(Sebastes spp.),* Eulachon *(Thaleichthes pacificus),* Capelin *(Mallotus villosus),* Arrowtooth flounder *(Atheresthes stomas),* and codfishes (Gadidae). Non teleost prey included squid and spiny dogfish *(Squalus acanthias).* All sharks sampled for stomach contents were captured in July and August, during the period of peak Pacific salmon spawning aggregations in the PWS region.

To-date, none of the sharks released with Star -Oddi data storage tags in their stomachs have been recovered. Two Roto tags have since been spotted on sharks as they swam at the surface; tag #6 (Star-Oddi tag *'00-6)* was spotted in Port Gravina in mid-August, *2001* (Trowbridge, C., personal communication, *2000*)*,* and tag: #12 (Star-Oddi tag '00-12) was seen in Port Gravina in May *2001* (Anka, D. personal communication, 2001).

Table 5. Summary of salmon shark diet from the contents of 51 stomachs collected in Prince William Sound during July and August 1999-2001 expressed as percent number (%N) and percent weight (%W).

Prey Items	%N	%W
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 (*Thaleichthes 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

Salmon shark prey consumption estimate (Objective 4)

We estimate that during 45 days in July and August 2000, salmon sharks consumed 263,000 kg of prey in Port Gravina. The time period corresponds to the estimated period of peak seasonal abundance of salmon sharks and Pacific salmon in the bay.

The biomass (B) of prey consumed by salmon sharks in Port Gravina in 2000 was calculated as;

$$B = DxRxSxW,$$

where D is the estimated number of days the sharks occupy focal foraging areas in Port Gravina (= 45 days), *R is the estimate of salmon shark daily ration expressed as % body weight (= 2%), S is the estimated number of salmon sharks foraging in the bay in '00 (= 2000), and W is the mean body weight of salmon sharks caught in the region (= 146 kg; n = 18). *We had hoped to refine our daily ration estimates with archived depth and temperature data from Star-Oddi deployed in 12 shark stomachs. However, we were unable to recover any of the tags. Therefore, we deferred to the estimate for daily ration used by Nagasawa (1998).

DISCUSSION/SUMMARY

What is the role of the salmon shark as a top predator in the trophic ecology of PWS during summer? The project was designed to address this question by estimating the biomass and composition of prey consumed by salmon sharks during the period of peak seasonal residency of salmon sharks in Port Gravina. Our field sampling objectives focused on estimating consumption calculation parameters by (1) estimating the period of peak salmon shark residency in PWS and Port Gravina by describing shark movements from conventional tag recoveries and locations provided by satellite tag transmissions, (2) estimating salmon shark abundance during the period of peak seasonal residency in Port Gravina during summer 2000 based on aerial strip surveys, and (3) estimating salmon shark diet composition during summer in PWS and refining existing estimates of daily ration (Nagasawa 1998) with archived stomach temperature data from data storage tags deployed in shark stomachs, (4) estimating the average weight of salmon sharks inhabiting PWS during summer by measuring the weight of sharks caught during summer field sampling operations. From these parameters we calculated the estimated annual biomass and species composition of prey consumed by salmon sharks in Port Gravina in July and August 2000.

Salmon shark movements and seasonal residency - Based on our observations, we propose four modes of movement for salmon sharks in the GOA and eastern North Pacific Ocean: focal foraging movements, foraging dispersals, directed migrations, and annual fidelity to PWS focal foraging areas. Focal foraging movements are constrained to relatively small geographic regions at adult Pacific salmon migration corridors and staging areas. As the summer salmon runs taper off, the sharks disperse; some continue to reside in PWS and the GOA into fall and winter, while others undergo directed, often neatly linear southeasterly migrations hundreds to thousands of kilometers toward the west coasts of Canada and the continental United States. Recaptures near release locations after 1-3 years at-large suggests some degree of seasonal affinity to focal foraging areas in PWS.

Salmon sharks exhibit a high degree of site fidelity during summer within two distinct focal foraging areas in PWS, located where adult salmon concentrate as they return to streams and hatcheries in summer. Port Gravina is one of many staging areas where adult salmon aggregate before entering their natal streams. Hinchinbrook Entrance is one of four narrow passes, or migration corridors through which adult salmon must converge as they migrate into PWS from the GOA. The sharks begin aggregating in late June as early chum salmon runs move into PWS. Nearly continuous pulses of chum, pink, and coho salmon concentrate and hold large numbers of foraging salmon sharks as late as September. Our observations indicate that principal large salmon shark aggregations in PWS coincide in time and space with adult salmon spawning migrations during July and August. Salmon sharks have also been observed in PWS near Pacific herring overwintering aggregations (Oct. -Feb.), and spawning aggregations (primarily April-May) (Moffitt, S., personal communication, 2000). Salmon sharks inhabit the GOA throughout the year (Hart 1973), but large aggregations typically disperse from focal foraging areas in PWS as salmon runs taper off in fall.

Salmon shark diet composition and daily ration - How important are species other than salmon in the diet of salmon sharks in PWS during summer when salmon are abundant? Adult Pacific salmon are the principal prey during summer months in PWS, but salmon sharks appear to be opportunistic predators and consume sablefish, walleye pollock, herring, rockfish and squid even when adult salmon are abundant. Nearly 24% of the prey biomass found in salmon shark stomachs from PWS was represented by species other than salmon. Sablefish appears to important in salmon shark diet, perhaps because of their high oil content. The sharks sampled for diet in Port Gravina had only salmon and squid beaks in their stomachs and salmon appear to be the principle prey consumed in the bay during July and August.

Because salmon sharks are endothermic and maintain high body temperatures (25-26 ºC) in cold ambient water, their energetic demands could require daily rations in the order of 4-8% (or more) of their body weight per day (Block, B., personal communication, 1999). Because were unable to recover any of the archival stomach tags that we hoped would enable us to develop empirical estimates of daily ration, we deferred to Nagasawa's (1998) daily ration estimate of 2% body weight per day for our biomass calculations.

Salmon shark abundance estimates - Confidence in the precision of our overall consumption estimate depended largely upon the success of a statistical abundance estimation based on sharks counted along line transects with hydroacoustic remote sensing gear. Unfortunately, the acoustic gear we used either failed to effectively discern sharks in the water column, or the sharks were not present in significant numbers. Explanations for non detection of sharks by the remote sensing gear include: (1) the sharks were missed because of the narrow area swept by the acoustic beams, (2) the echo strength from salmon sharks was indiscernible from salmon or other teleost targets in the region, (3) the 120 kHz single beam systems we used might be better suited to discerning smaller fish, (4) salmon sharks are poor sound reflectors because they have no swim bladder, and (5) the sharks were not present. However, observations of numerous sharks breaching at the surface and success with "blind" fishing with purse seine and hand lines when sharks were not observed at the surface strongly suggests to the authors that salmon sharks were abundant when and where we sampled with the hydroacoustic gear.

We ultimately based our overall abundance estimate on aerial counts made along strip transects in 2000. From aerial survey counts in Port Gravina we estimated there were at least 500 sharks at the surface on July 6, 2000, and on August 16, 2000 there were at least 2,000 sharks at the surface. We based our overall abundance estimate on the largest of the two estimates because both of the estimates only consider sharks that were only visible at the surface in relatively small regions of Port Gravina and were therefore likely quite conservative.

