



# New insights into spatial segregation by sex and life-history stage in blue sharks *Prionace glauca* in the northwestern Pacific

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**ABSTRACT:** Spatial segregation is a key component to understand the ecology of highly migratory species; however, this aspect is poorly known for many pelagic shark species. We investigated spatial segregation by sex and life-history stage in blue sharks *Prionace glauca* in the northwestern Pacific, using satellite tracking data gathered from 74 electronic tags as well as fisheries-dependent size-measurement datasets, which allowed us to update a schematic diagram of the migration patterns of this population. Blue sharks were tracked for 30 to 271 d (mean 125 d) during which they moved extensively between temperate and subtropical waters. Juveniles were distributed mainly in the North Pacific Transition Zone (30°–45° N), but expanded their range southward as they grew, while adults in the entire northwestern Pacific showed clear spatial segregation by sex. Adult females migrated seasonally between temperate and subtropical areas for reproduction, while adult males occupied a broad distribution area yet mainly in temperate waters (30°–40° N), and their habitats partially overlapped with those of juveniles of both sexes. These findings provide new insights for updating the schematic migration diagram of this population, especially because adult males were previously thought to distribute mainly in tropical and subtropical waters. Furthermore, a majority of adult females found north of 30° N exhibited fresh mating scars; this observation suggests that the mating ground of blue sharks in the northwestern Pacific is broader (20°–40° N) than previously thought (20°–30° N), and partially overlaps with the parturition and nursery grounds of this species (30°–50° N).

**KEY WORDS:** Sexual segregation · Habitat use · Migration · Mating ground · Horizontal movement · Distribution · Satellite tracking

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## 1. INTRODUCTION

Spatial segregation by sex and life-history stage is a widespread behavior and evident in many species of elasmobranchs (Klimley 1987, Sims 2005); adult males and females often use different habitats either within the same area or between different areas. Their spatial segregation can result from both social and ecological factors such as temporal mating patterns,

intraspecific competition, population density, prey availability, and energetic requirements (Wearmouth & Sims 2008, 2010, Mucientes et al. 2009). Knowledge of spatial segregation in sharks is key to understanding their ecology and population dynamics and has resonance in the successful management and conservation of populations (Wearmouth & Sims 2010).

The blue shark *Prionace glauca* (Carcharhinidae) is an ecologically and economically valuable species

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that plays an important role in pelagic ecosystems. This species is one of the most abundant pelagic predators, with a circumglobal distribution in temperate to tropical waters (Nakano & Stevens 2008) owing to higher productivity with faster growth and larger numbers of offspring compared to other pelagic sharks (Fujinami et al. 2017, 2019, Kai & Fujinami 2018). Blue sharks are a common bycatch in longline fisheries targeting swordfish (Campana 2016) in addition to being a target of commercial fisheries (e.g. Hiraoka et al. 2016). Stock assessments of this species have been conducted by several regional tuna fisheries management organizations to implement appropriate management measures.

Based on fisheries-dependent data (i.e. catch and size-measurement data), Nakano (1994) defined a schematic migration model for blue sharks in the North Pacific, wherein (1) mating takes place in early summer in subtropical waters at 20°–30°N; (2) parturition occurs during spring in temperate waters at 30°–40°N; (3) juvenile males are found mainly at 30°–35°N, whereas juvenile females predominate above 35°–40°N; and (4) adults inhabit the entire North Pacific between the Equator and 45°N, and they spatially segregate by sex. Similar distributions and migration patterns have been observed for blue sharks in the North Atlantic and South Atlantic, based on bycatch and tracking data (e.g. Montealegre-Quijano & Vooren 2010, Vandeperre et al. 2014a,b, 2016). A recent study using pop-up satellite archival tags (PSATs) of pregnant blue sharks in the northwestern Pacific revealed seasonal northeast–southwest migration (Fujinami et al. 2021) and strongly supported the adult female migration patterns proposed by Nakano (1994). However, the migration patterns of adult males and other life-history stages (i.e. juveniles of both sexes) have not yet been verified by satellite tracking data in the northwestern Pacific. Moreover, the mating ground proposed by Nakano (1994) remains uncertain because of a paucity of data on mating scars on females (Suda 1953).

Developments in satellite tracking technology allow us to investigate animal behaviors in oceanic environments where direct observation is not possible. To date, several authors have reported ample information about the movements of blue sharks using satellite tags deployed in the Atlantic (Queiroz et al. 2010, 2012, Campana et al. 2011, Vandeperre et al. 2014a, 2016, Howey et al. 2017), Indian (Heard et al. 2018), and Pacific Oceans (Stevens et al. 2010, Musyl et al. 2011, Maxwell et al. 2019, Fujinami et al. 2021). These previous telemetry studies revealed various patterns of migration (e.g. seasonal, trans-Atlantic,

and latitudinal) and vertical movement (e.g. diel vertical). Several reports have described spatial segregation in blue sharks (e.g. Vandeperre et al. 2014a, Howey et al. 2017), and one study (Maxwell et al. 2019) revealed that adult males and juvenile females partially overlap in some habitats in the northeastern Pacific. Although a recent tagging study described the migration pattern of pregnant blue sharks in the northwestern Pacific (Fujinami et al. 2021), information from satellite tags about the movements of blue sharks in the central and western North Pacific is lacking compared with other oceans (Queiroz et al. 2019).

We aimed to verify spatial segregation by sex and life-history stage in blue sharks in the northwestern Pacific, using both fishery-independent data (satellite-tracking data gathered from 74 electronic tags) and fishery-dependent data (broad-scale size-measurement datasets), and to update the schematic diagram of sex-specific migration patterns for juvenile and adult sharks, including the populations' mating ground and habitats during different life-history stages, as presented by Nakano (1994). We re-evaluated the spatial extent of the mating ground for blue sharks in the northwestern Pacific based on our observations of the existence and condition of mating scars on adult females, in both temperate and subtropical waters, in conjunction with information gathered about the migrations of adult sharks.

## 2. MATERIALS AND METHODS

### 2.1. Satellite tagging

Blue sharks were captured by a Japanese research vessel (RV 'Shunyo-maru') and a chartered vessel ('Den-maru No. 37') equipped with longline gear, operating in the northwestern Pacific (18°–37°N, 130°–158°E), in October 2015–2016 and May 2017, and in April–May 2017–2019, respectively. Live blue sharks captured by the research vessel were retrieved from the water using a 'scooper' (a square basket-like device on the vessel designed to scoop up large-sized fish; Nakano et al. 2003, Fujinami et al. 2021) and were physically restrained using 2 ropes around the body while they remained on the scooper, whereas sharks captured by the commercial vessel were brought on board for the tagging procedure. During tagging, the gills of sharks were ventilated using seawater irrigation and their eyes were covered with a damp black cloth to reduce stress. Sex was visually determined by the presence or absence

of claspers (present in males). Dorsal length (DL, to the nearest cm) was measured as the distance from the first-dorsal-fin origin to the second-dorsal-fin origin. For the data analysis, DL was converted to precaudal length (PCL, distance from the tip of the snout to the precaudal pit) using the relationships:  $PCL = 2.51DL + 12.33$  for males, and  $PCL = 2.62DL + 7.48$  for females (Fujinami et al. 2017). The maturity stage of tagged males was identified as adult or juvenile (including subadults) based on clasper condition (adult males have calcified claspers). For females, pregnancy state (pregnant or not) was judged based on direct observation via ultrasonography (Fujinami et al. 2021) and/or by analysis of sex steroid hormones in the blood (Fujinami & Semba 2020). In case such measurements were unobtainable, the maturity stage was inferred from length at 50% maturity for North Pacific blue sharks (160.9 cm PCL for males, 156.6 cm PCL for females: Fujinami et al. 2017).