Salmon shark prey consumption estimate - Based on our estimates for the preceding parameters, we calculated that salmon sharks consumed at least 263,000 kg of prey in Port Gravina during summer, 2000. Is this a realistic estimate? In 2000, pink salmon averaged 1.5 kg and chum salmon averaged 3.7 kg in Port Gravina (Moffitt, S., personal communication, 2003). If we assume the sharks consumed equal proportions of pink and chum salmon by weight the sharks would have consumed 116,000 pink salmon and 36,000 chum salmon. Based on the ADF&G escapement and commercial harvest estimates for Port Gravina in 2000, the sharks would have consumed 80% of the pink salmon escapement (145,242 fish), 14% of the pink salmon commercial harvest (842,364 fish), 54% of the chum salmon escapement (66,862 fish), and 63% of the chum salmon harvest (56,906 fish; Johnson et al. 2002; Moffitt, S., personal communication, 2003). We believe our overall consumption estimate (263,000 kg) is conservative because: (1) we likely underestimated daily ration because salmon sharks are endothermic and their energetic demands likely require more than the 2% body weight per day estimate we used in our calculations, and (2) we likely underestimated salmon shark abundance in Port Gravina because we only counted sharks we could see from our spotter aircraft.

While the accuracy of the estimate can certainly be debated as to how conservative, the direction and significance of the consumption to the salmon run is real. Low salmon runs at a time of high salmon shark survival could be devastating until shark numbers decline or redistribute (in other words, switch prey) away from adult salmon staging areas.

What environmental and human induced changes have taken place in the north Pacific Ocean that could have affected salmon shark abundance in the Gulf of Alaska?

Anecdotal reports of large surface aggregations of salmon sharks, often numbering in the thousands, increased abruptly in the northeast GOA during the mid 1990s. Have environmental and or human induced changes taken place in the north Pacific that could affect salmon shark abundance in PWS? There has been much speculation whether perceived salmon shark increases in PWS during the mid-1990s represent an actual population increase, or whether the sharks simply discovered under-utilized prey-fields during summer in PWS. Quantitative data do not exist to support anecdotal evidence of increases in salmon shark abundance in eastern North Pacific Ocean during the 1990s. However, a recent report indicates that salmon shark catch rates in the western and central North Pacific Ocean was low from 1984 to 1993, but increased sharply in 1996 and thereafter remained at a high level (Nagasawa et al. 2002). Considerable numbers of juvenile salmon sharks were taken as bycatch from 1978 to 1992 in large-scale pelagic driftnet fisheries in the North Pacific. A moratorium on these fisheries in 1992 eliminated an important source of salmon shark removals on the high seas. Near elimination of those fisheries by 1992 could have contributed to an increasing salmon shark population throughout the north Pacific Ocean.

Salmon sharks often segregate geographically by size and sex (Nagasawa 1998, Tanaka 1980; Sano 1962). Nakano and Nagasawa (1996) and Blagoderov (1994) suggest that salmon shark nursery grounds are situated in open waters of the North Pacific Ocean adjacent to the highly productive subarctic boundary and transitional domain (Figure 13). Small salmon sharks (70-110 cm total length) were caught in Japanese salmon research gillnets and were concentrated adjacent to parturition grounds suggested by Blagoderov (1994). Adult salmon sharks are distributed north of the subarctic boundary (Nakano and Nagasawa 1996), with the largest sharks in the western North Pacific found in the Sea of Okhotsk and Bering Sea (Blagoderov 1994). Patterns of sexual segregation also increase with increasing latitude. Sexual composition in the western North Pacific Ocean is male dominated; 90% are males north of 52ºN (Sano 1962, Nagasawa 1998). Salmon shark sexual composition in the eastern North Pacific Ocean is female dominated with increasing latitude; 85-92% are females north of 50ºN (Goldman and Musick 2000). Of the 91 sharks sexed during our study in PWS (60ºN, 87 (95.6%) were females.

Data from multinational observer programs beginning in the late 1980s and Japanese high seas salmon gillnet surveys from 1981 to 1991 suggest the majority of salmon sharks taken in high seas gillnet fisheries were juveniles (McKinnell and Seki 1998, Nakano and Nagasawa 1996). The mean total length of salmon sharks sampled in the Japanese flying squid driftnet fishery in 1991 (35ºN- 46ºN; 145ºW-170ºE) was 117.8 cm (SD = 39.2 cm, n = 69). The mean pre-caudal length of female salmon sharks caught during our study was 178 cm; average weight was 146 kg. Size at maturity for female salmon sharks in the western North Pacific Ocean has been estimated to occur at 8-10 years and 170-180 cm pre-caudal length (Tanaka 1980). Yatsu et al. (1993) estimated 56,029 salmon sharks averaging 38.7 kg were caught in the Japanese flying squid driftnet fishery in 1990. Preliminary analyses of maturity from female salmon shark reproductive tracts and age analyses from vertebrae suggest the majority of the female salmon sharks aggregating in PWS are just coming into maturity and represent strong year classes corresponding to the moratorium on pelagic driftnet fisheries in 1992 (Gallucci, V., 2002 personal communication).

Prior to 1992, recruitment of juvenile salmon sharks into the adult population was likely reduced during many years of bycatch in the North Pacific Ocean by industrial fishing fleets. Regions of high fishing pressure often overlapped with salmon shark parturition and nursery grounds suggested by Blagoderov (1994; Figure 13). Until 1992, Japan, the Republic of Korea and Taiwan participated in large-scale pelagic driftnet fishing in the North Pacific Ocean. Japanese mothership driftnet salmon fisheries operating in the North Pacific beginning in 1952 were significantly reduced in 1977, mainly due to the declaration of 200-mile exclusion zones (Yatsu et al. 1993). From the late 1970s to 1992, large-scale pelagic driftnet fisheries in the North Pacific targeted flying squid *(Ommastrephes bartrami),* tunas (Scombridae), and billfishes (Istiophoridae; McKinnell and Seki 1998). The monthly northern fishing boundary fluctuated between 40ºN and 46ºN to minimize the incidental take of salmonids, with fishing effort mostly confined within three degrees of latitude from the northern boundary (Yatsu et al. 1993). This strategy concentrated fishing effort within or adjacent to salmon shark nursery grounds.

Apparent salmon shark increases in GOA during the mid-1990s followed 10-15 years after a trophic regime shift in the northeast Pacific Ocean, which was initiated by an increasing frequency of warm ocean climate events beginning in winter 1977 (Anderson and Piatt 1999; McGowan et al. 1998; Anderson et al. 1997; Bechtol 1997; Bailey et al. 1995). Biological consequences following the ocean climate shift included a marked improvement of groundfish production and improved Pacific salmon marine survival (Hilborn and Eggers 2000; Downton and Miller 1998; Francis and Hare 1994; Beamish and Bouillon 1993). These changes and increased salmon hatchery output in the 1980s resulted in sharply increasing trends in north Pacific salmon and groundfish production in the GOA. The overall increase in salmon shark prey species likely benefitted the sharks.

The convergence of environmental and human induced changes in the northeast Pacific Ocean help explain strong anecdotal evidence of a rapid increase in salmon sharks in the region. We propose the apparent increase in salmon shark abundance in the GOA is due to a convergence of factors, including: (1) the moratoria on high seas industrial driftnet fishing in 1992; (2) trophic regime shifts which resulted in sharp increases in salmon, cod, and flatfish production during the 1980s and 1990s; (3) Pacific salmon hatchery production in PWS, Kodiak Island, and Southeast Alaska during the 1980s and 1990s, and; (4) a northward shift in range as the as the salmon shark population matures. Due to these factors and salmon sharks' longevity, we predict their abundance and importance as top predators in PWS and the GOA will likely increase. Because salmon sharks occupy the highest trophic level in the food web of subarctic waters, and their apparent increase during the 1990s, we believe salmon sharks should be more closely monitored as a possible keystone species.

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FIGURES

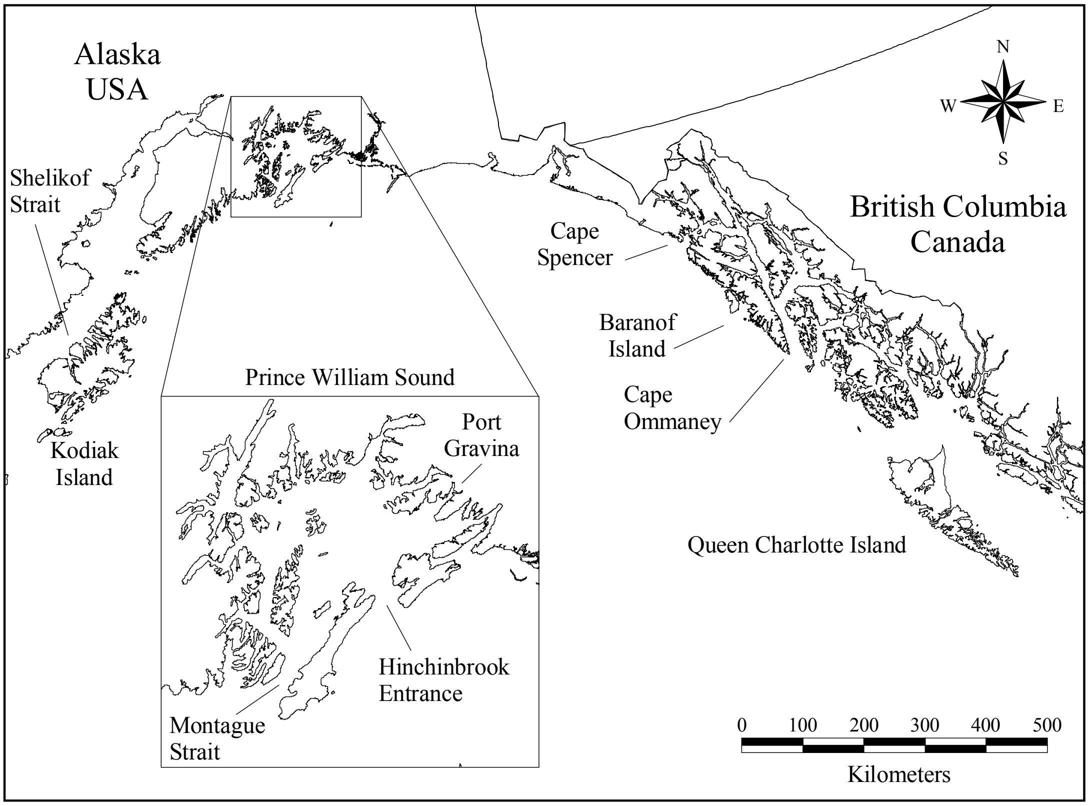

Figure 1. Location of directed salmon shark study (Port Gravina and Hinchinbrook Entrance, Prince William Sound, Alaska), and place names in the Gulf of Alaska and northeast Pacific Ocean.

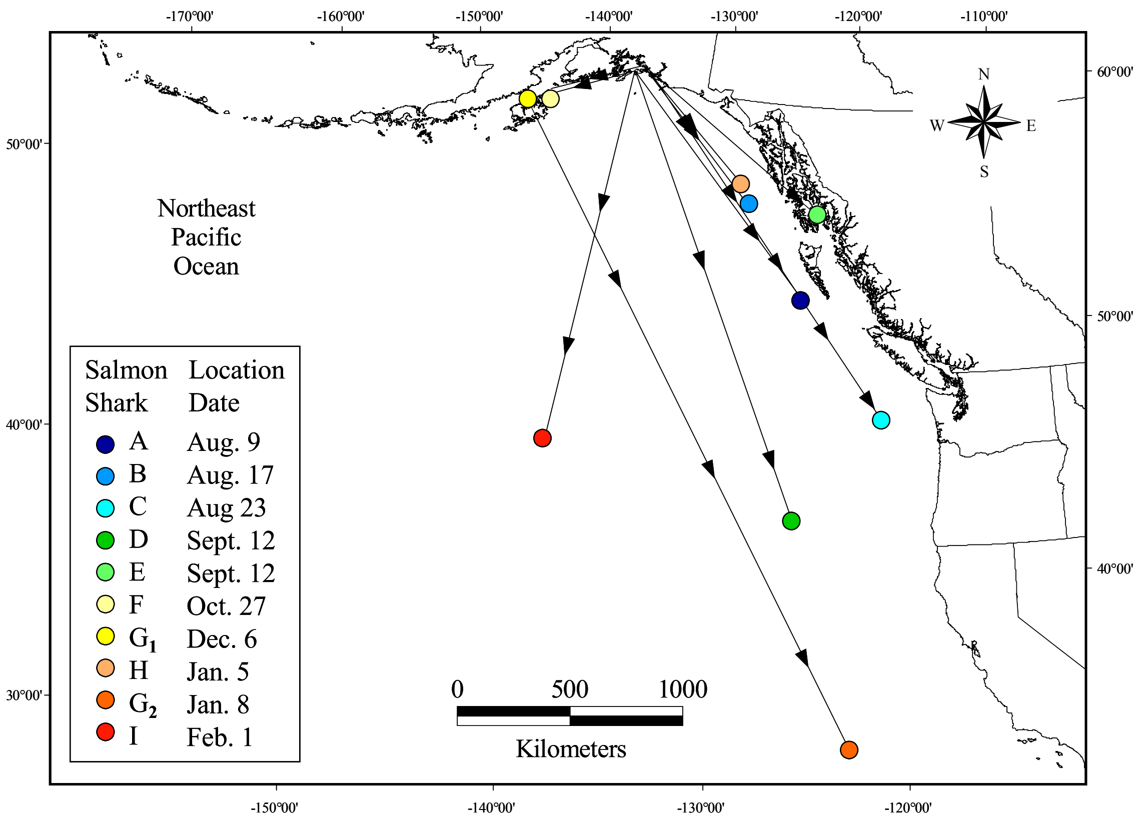

Figure 2. *Lamna ditropis.* Large-scale movements of salmon sharks tagged in Prince William Sound during July 1999-2001. Locations are from Global Positioning System at time of release, recapture location (shark E), and Argos Satellite-derived end-point positions (sharks A, B, C, D, F, G, H, and I). The two locations indicated for shark G are just prior to a directed southerly movement (G_1), and the final location obtained from tag transmissions (G_2).