We tagged 92 blue sharks with either a PSAT (MiniPAT, Wildlife Computers) or a smart position or temperature transmitting (SPOT) tag (SPOT6, Wildlife Computers), and 5 individuals in 2019 were double tagged with both a PSAT and a SPOT tag. PSATs ( $n = 90$ ) were attached to sharks using a plastic umbrella dart (Domeier et al. 2005) inserted into the dorsal musculature lateral to the first dorsal fin. The umbrella tip was attached to the PSAT with a fluorocarbon tether secured with crimps and encased in silicone tubing; the posterior part of the tag was fixed to prevent swing of the PSAT (Fujinami et al. 2021). The PSATs archived a time-series of data for ambient water temperature ( $\pm 0.1^\circ\text{C}$ ), depth ( $\pm 0.5$  m) at 600 s intervals, and relative light intensity (in the range of  $5 \times 10^{-12}$  to  $5 \times 10^{-2} \text{ W cm}^{-2}$ ) after the tagged sharks were released. These tags were programmed to automatically detach from the shark if (1) the user-defined deployment period (180, 240, or 270 d) was over; (2) the shark showed no significant vertical movement (within a range of  $\pm 2.5$  m) recorded over 5 d; or (3) the shark descended to a depth of over 1700 m. SPOT tags ( $n = 12$ ) were fixed to the first dorsal fin of sharks using 3 nylon bolts and stainless-steel locknuts, and washers (Kai & Fujinami 2020). The bolts were passed through holes that were drilled through the fin using a cordless drill. When the tag antenna is above the sea surface and the wet/dry sensor on the tag reads 'dry state,' the tag activates transmission to the Argos system and provides the geographic position with a high degree of accuracy. A conventional tag was also attached to the dorsal musculature behind the first dorsal fin of each satellite-tagged shark. After the tagging procedure, if possible, any hook was removed

from the shark's mouth before it was released. Sharks were retained on the scooper or boat deck for 3–6 min to complete the tagging and measurements.

## 2.2. Analysis of satellite tracking data

Light-based geolocation of the PSATs was performed using a hidden Markov state-space model (manufacturer's proprietary Global Position Estimator 3 software: GPE3, Wildlife Computers) based on the methods of Pedersen et al. (2011) and Basson et al. (2016). The GPE3 uses recorded data (dawn and dusk light readings, depth, sea surface temperature [SST], and the tagging and pop-up locations) and corresponding reference data on satellite-based SST (NOAA Optimum Interpolation [OI] SST version 2 High-Resolution Dataset, <https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html>) and bathymetry with 1-degree step (NOAA ETOPO1 Global Relief Model, version Bedrock, <https://www.ngdc.noaa.gov/mgg/global>). The speed parameter in GPE3 was used to build daily diffusion kernels that govern allowable movement distance of individuals per day. We chose 7 individuals with longer deployments (Sharks 3, 16, 26, 39, 48, 58, 71) to set the multiple speed parameter ( $1\text{--}7 \text{ km h}^{-1}$ ). Model runs with  $7 \text{ km h}^{-1}$  as the speed parameter yielded the highest location scores and were deemed appropriate. Since the output of the GPE3 model can provide a probability distribution across the state-space, at each time step in the model, at a resolution of  $0.25^\circ$ , we used the location with the highest probability per day (only the midnight estimates) for the track of each individual in the movement analyses. This type of light-based model has been shown to produce accurate location estimates from tag data with root-mean-squared error values of  $<2.4^\circ$  in latitude and  $<0.52^\circ$  in longitude, when compared with known locations (Basson et al. 2016, Nasby-Lucas et al. 2019). To determine differences in the SST experienced by tagged sharks, by sex and life-history stage, recorded temperature–depth profiles were interpolated to 1 m intervals using a smoothing spline to account for differences in the sampling intervals between profiles (Fujinami et al. 2021). To compare the environmental preference among 4 components (JM: juvenile males; JF: juvenile females; AM: adult males; AF: adult females), the density of SST records was plotted by sex and life-history stage for 2 areas (temperate and subtropical waters) divided by the latitude  $35^\circ\text{N}$ , which was determined to be the thermal front boundary for the Kuroshio–Oyashio Transi-

tion Zone (TZ), with Area 1 to the north of 35° N and Area 2 to the south.

SPOT tags transmit to the Argos satellite system that estimates the location and accuracy of the position by calculating a Doppler-based geolocation while passing over a tagged shark, with associated location error when the shark is at the sea surface, referred to as location class (LC). The position accuracy was classified as either LC 3 (<250 m), LC 2 (250–500 m), LC 1 (500–1500 m), LC 0 (>1500 m), LC A or LC B (non-guaranteed accuracy), or LC Z (invalid). Firstly, we removed the LC Z data for the subsequent analyses. To remove unrealistic outlier locations, the remaining data of raw position estimates (LC 3, 2, 1, 0, A, B) were analyzed point-to-point with a 3 m s<sup>-1</sup> course speed filter using the 'argosfilter' package (Freitas et al. 2008) in R software (version 3.6.1, R Core Team 2019). Subsequently, a regular time-series of locations per day was estimated for each individual track using a continuous-time correlated random walk model ('crawl' package in R; Johnson et al. 2008), while accounting for Argos location error.

To examine the seasonal spatial segregation patterns of blue sharks, by sex and life-history stages, we estimated seasonal home-range parameters using kernel utilization distributions (KUDs) based on the most probable daily locations. We formatted the location data from the electronic tags as a 'SpatialPoints' object using the 'sp' package (Pebesma & Bivand 2005). The KUDs were estimated using the 'kernelUD' function of the 'adehabitat HR' package (Calenge 2006, 2019) with a reference bandwidth ('href') for all datasets. Equal grid intervals (number of grid intervals = 150) were used to estimate 50% (core home range) and 95% (home-range extent) KUDs of blue sharks by sex and life-history stage. A 95% utilization distribution overlap index (UDOI) (Fieberg & Kochanny 2005) derived from the 'kernel-overlaphr' function of the 'adehabitat HR' package was also used to elucidate spatial overlap of habitat range among the sexes and life-history stages. A minimum value of 0 in UDOI indicates no dyadic overlap, and a maximum value of 1 indicates high overlap with uniformly distributed ranges. Four seasons (quarters: qt) were defined as follows: qt 1 = January to March; qt 2 = April to June; qt 3 = July to September; and qt 4 = October to December.

### 2.3. Analysis of fisheries-dependent data

To supplement our determination of the migration patterns of blue sharks estimated from the satellite

tracking data, we used fisheries-dependent size-measurement datasets for blue sharks, collected between 1967 and 2018 by Japanese research and training vessels (longline and driftnet fisheries), and Japanese commercial longline fisheries operating in the northwestern Pacific (0°–50° N, 125°–180° E). The datasets (n = 122 135 individuals), which included operational time (year, month, and day), fishing location (the latitude and longitude in each operation were converted to 1° × 1° grid spacing), and sex and body size of the specimens, were used for evaluating the sex distribution and seasonal spatial distribution of blue sharks for different sizes. Maturity stages for both sexes were identified based on length at 50% maturity for North Pacific blue sharks (Fujinami et al. 2017).

A generalized additive model (GAM) with a binomial error distribution and logit link function was used to predict season-, sex-, and life-history-stage-specific probability of presence for blue sharks. To compile presence or absence datasets by season, sex, and life-history stage, the size-measurement dataset was aggregated by cruise and set information. The presence or absence of each component by set across the survey area (n = 28 320 sets) was defined as the response variable. Location (interaction term between latitude and longitude) defined as a continuous smoothed explanatory variable was estimated using thin-plate regression splines. Model parameters were estimated using the R package 'mgcv' (Wood 2019). We assumed that the blue sharks have different distribution patterns by season, sex, and life-history stage. Since 'mgcv' cannot simultaneously treat more than 3-way interactions, we predicted a probability of presence for blue sharks by each season and sex/life-history stage component (i.e. JM, JF, AM, AF) separately and mapped along the survey area with 1° × 1° grid spacing for each model.

### 2.4. Observation of mating scars on adult females

To elucidate the mating ground of blue sharks in the northwestern Pacific, we observed AF for the presence of mating scars (i.e. bite wounds or scars) and their condition (fresh [bleeding or open wound]: shortly after mating; or healed [no bleeding and closed wound]: several weeks or months have passed after mating behavior) among sharks caught in both temperate and subtropical waters during the parturition and mating season (i.e. spring–summer; Fujinami et al. 2017). Mating scars, which are regularly observed on the body or fins of females, are made by

males during courtship and mating (e.g. Stevens 1974, Pratt 1979). In this observation analysis, we used records gathered from Japanese research vessels and photo or film data collected by a Japanese scientific observer program. We regarded the waters where females with fresh mating scars were observed during the mating season as the mating grounds.