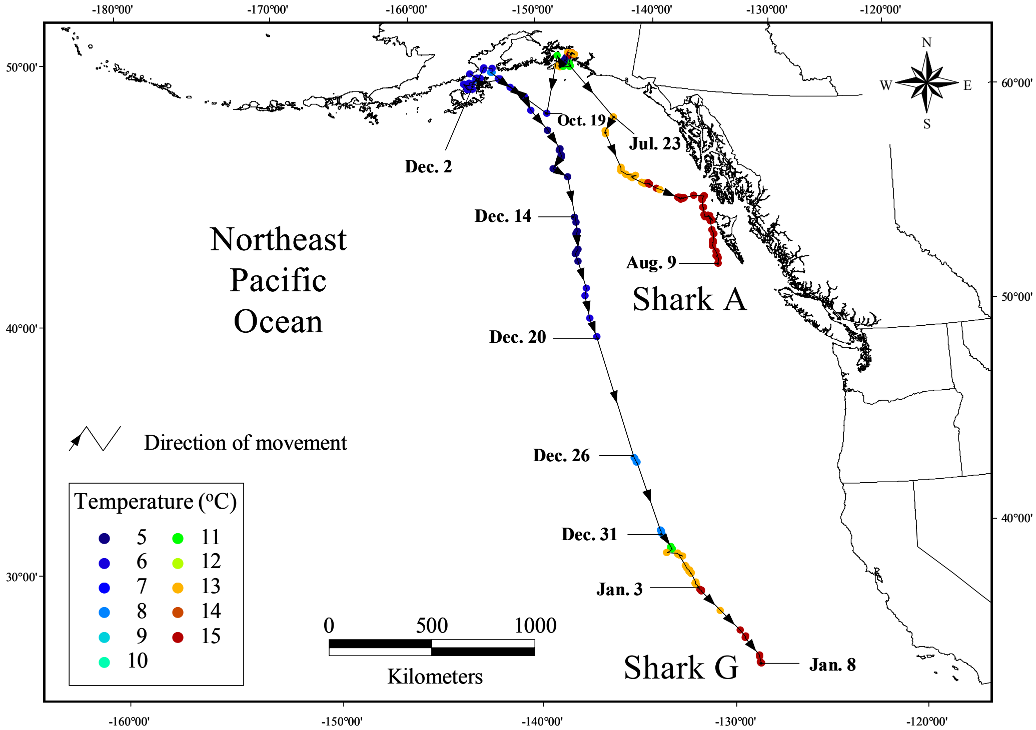

Figure 3. *Lamna ditropis*. Migratory movements and temperature modes of salmon sharks A and G during summer-winter 2001-2002. The data are Argos satellite-derived locations from SPOT2 tag transmissions, and color coded ambient temperature modes encountered by the sharks. Both sharks were released at Hinchinbrook Entrance, Prince William Sound, on July 18, 2001. The location points are connected in chronological order; black lines with arrows indicate overall direction of movement between locations.

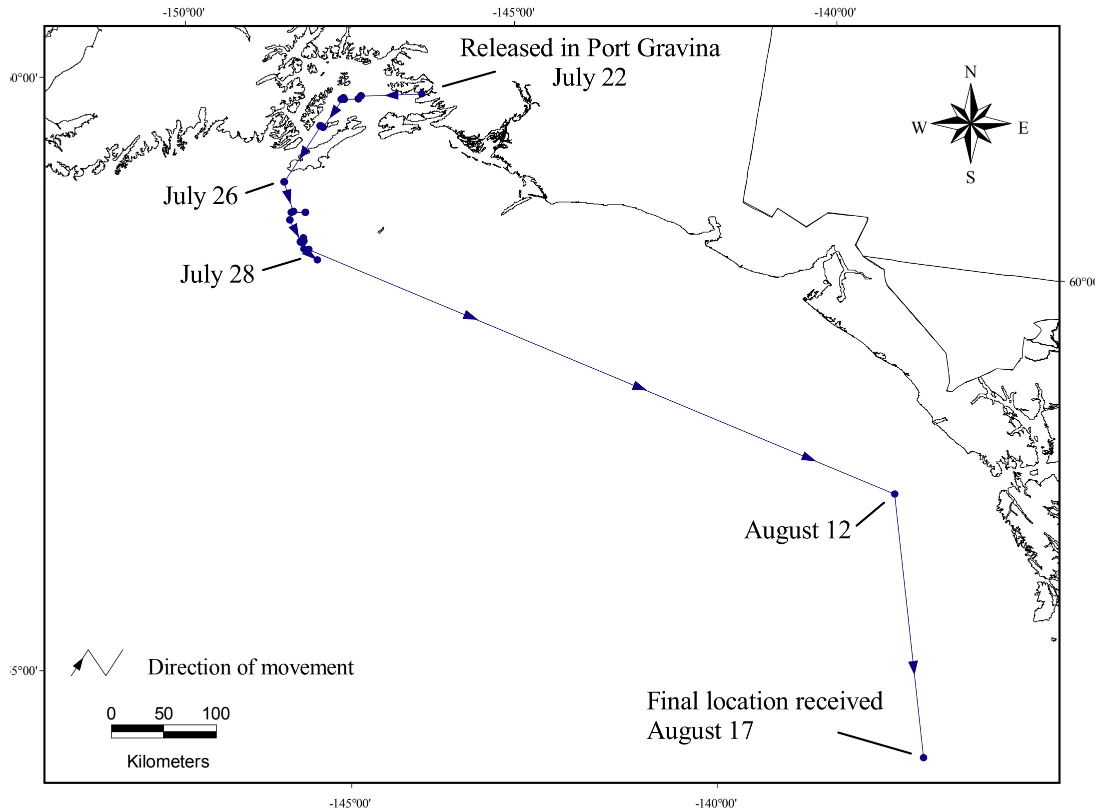

Figure 4. *Lamna ditropis.* Migratory movements of salmon shark B during July and August 2000. The data are Argos satellite-derived locations from a KiwiSat tag. The shark was released at Port Gravina, Prince William Sound, on July 22, 2000. The location points are connected in chronological order; blue lines with arrows indicate overall direction of movement between locations.

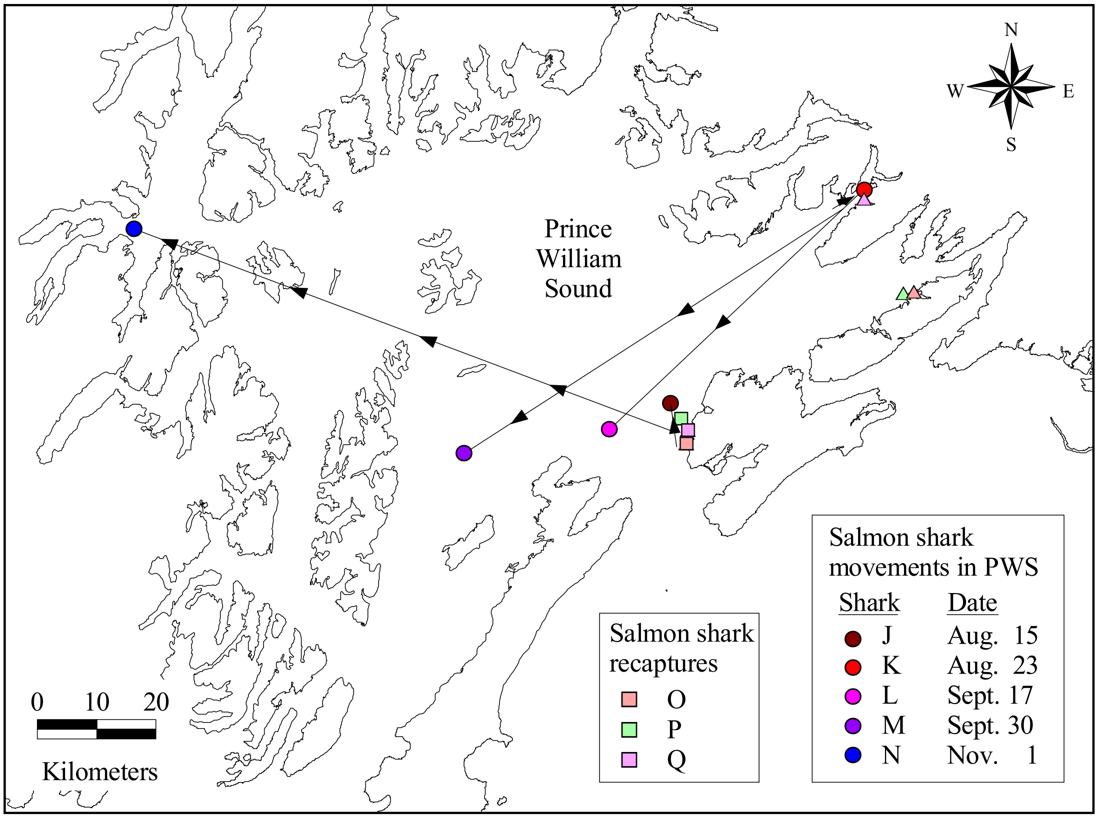

Figure 5. *Lamna ditropis*. Salmon shark movements from Argos satellite-derived end-point locations (circles, sharks J-N), and the release (triangles) and recapture (squares) locations of conventionally tagged sharks (sharks O - Q), within Prince William Sound. Sharks O - Q were recaptured by sport fishermen 3, 3, and 1 years after release, respectively. Lines with arrows indicate overall direction of movement from the release locations.

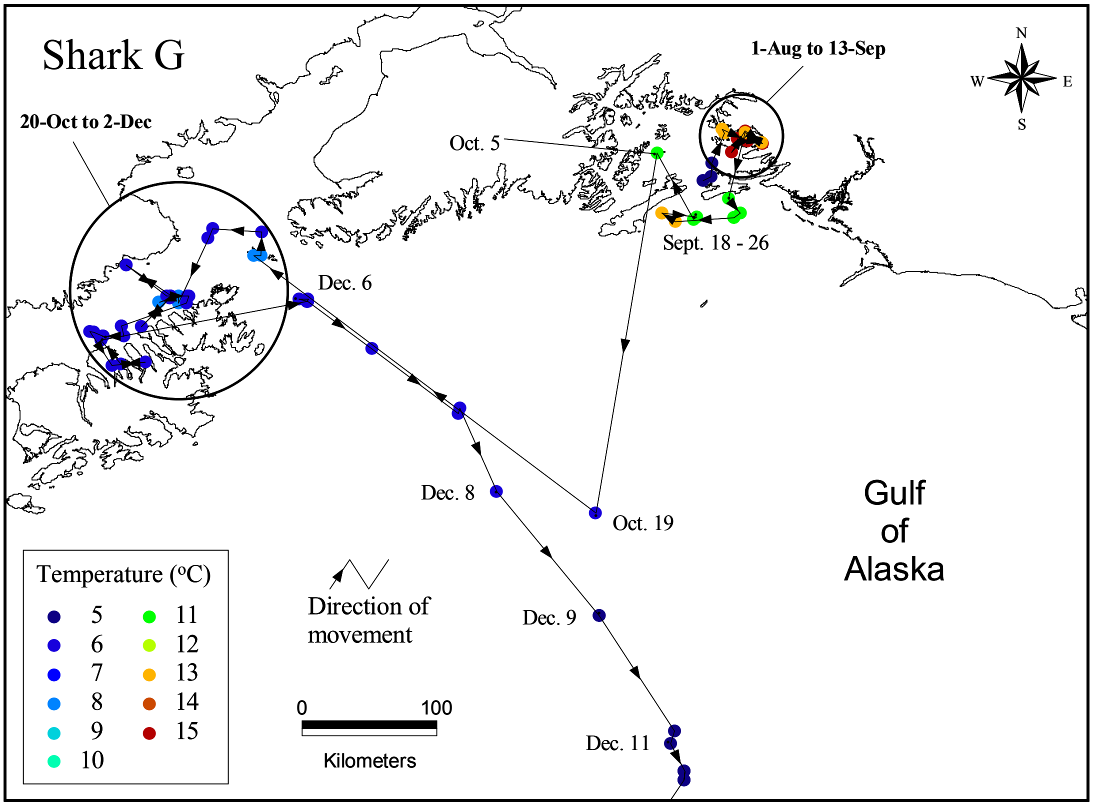

Figure 6. *Lamna ditropis*. Foraging movements and temperature modes of salmon shark G in northern Gulf of Alaska. The figure is a detail of shark specimen G movements in the northern extent of it's range during fall/winter 2001 (see Figure 4). The data are Argos satellite-derived locations from SPOT2 tag transmissions, and color coded ambient temperature modes encountered by the shark. Shark G was released at Hinchinbrook Entrance, Prince William Sound, on July 18, 2001. The location points are connected in chronological order; black lines with arrows indicate overall direction of movement between locations.