### 3. RESULTS

#### 3.1. Movement patterns

Of the 102 tags deployed on 97 blue sharks, 85 tags (75 PSATs and 10 SPOT tags) successfully transmitted data on their movements via the Argos system (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m696p069\\_supp.pdf](http://www.int-res.com/articles/suppl/m696p069_supp.pdf)). Among the 85 tags, the data of 11 PSATs that had popped up within 30 d of tagging were excluded from subsequent analysis because the data strongly suggested that the shark had either died (i.e. the shark suddenly sank to a depth of over 1700 m within a short period after tag-

ging) or the tag had been preyed on (the temperature recorded by the tag increased suddenly to  $>25.0^{\circ}\text{C}$  irrespective of the water depth). We did not use the vertical movement data in this study; but when we checked, evidence of abnormal behavior caused by tag attachment was not observed in the remaining tag data, so we used all tracking data from the deployment start to the deployment end. Tracking periods of the sharks with the remaining 74 tags ranged from 30 to 271 d (total 8855 d, mean tracking duration 125 d). The PCL ranges of tagged sharks were 120.3–168.0 cm ( $n = 18$ , mean 149.6 cm) for JM, 109.7–138.5 cm ( $n = 2$ ) for JF, 165.4–233.2 cm ( $n = 27$ , mean 191.1 cm) for AM, and 141.1–243.3 cm ( $n = 24$ , mean 187.3 cm) for AF (Fig. S1). Most juveniles of both sexes were considered to be subadults. Overall, the satellite-tracked sharks displayed wide-ranging movements in the northwestern Pacific (Fig. 1) and they traveled distances ranging from 938 to 13419 km (mean 4014 km). However, none of the tagged sharks crossed the international date line or the Equator.

Among juvenile blue sharks, JM displayed extensive movements, especially latitudinally between

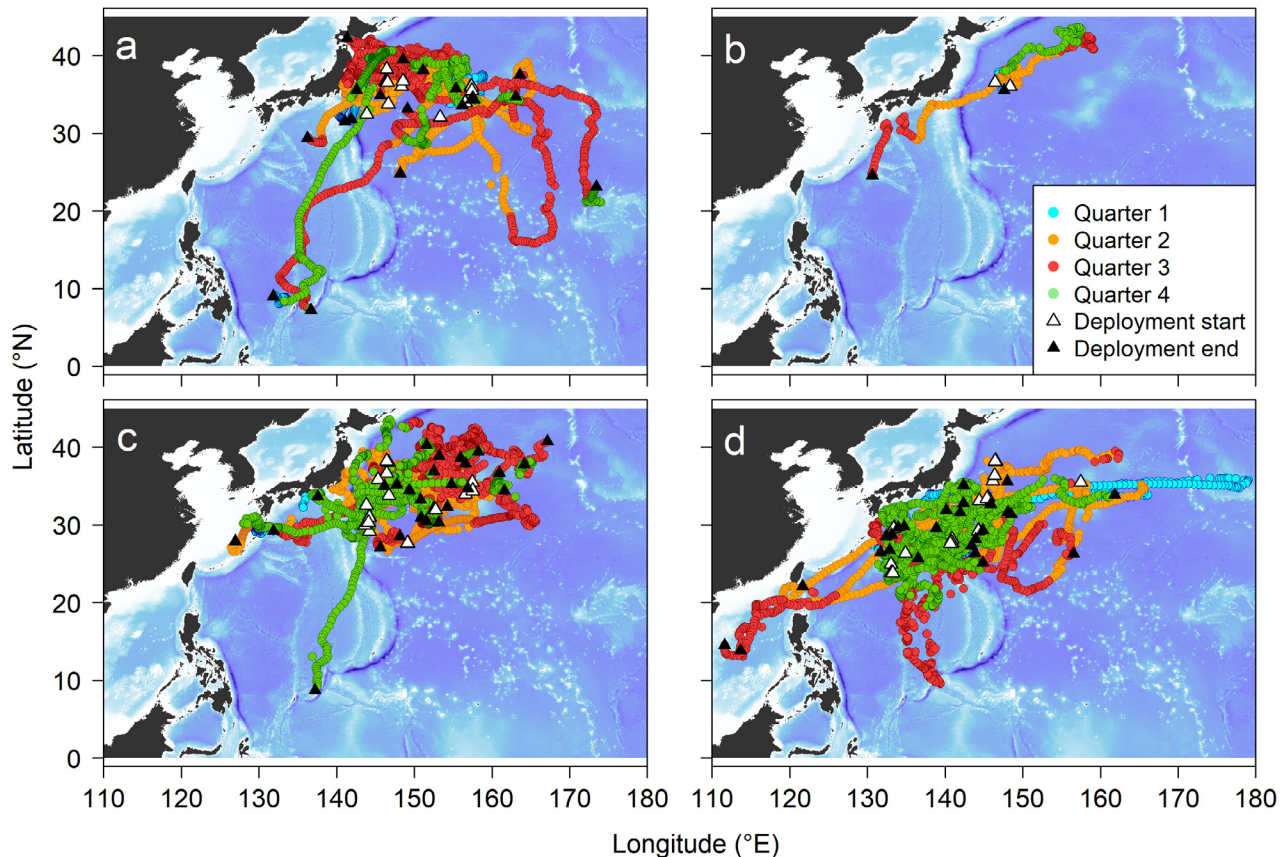


Fig. 1. Quarterly reconstructed most probable daily locations of tagged blue sharks in the northwestern Pacific, for (a) juvenile males ( $n = 18$ ), (b) juvenile females ( $n = 2$ ), (c) adult males ( $n = 27$ ), and (d) adult females ( $n = 24$ ), in Quarter 1 (January–March), Quarter 2 (April–June), Quarter 3 (July–September), and Quarter 4 (October–December)

7.2° and 42.2° N (Fig. 1a). Although the majority of JM ( $n = 13$ ) were distributed in the temperate waters north of 30° N, 5 of these (Sharks 6, 46, 51, 54, and 61) moved to subtropical waters south of 30° N; in particular Shark 51 (152.9 cm PCL) and Shark 61 (130.3 cm PCL) traveled farther south during qt 3 and qt 4, to 7.2° and 8.0° N, respectively. Although only 2 JF were tagged, these individuals showed opposing movement patterns: the smaller JF (Shark 58, 109.7 cm PCL) moved northward from the tagging location and reached 43.7° N in qt 3, and then returned to near the tagging location (37.9° N) in qt 4 (Fig. 1b); in contrast, the larger JF (Shark 38, 138.5 cm PCL) moved only southward, from 36.6° to 24.6° N, during qt 2 and qt 3.

For adult blue sharks, the movement patterns of AM (Fig. 1c) resembled those of JM (Fig. 1a). However, AM distributed in a limited latitudinal range (26.6°–43.6° N, mean 33.3° N), except for 1 specimen (Shark 13, 180.5 cm PCL) in qt 4 (Fig. S2). Although that AM moved to a tropical latitude (7.2° N) in qt 4, similar to the movements of some JM, the other AM remained in temperate waters at 30°–40° N throughout the year (Fig. 1c). In addition, AM tended to perform an east–west seasonal shift in their movements (Fig. S3). In contrast, AF clearly showed annual latitudinal migration between temperate and subtropical waters (9.8°–39.5° N; Fig. 1d; Fig. S2), and they displayed southward movements from more temperate locations in qt 2 to subtropical waters during qt 3, returning to temperate waters during qt 4 and qt 1.

Blue sharks were present over a wide range of SST (9.9–33.3°C, median 24.9°C). The SST experienced by blue sharks in Area 1 (temperate waters, 35.0°–43.6° N) was 14.1–31.6°C (median 21.1°C) for JM, 9.9–22.5°C (median 15.6°C) for JF, 17.8–28.8°C (median 23.3°C) for AM, and 13.2–24.8°C (median 20.0°C) for AF (Fig. 2). The SST experienced by sharks in Area 2 (subtropical waters, 8.1°–34.9° N) was 14.0–30.9°C (median 27.9°C) for JM, 21.7–31.2°C (median 27.0°C) for JF, 12.4–30.7°C (median 25.8°C) for AM, and 14.8–33.3°C (median 26.8°C) for AF (Fig. 2). In both areas, the SST differed significantly between sexes and life-history stages (Kruskal–Wallis test,

$\chi^2 = 1543.9$ ,  $p < 0.001$  in Area 1, and  $\chi^2 = 461.6$ ,  $p < 0.001$  in Area 2). In Area 1, females were more often located in the lower SST zone compared to males, regardless of their life-history stage (difference in median SST between sexes: 5.5°C for juveniles and 3.3°C for adults).

### 3.2. Spatial segregation and habitat overlap

The seasonal 50 and 95% KUDs of blue sharks were highly distorted for different combinations of sex and life-history stage (Table 1, Fig. 3). Core habitat of JM appeared to be from coastal areas of Japan to offshore areas at around 160° E during qt 2 (Fig. 3b) and qt 3 (Fig. 3c), and 2 hot spots appeared, in temperate and subtropical waters, during qt 4 (Fig. 3d) and qt 1 (Fig. 3a). Overall, JM tended to extend their habitat selection to subtropical waters during qt 3 and qt 4. For JF, 2 hot spots also appeared, as seen for JM, but the hot spots were inconsistent be-

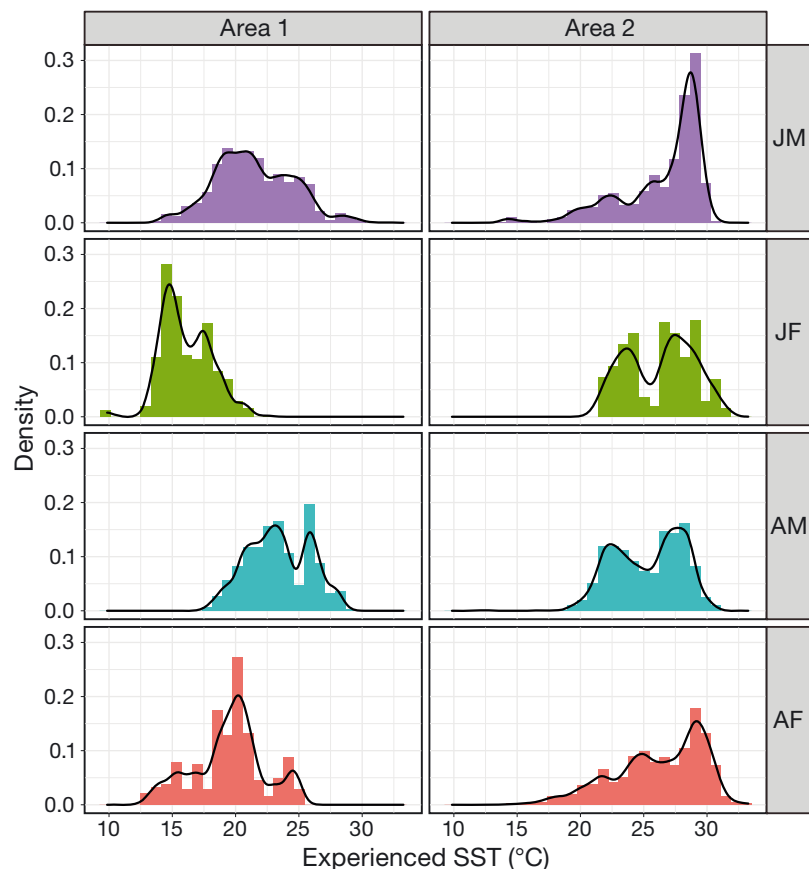


Fig. 2. Density plots and histograms of sea surface temperature (SST) experienced by tagged blue sharks by sex and life-history stage (JM: juvenile males; JF: juvenile females; AM: adult males; AF: adult females) in waters north (Area 1) and south (Area 2) of 35° N

Table 1. Quarterly kernel utilization distribution (KUD) areas (km<sup>2</sup>) for blue sharks in the northwestern Pacific, by sex and life-history stage. JM: juvenile males; JF: juvenile females; AM: adult males; AF: adult females; n: number of daily points for the KUDs for each group (season, sex, and life-history stage). Quarter 1: January–March; Quarter 2: April–June; Quarter 3: July–September; Quarter 4: October–December

Life-history stage	Quarter 1			Quarter 2			Quarter 3			Quarter 4		
	50% KUD	95% KUD	n	50% KUD	95% KUD	n	50% KUD	95% KUD	n	50% KUD	95% KUD	n
JM	223.8	913.9	184	82.9	408.4	746	120.9	928.6	1157	180.7	923.6	521
JF	1.4	5.6	37	56.6	225.5	85	131.3	672.9	130	17.6	81.2	92
AM	124.1	589.4	157	84.5	368.9	902	89.1	413.9	1104	118.3	599.2	806
AF	203.2	818.4	427	204.8	792.1	577	210.7	946.5	778	71.2	278.0	1245

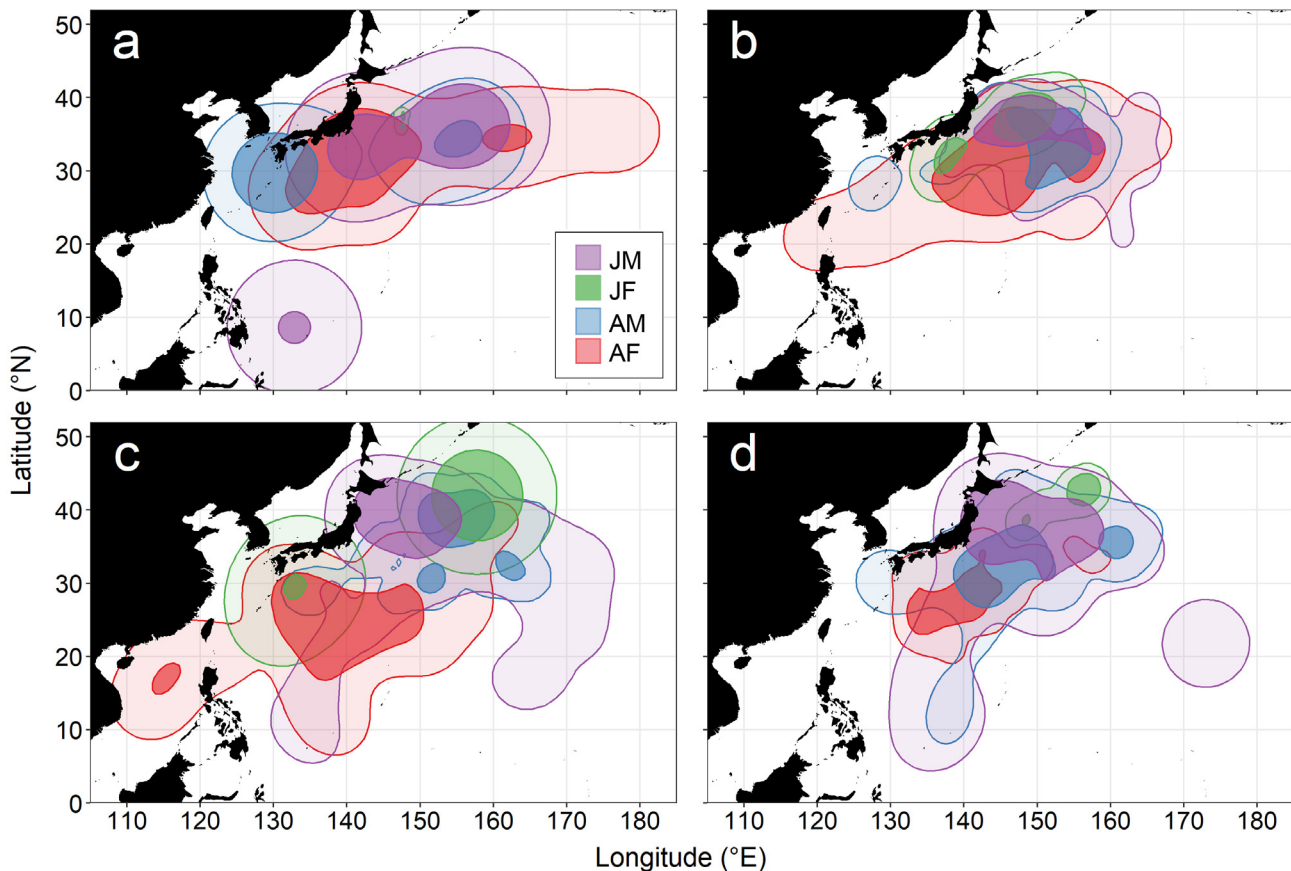


Fig. 3. Seasonal 50% (darker shades) and 95% (lighter shades) kernel utilization distributions for tagged blue sharks in the northwestern Pacific, by sex and life-history stage (JM: juvenile males; JF: juvenile females; AM: adult males; AF: adult females), in (a) quarter (qt) 1, January–March; (b) qt 2, April–June; (c) qt 3, July–September; and (d) qt 4, October–December

tween individuals ( $n = 2$ ). The hot spots of the larger JF appeared off the southern coast of Japan in qt 2 (Fig. 3b) and qt 3 (Fig. 3c), while those of the smaller JF appeared in the subarctic area around 40°N in all seasons, and the area occupied was further north than for AF. Sexual segregation between AM and AF was obvious in qt 3 (UDOI = 0.08; Fig. 3c); AF were located in subtropical waters, while AM were found mainly in a more limited range at 30°–40°N.