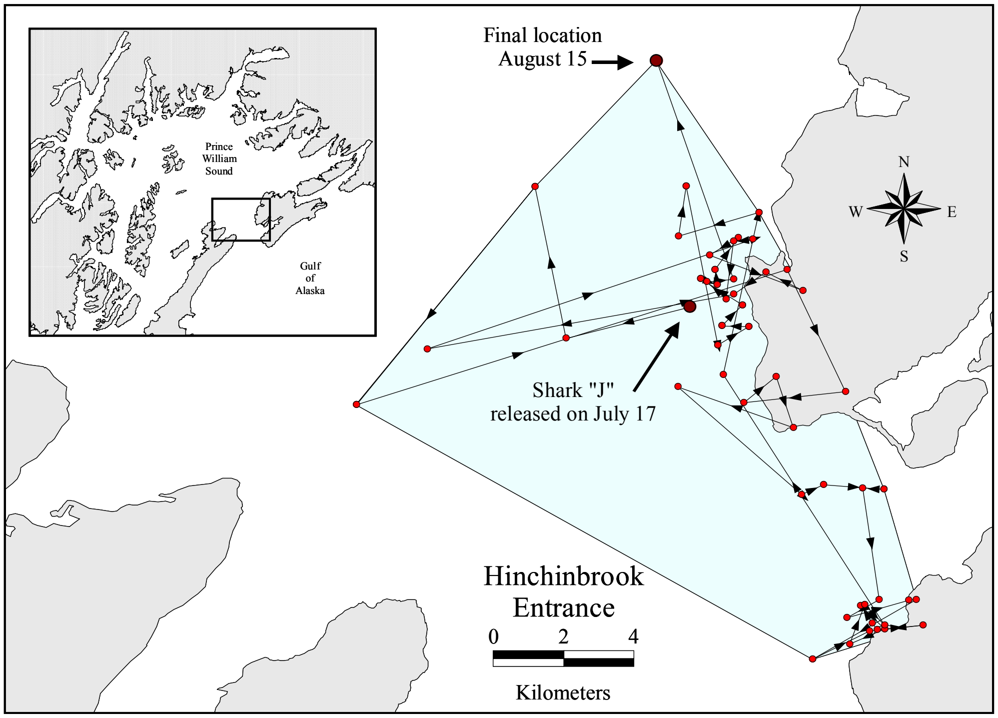

Figure 7. *Lamna ditropis*. Focal foraging area and movements of salmon shark J at Hinchinbrook Entrance, Prince William Sound; July 17 to August 15, 2001. Location points (red dots) are connected in chronological order; black lines with arrows indicate overall direction of movement between locations. The focal foraging area (blue area) was estimated using the minimum convex polygon method (MCP; Mohr 1947).

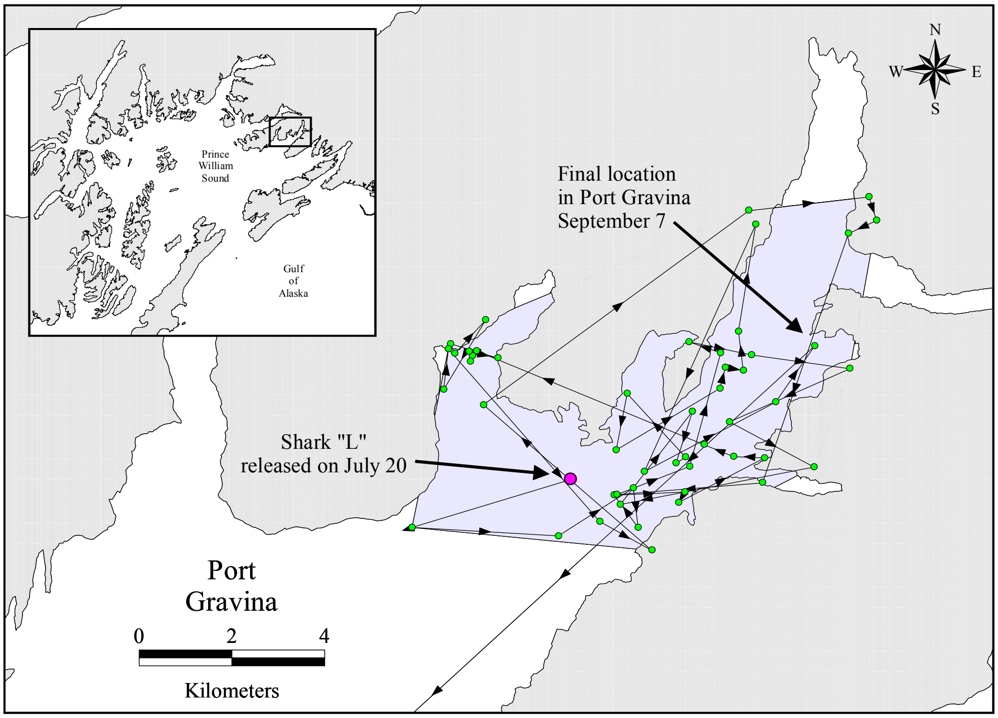

Figure 8. Lamna ditropis. Focal foraging area and movements of salmon shark L in Port Gravina, Prince William Sound; July 20 to September 7, 2000. Location points (green dots) are connected in chronological order; black lines with arrows indicate overall direction of movement between locations. The focal foraging area (purple area) was estimated using the minimum convex polygon method (MCP; Mohr 1947).