Overlap of the home range was observed for different combinations of sex and life-history stage, and a high level of overlap was observed between juveniles (but especially JM) and adults (Table 2). For qt 1, the overall KUDs partially overlapped between JM and adults of both sexes (UDOI = 0.57 for JM–AF; UDOI = 0.31 for JM–AM). For qt 2, overlap of the home range occurred for all combinations of sex and life-history stage; especially, the habitats of JM

Table 2. Quarterly 95% utilization distribution overlap index (UDOI) for blue sharks in the northwestern Pacific, by sex and life-history stage. A minimum UDOI value of 0 indicates no dyadic overlap (lighter gray), and a maximum value of 1 shows high overlap with uniformly distributed ranges (darker gray). JM: juvenile males; JF: juvenile females; AM: adult males; AF: adult females; n: number of daily points for the kernel utilization distributions for each group (season, sex, and life-history stage); Quarter 1: January–March; Quarter 2: April–June; Quarter 3: July–September; Quarter 4: October–December

Season	Life stage	n	JM	JF	AM	AF
Quarter 1	JM	184	X			
	JF	37	0.009	X		
	AM	157	0.31	0.003	X	
	AF	427	0.57	0.008	0.40	X
Quarter 2	JM	746	X			
	JF	85	0.66	X		
	AM	902	0.89	0.40	X	
	AF	577	0.60	0.35	0.61	X
Quarter 3	JM	1157	X			
	JF	130	0.17	X		
	AM	1104	0.58	0.50	X	
	AF	778	0.07	0.13	0.08	X
Quarter 4	JM	521	X			
	JF	92	0.11	X		
	AM	806	0.69	0.03	X	
	AF	1245	0.12	0.00	0.46	X

highly overlapped with those of AM (UDOI = 0.89). For qt 3, the KUDs largely overlapped between juveniles of both sexes and AM (UDOI = 0.58 for JM–AM, UDOI = 0.50 for JF–AM). For qt 4, overlap of the home range occurred between AM and AF (UDOI = 0.46) and between JM and AM (UDOI = 0.69).

### 3.3. Probability of presence

A summary of the fisheries-dependent size-measurement data for blue sharks by sex and life-history stages, across all seasons, showed PCL ranges of 32.0–160.4 cm (median 140.0 cm,  $n = 52\,635$ ) for JM, 41.0–156.0 cm (median 135.0 cm,  $n = 23\,605$ ) for JF, 160.9–294.0 cm (median 173.5 cm,  $n = 33\,699$ ) for AM, and 156.7–291.0 cm (median 166.0 cm,  $n = 12\,196$ ) for AF (Fig. S4). Spatial plots of the size-measurement data revealed that most smaller juveniles (<100 cm PCL) of both sexes occurred north of 35°N, and larger juveniles (i.e. subadults) of both sexes occurred in both temperate and tropical waters (Fig. 4). In waters north of 35°N, a large number of blue sharks were observed, and the population was

mainly composed of JM larger than 100 cm PCL (Figs. S4 & S5). In contrast, in waters south of 35°N, the observed number of blue sharks was low and mainly consisted of subadults and adults. Large-sized AM were observed at 15°–30°N in qt 1–2 and mainly north of 30°N in qt 3–4 (Fig. 4).

Diagnostic plots of the GAMs showed normality and homoscedasticity for their residuals, indicating that the modeling was appropriate (Figs. S6–S9). A high presence probability (>90%) for JM and JF was observed for waters north of 35°N throughout the year (Fig. 5), while a high presence probability (>90%) in subtropical waters (south of 30°N) was observed in qt 3 for JF, and in qt 1 and qt 4 for JM. For AM, a high presence probability occurred for the broad area from temperate to subtropical waters, in all seasons (Fig. 6). A high probability presence of AF was observed for waters north of 32°N in qt 1, south of 18°N in qt 2 and qt 3, and in subtropical waters at 18–25°N in qt 4 (Fig. 6).

### 3.4. Mating scars on adult females

Females with fresh mating scars ( $n = 131$ ) were observed over a broad range, from 3.8° to 42.2°N (median 34.0°N); of these females, 62.6% were found north of 30°N (Fig. 7). Among them, pregnant females ( $n = 21$ ) were observed in waters between 33.4° and 38.4°N (median 36.4°N). Females with well-healed mating scars ( $n = 63$ ) were found in subtropical waters, between 3.4° and 24.2°N (median 20.4°N) (Fig. 7). Overall, the females with fresh mating scars were mostly distributed in northern waters compared with those with well-healed mating scars (Wilcoxon rank-sum test,  $W = 7320$ ,  $p < 0.001$ ). Females without mating scars ( $n = 39$ ) were observed between 21.6° and 39.8°N (median 35.1°N).

## 4. DISCUSSION

Using fishery-independent and fishery-dependent data (PSAT and SPOT tags) of 3 types, we used a holistic approach to reveal spatial segregation by sex and life-history stage for blue sharks in the northwestern Pacific. Overall, analysis based on the satellite tracking data and fisheries-dependent size-measurement data showed similar movement and distribution patterns. Interestingly, we noted seasonal changes in the overlap of areas occupied by adults (especially AM) and juveniles in temperate waters. Juveniles occur mainly around the TZ in tem-



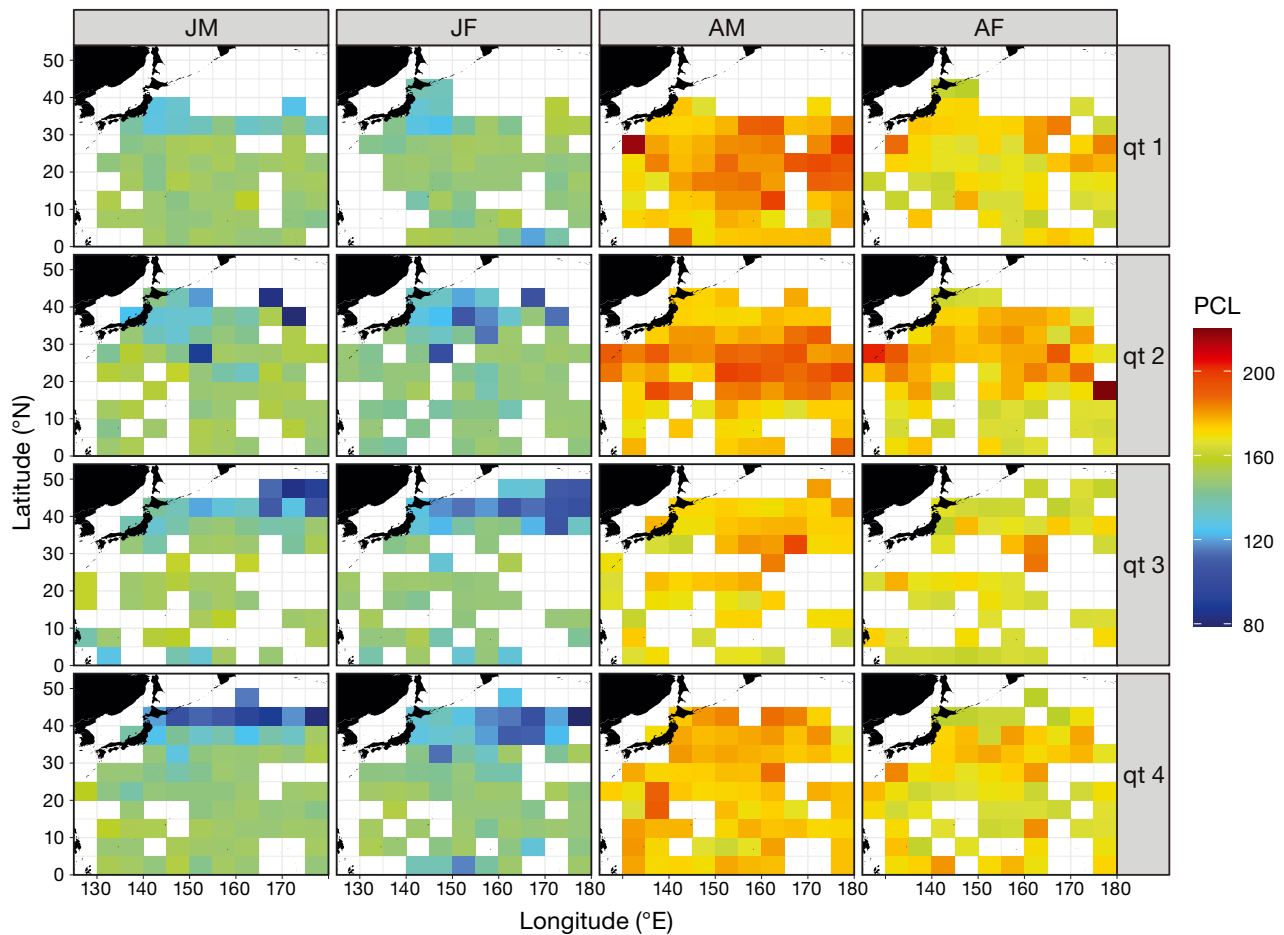


Fig. 4. Quarterly spatial distributions ( $5^{\circ} \times 5^{\circ}$  grid spacing) by mean body size (precaudal length: PCL, cm) of blue sharks, by sex and life-history stage (JM: juvenile males; JF: juvenile females; AM: adult males; AF: adult females) in the northwestern Pacific, based on fisheries-dependent size-measurement data. qt (quarter) 1: January–March; qt 2: April–June; qt 3: July–September; qt 4: October–December