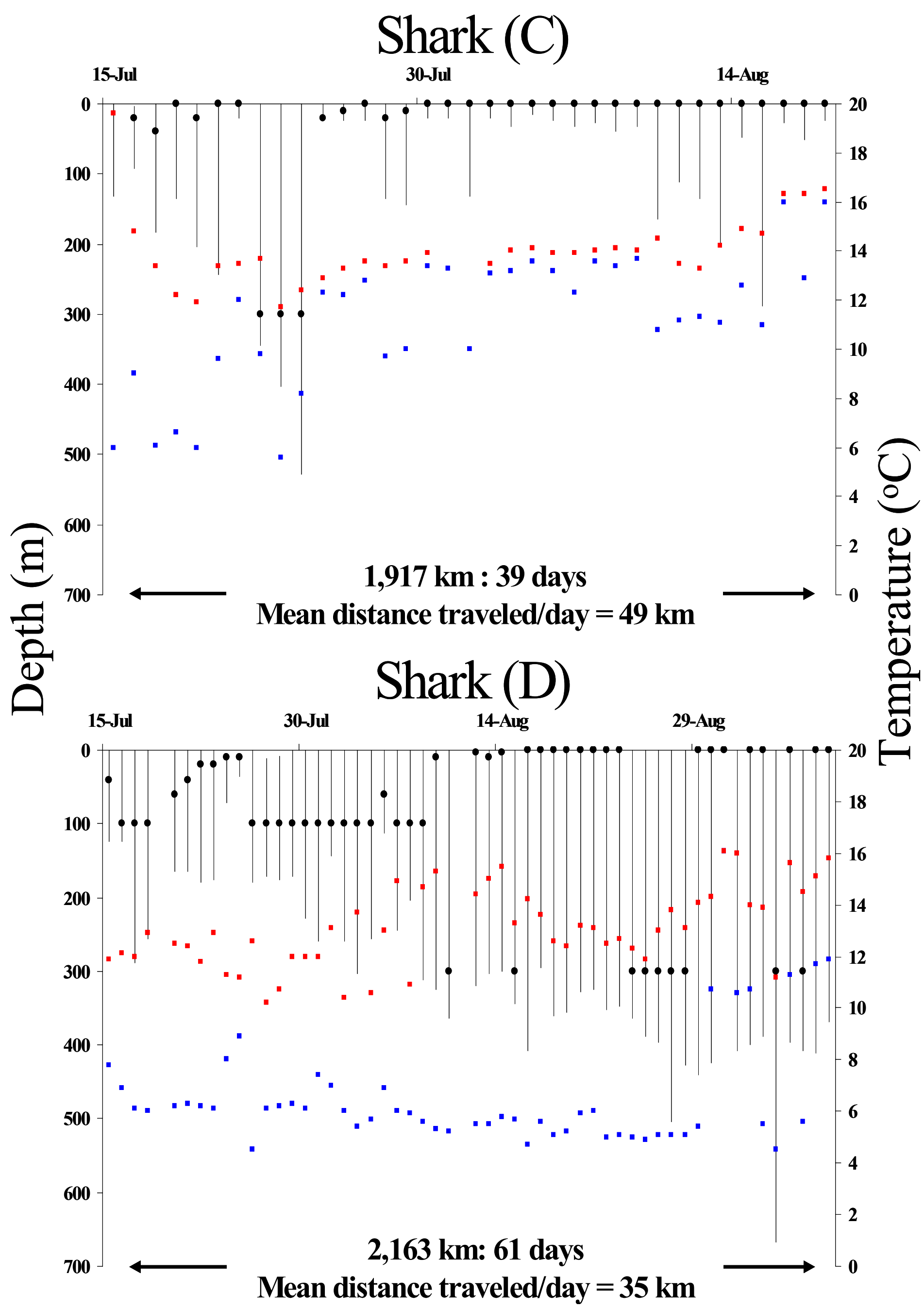

Figure 9. *Lamna ditropis*. Daily depth and temperature range and depth mode for salmon sharks C and D. Both sharks were tagged in Port Gravina in mid-July, 2001. The data were obtained from Wildlife Computers PAT tag transmissions to the Argos satellite system. Figure 2 shows the shark's locations at time of pop-up. Vertical black lines are daily depth range, black points are daily depth mode. Red and blue points are the maximum and minimum daily ambient temperatures encountered by the sharks, respectively.

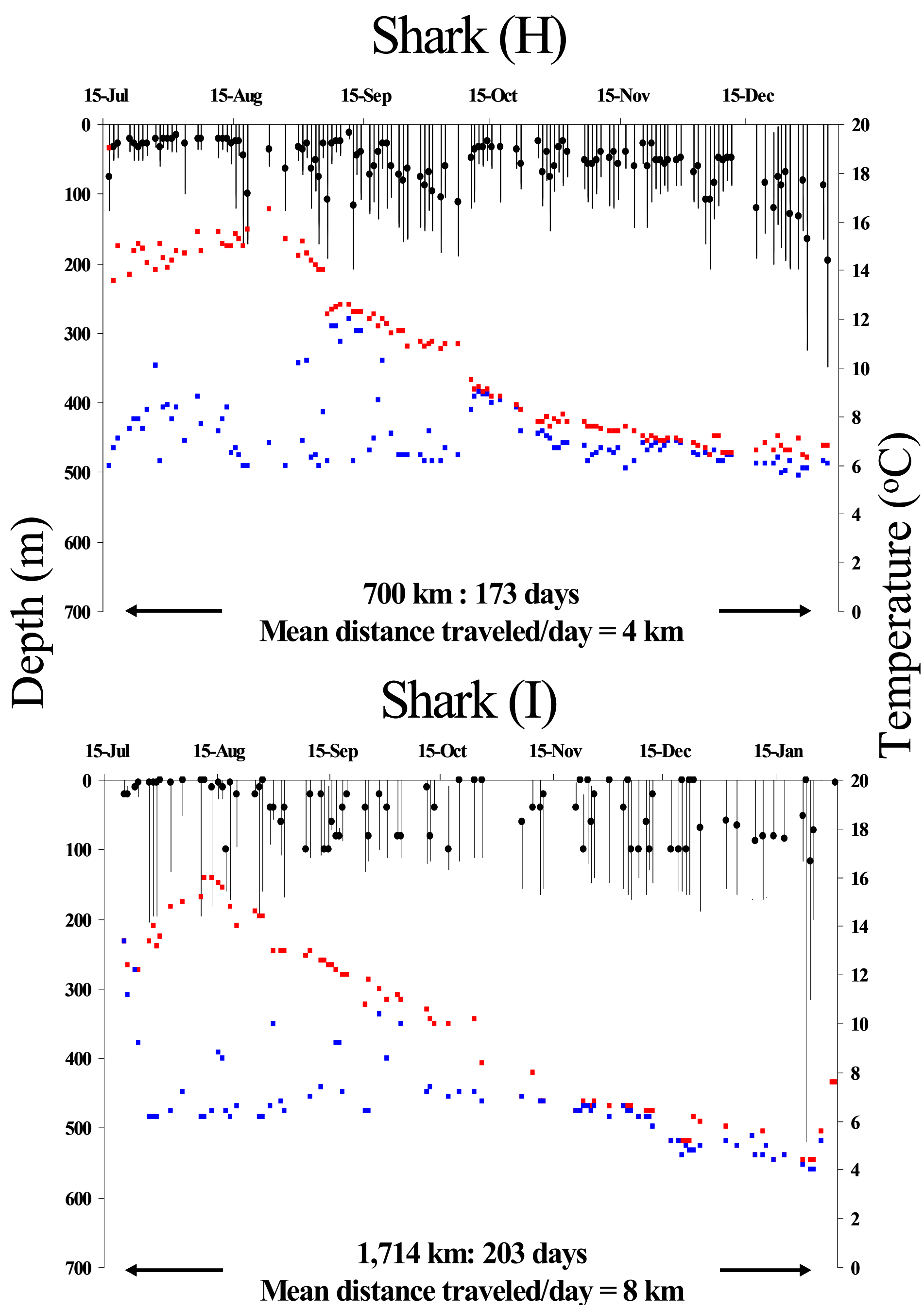

Figure 10. *Lamna ditropis*. Daily depth and temperature range and depth mode for salmon sharks H and I. Both sharks were tagged in Port Gravina in mid-July, 2001. The data were obtained from Wildlife Computers PAT tag transmissions to the Argos satellite system. Figure 2 shows the shark's locations at time of pop-up. Vertical black lines are daily depth range, black points are daily depth mode. Red and blue points are the maximum and minimum daily ambient temperatures encountered by the sharks, respectively.

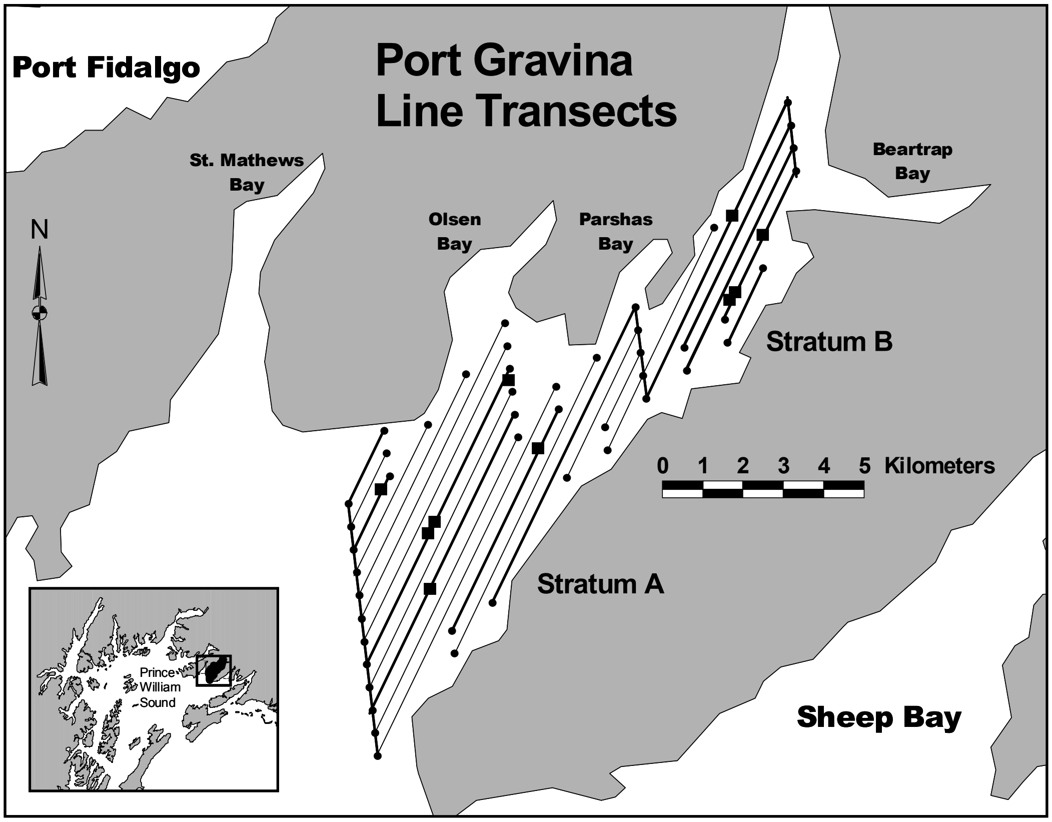

Figure 11. Stratified systematic line transects sampled during July 2000 in Port Gravina, Prince William Sound with simultaneous side-looking and down-looking Biosonics hydroacoustic systems. Squares indicate locations of salmon sharks visually spotted at the surface during the survey. Sampled transects were randomly selected and are indicated by the thick lines. Stratum A was chosen to represent an area of low shark concentration and Stratum B was chosen to represent an area of high shark concentration based upon aerial survey data.

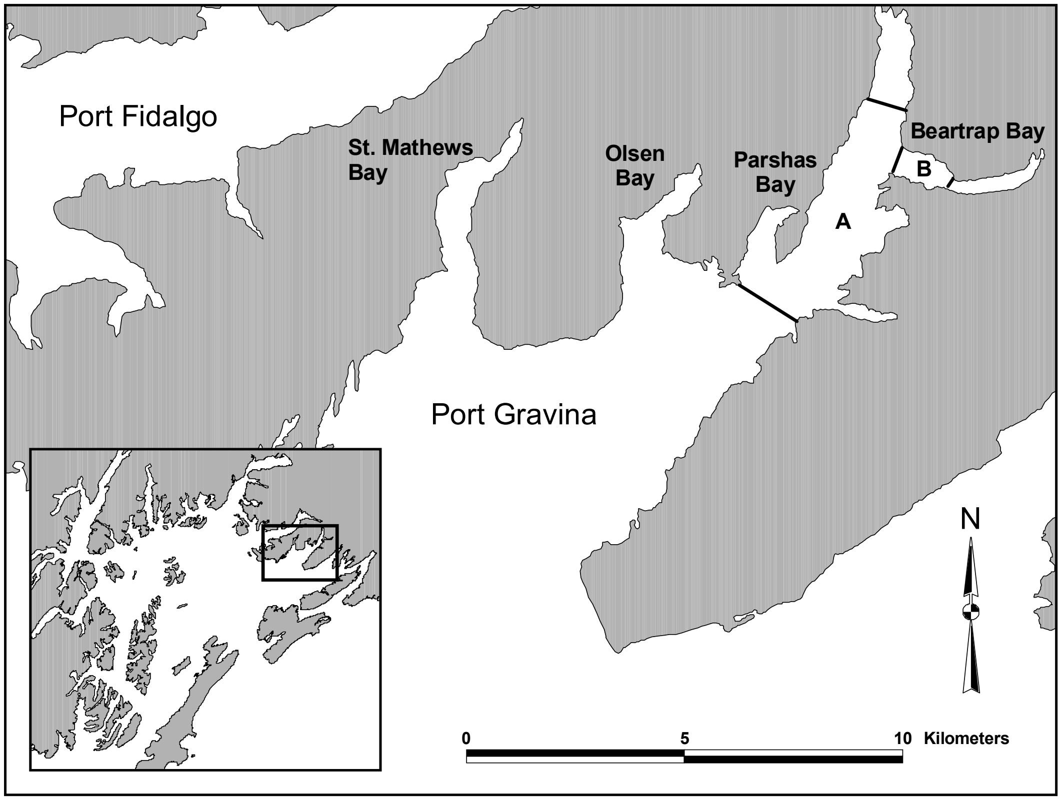

Figure 12. Geographic location of areas where intensive strip search patterns were flown by a spotter pilot for the purpose of estimating salmon shark abundance. An estimated 500 salmon sharks were at or near the surface of region A on the morning of July 6, 2000; and 2000 salmon sharks were estimated to be at or near the surface of region B on the afternoon of August 16, 2000.

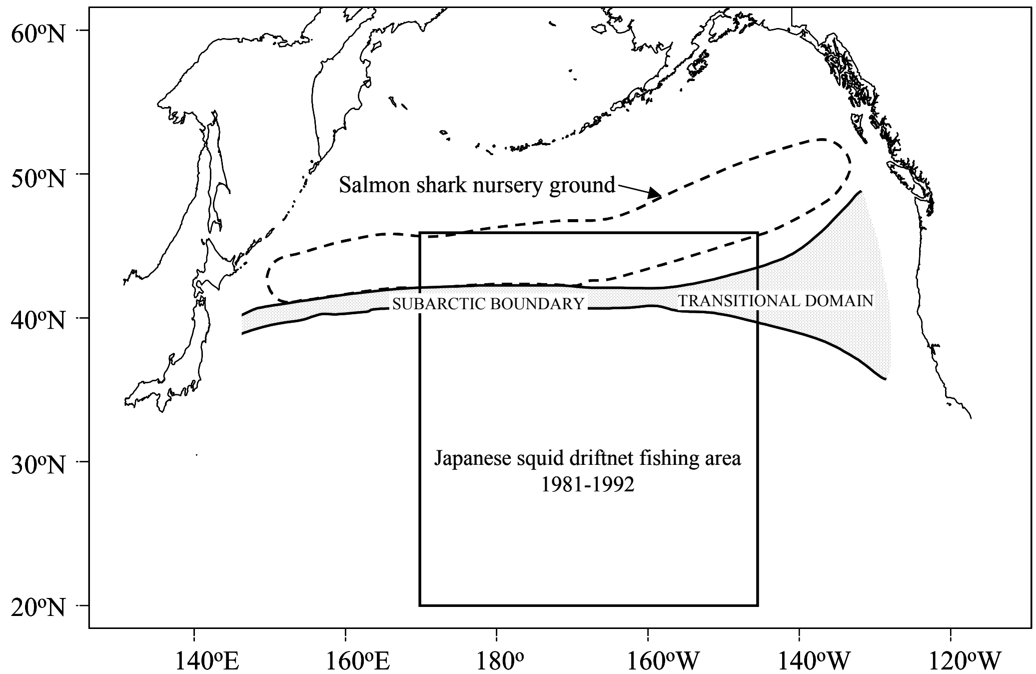

Figure 13. Schematic map of proposed salmon shark nursery grounds (after Nakano and Nagasawa 1996), and Japanese driftnet fishing grounds for flying squid, 1981-1992 (after Yatsu et al. 1993).