perate waters: JM primarily in waters between  $30^{\circ}$  and  $40^{\circ}$  N, and JF primarily in waters between  $40^{\circ}$  and  $50^{\circ}$  N. AF undertake an annual north–south migration between temperate and subtropical waters, while AM occur in the broad area from temperate to subtropical waters yet remain mainly in temperate waters throughout the year, and in temperate waters, the area of AM distribution partially overlaps areas occupied by juveniles. Notably, the mating ground of blue sharks, based on observation of females with fresh mating scars, was found to be much broader ( $20^{\circ}$ – $40^{\circ}$  N) than that depicted in the schematic diagram of migration patterns of this population presented by Nakano (1994). In addition, no satellite-tagged blue sharks moved beyond the Equator; all stayed within the North Pacific. Considering these new findings on the distribution patterns of AM and the spatial extent of the mating ground, plus information from previous studies (discussed below), we

present a revised schematic diagram of the migration patterns of blue sharks in the northwestern Pacific (Fig. 8).

Despite no tracking data on neonates in this study, yet consistent with our analysis of the size-measurement datasets and several findings from previous studies (e.g. Nakano 1994, McKinnell & Seki 1998, Vandeperre et al. 2014a, 2016, Coelho et al. 2018, Fujinami et al. 2021), we suggest that the parturition ground is in temperate water, and that the distribution of neonates is from temperate areas to the subarctic boundary. We found that juveniles are largely distributed in temperate waters, although smaller juveniles may shift towards the subarctic boundary where prey items will be plentiful (Figs. 4 & 5). Likewise, several studies in the Atlantic (Mejuto & García-Cortés 2005, Vandeperre et al. 2014a, 2016, Coelho et al. 2018), Indian (Coelho et al. 2018), and North Pacific Oceans (Nakano 1994) reported that neonates and smaller ju-

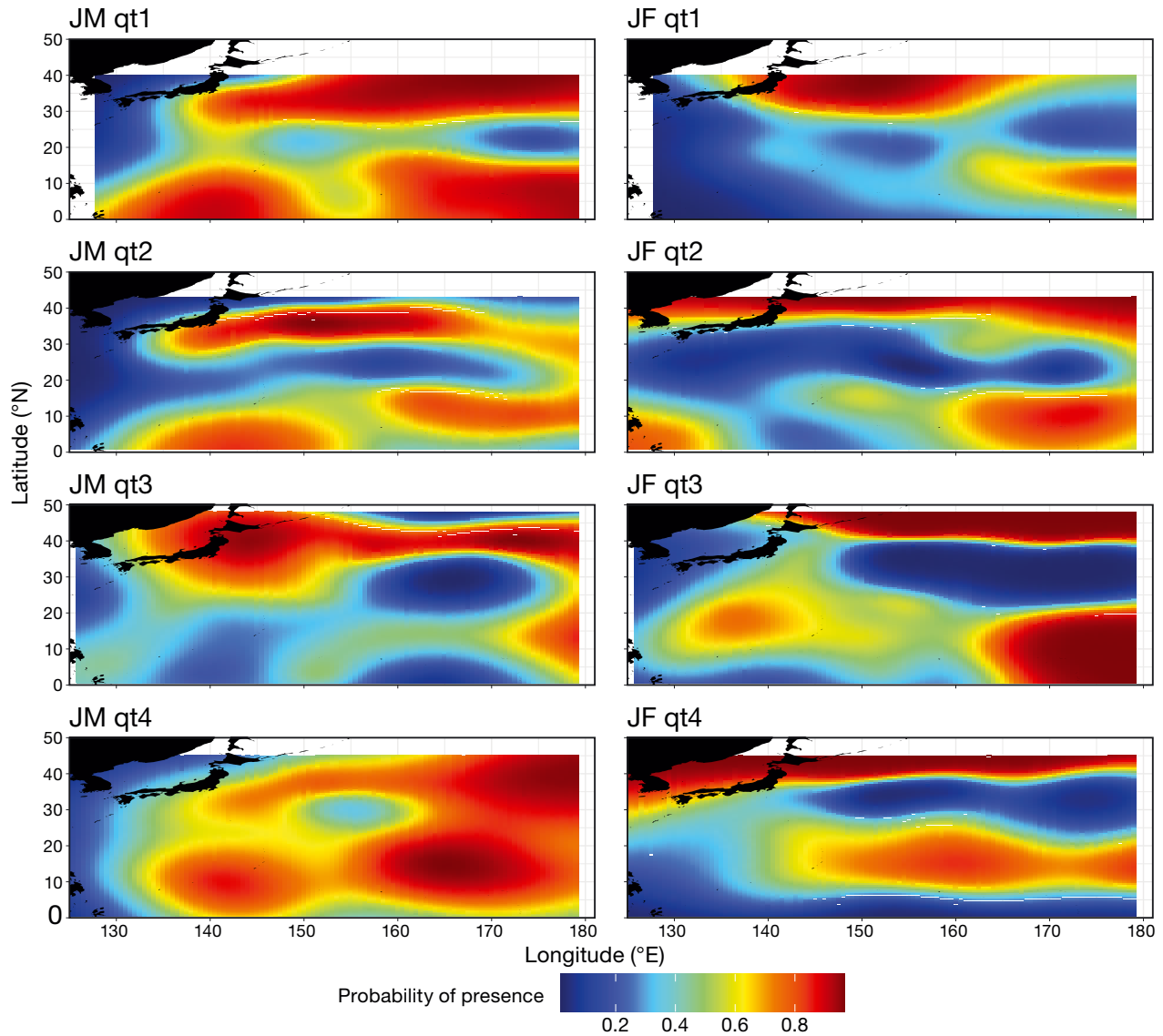


Fig. 5. Quarterly spatial predictions ( $1^{\circ} \times 1^{\circ}$  grid spacing) of probability of presence for juvenile blue sharks by sex, based on size-measurement datasets. JM: juvenile males; JF: juvenile females; qt 1: January–March; qt 2: April–June; qt 3: July–September; qt 4: October–December

veniles predominated at higher latitudes. Moreover, recent satellite tracking data in the northwestern Pacific showed that pregnant blue sharks with full-term embryos moved towards the TZ (Fujinami et al. 2021).

Sexual segregation of blue sharks is well known in the Atlantic (Vandeperre et al. 2014a, Howey et al. 2017), Indian (Coelho et al. 2018), and Pacific (Nakano 1994, Ohshimo et al. 2016, Maxwell et al. 2019) Oceans. Our findings showed patterns of segregation similar to those reported in previous studies, and indicated that JM and JF start to segregate from each other before reaching sexual maturity. We believe that JM mainly occur in the area around the TZ and gradually extend their habitat selection to subtropical

waters, as far south as  $30^{\circ}$  N, as they grow (Figs. 3–5). Based on our results from the fishery-dependent size-measurement data, we propose that smaller-sized JF occur mainly in subarctic water and possibly spatially segregate from both JM and adults (Figs. 4 & 5), whereas larger-sized JF likely extend their distribution to subtropical waters (Fig. 4). This theory is supported by the limited tracking data for JF ( $n = 2$ ), wherein the smaller JF (Shark 58, PCL 109.7 cm) moved northward from  $35.6^{\circ}$  to  $43.7^{\circ}$  N, while the larger JF (Shark 38, PCL 138.5 cm) moved southward from  $36.6^{\circ}$  to  $24.6^{\circ}$  N. These data may indicate that the small JF was not yet at the stage of expanding its habitat to subtropical waters, and that the large JF

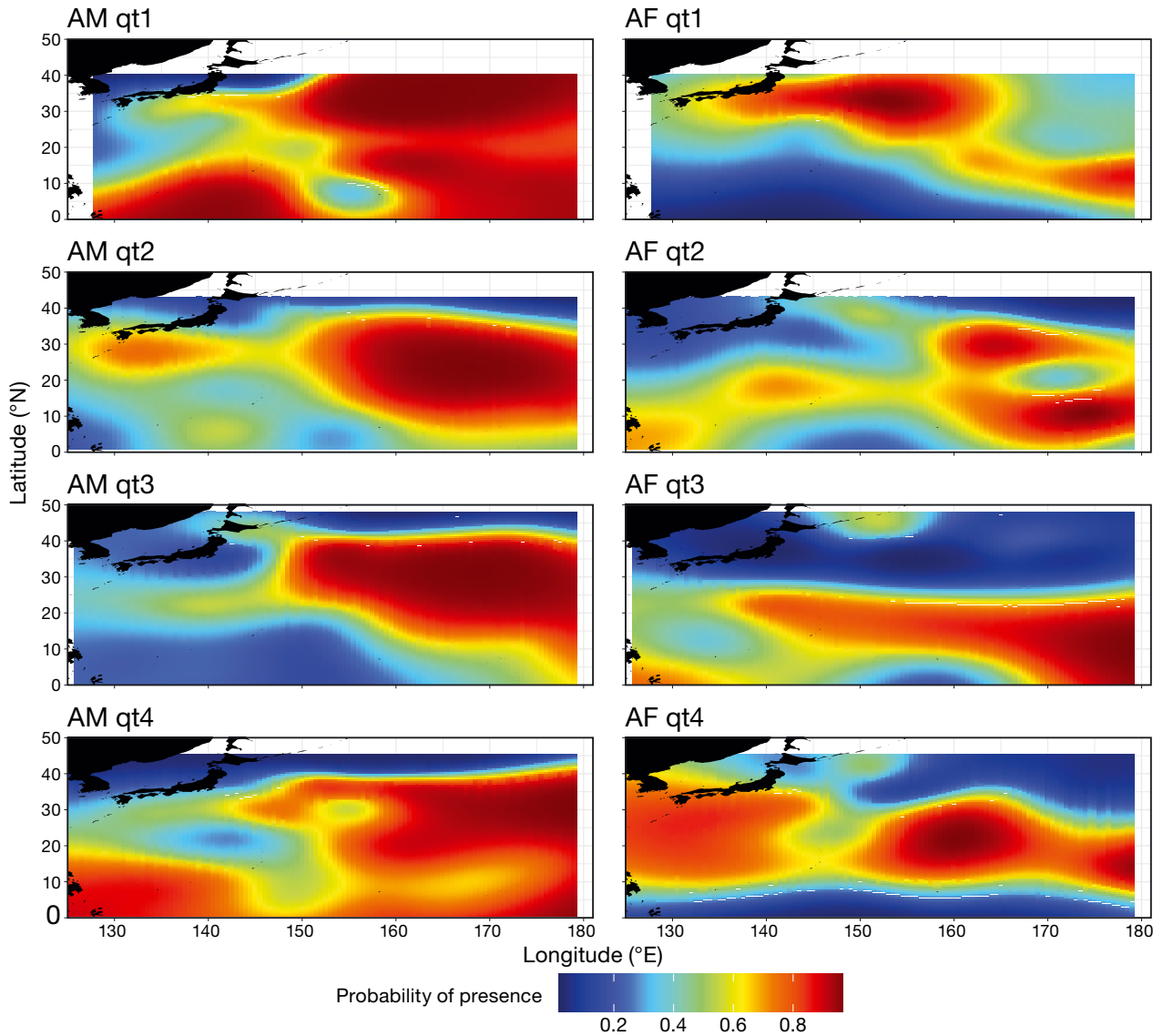


Fig. 6. Quarterly spatial predictions ( $1^\circ \times 1^\circ$  grid spacing) of probability of presence for adult blue sharks by sex based on size-measurement datasets. AM: adult males; AF: adult females; qt 1: January–March; qt 2: April–June; qt 3: July–September; qt 4: October–December

was at the stage of beginning large-scale latitudinal migration, similar to AF (Fujinami et al. 2021). Evidence from the northeastern Pacific showed that larger JF (136.9–180.1 cm fork length, or 125.7–165.5 cm PCL when converted using the relationship described by Fujinami et al. 2017) were found between  $32^\circ$  and  $45^\circ\text{N}$  during summer and then moved south of  $35^\circ\text{N}$  in the fall (Maxwell et al. 2019). Considering research showing that AM in the North Atlantic attempted to mate aggressively with JF (Calich & Campana 2015), the latitudinal migration of large JF might constitute an ecological adaptation to avoid the aggressive mating behavior of males, as hypothesized by Vandeperre et al. (2014a) and Howey et al. (2017).

Our findings strongly suggest that the mating ground of blue sharks in the North Pacific extends over a wide range, from temperate to subtropical waters ( $20^\circ$ – $40^\circ\text{N}$ ; Figs. 7 & 8). During the mating season (spring–summer: Fujinami et al. 2017), about two-thirds of the AF observed with fresh mating scars occurred north of  $30^\circ\text{N}$ , while those with well-healed mating scars occurred in subtropical waters (Fig. 7). The mating ground depicted in the previous migration model (Nakano 1994) was also based on a study of the mating scars on females (Suda 1953). Our data were collected from a broader area, in temperate and subtropical waters, and yield more information as we included both presence or absence and

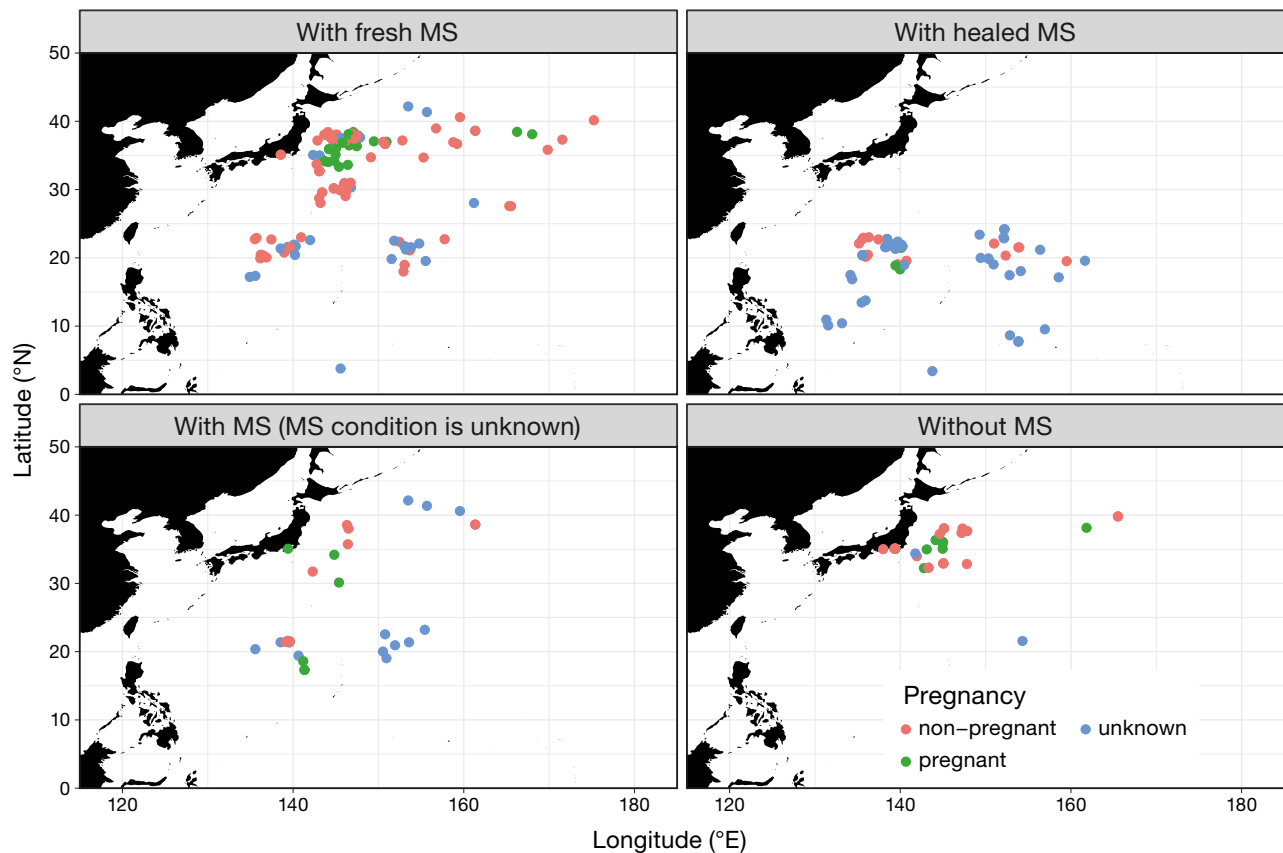


Fig. 7. Spatial distributions of adult female blue sharks observed with mating scars (MS) (fresh MS:  $n = 131$ ; well-healed MS:  $n = 63$ ; condition of MS unknown:  $n = 37$ ) or without MS ( $n = 42$ ), by pregnancy state, during the parturition and mating seasons (i.e. spring–summer; Fujinami et al. 2017)

condition (fresh or healed) of mating scars. The finding that the mating ground spans subtropical and temperate waters would suggest several ecological advantages for both sexes, including (1) the mating opportunities for AF in temperate waters increase soon after parturition, and (2) AM could intercept AF for mating in highly productive waters, with less expenditure of energy for broadscale annual migration like AF. Although our data also indicated a possibility that the blue shark mating ground in the northwestern Pacific might be biased westward (Figs. 3 & 7), evidence obtained in this study is still insufficient. Further research will be necessary to obtain sufficient data to elucidate the exact mating ground in the entire North Pacific.

Information from previous studies helps to clarify that AF in the northwestern Pacific migrate annually between temperate and subtropical waters for reproduction (mating in summer, gestation during summer and autumn, and parturition in the following spring; Fujinami et al. 2017, 2021) and shows that they give birth in the productive temperate region (Nakano 1994, Fujinami et al. 2021). Therefore, it is reason-

able to speculate that AF mate along a migration pathway from temperate to subtropical waters soon after parturition (Fig. 8). In the migration pathway seen in qt 2, AF would have opportunities to mate with AM in the overlapped area (UDOI = 0.61; Table 2). AF are able to ovulate and be fertilized again soon after parturition (Fujinami et al. 2017); hence, early embryonic growth would be helped by the female moving into the warmer water of the subtropical area (Hazin et al. 1994, Fujinami et al. 2021).

It has been generally thought that AM blue sharks inhabit mainly tropical and subtropical waters (e.g. Nakano 1994, Coelho et al. 2018). However, our study found that AM widely occurred from temperate to subtropical waters (Fig. 6; Fig. S5), and remained mostly in temperate waters according to satellite tracking data (Fig. 3). Hotspots of blue sharks in the North Pacific were observed in temperate waters, including the TZ, based on catch data from Japanese research, training, and commercial vessels (Kai et al. 2017, Kai 2019). Thermal fronts, including the TZ, act to aggregate top predators, including whales, tunas, billfishes, and sharks, with

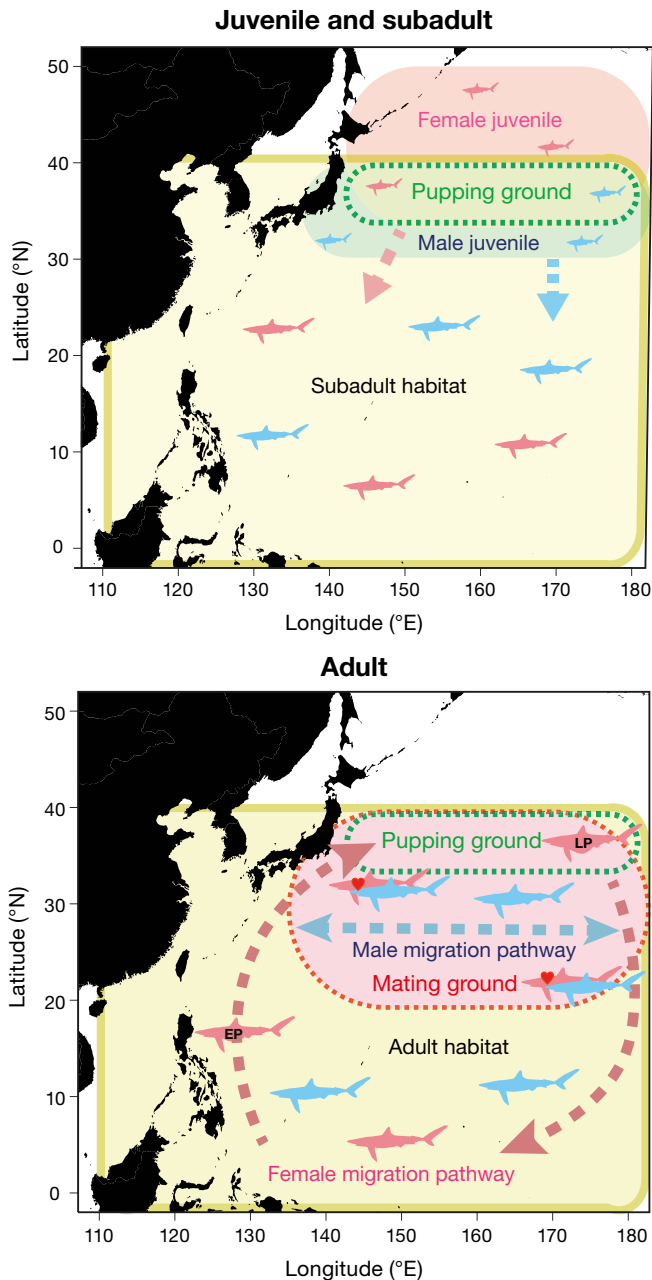


Fig. 8. Migration patterns of blue sharks by sex and life-history stage in the northwestern Pacific (revised from Nakano 1994). EP (LP): early (late) pregnancy

greater apparent mixing of the sexes owing to feeding or courtship opportunities (McKinnell & Seki 1998, Sims et al. 2000, Olson 2001). However, it is worth noting that fishing efforts of Japanese fleets targeting blue shark in the subtropical waters were generally lower than in temperate waters (Hiraoka et al. 2016, Kai et al. 2017), and that our tracking data for AM were mostly limited to waters north of 30° N.

Further tagging research for AM in subtropical and tropical waters will be important to fill in the gaps in our understanding. Kai et al. (2017) demonstrated the seasonal east–west movements of blue sharks using a spatio-temporal model with fishery-dependent data. Similarly, satellite tracking data for AM in the present study showed clear east–west seasonal shifts in their habitat selection (Fig. S3). AM likely perform mainly east–west movements within the temperate and subtropical waters rather than north–south movements like AF. Given the seasonal movement patterns of adults of both sexes within the wide mating ground, AM could intercept AF for mating as the sharks move between subtropical and temperate waters, but especially around the TZ. Several advantages for AM would ensue from such a movement pattern, including an increased probability of encounters with AF in the expansive pelagic waters, and energy spent on life-history needs other than migration (i.e. growth and reproduction). In general, male blue sharks grow larger than females, and the difference in growth rate clearly arises after sexual maturity (e.g. Nakano 1994, Joung et al. 2018, Fujinami et al. 2019).

Adult and juvenile blue sharks are characteristically known to spatially segregate in temperate waters (e.g. Nakano 1994, Vandeperre et al. 2014a, Coelho et al. 2018). However, our results indicated some spatial overlap between adults and juveniles within temperate waters (Fig. 3) as well as different water temperature preferences between sexes at the same life-history stage (Fig. 2). In temperate waters, the SSTs experienced by adults were relatively higher than those of juveniles, and were likewise higher for males than for females (Fig. 2). In the North Atlantic, female blue sharks occupied cooler water when compared with males irrespective of the life-history stage, suggesting that the optimal water temperature differs between sexes (Vandeperre et al. 2014a, Howey et al. 2017). There is evidence of fine-scale segregation between sexes and different life-history stages among blue sharks within the same horizontal habitat, based on preferences for specific environmental conditions, including water temperature (e.g. Nakano 1994, Vandeperre et al. 2014a, Maxwell et al. 2019). The skin of female blue sharks is typically thicker than that of males, which may allow them to expand their niche to cooler temperature zones (Howey et al. 2017). As discussed, water temperature is an important factor determining the habitat of blue sharks and their prey items; thus, fine-scale analyses that include oceanic environmental factors are still needed.

## 5. CONCLUSIONS

We holistically elucidated the spatial segregation patterns of blue sharks in the northwestern Pacific and also found some overlap in spatial distributions between sexes and life-history stages: (1) juveniles of both sexes were found predominantly in temperate waters, but their core habitat changes seasonally by sex as they grow; (2) AF performed annual north–south migrations for reproduction; and (3) AM tended to remain in temperate waters and display seasonal longitudinal migrations. The migration pattern of AM is a new finding because AM were previously considered to mainly occupy equatorial and tropical/subtropical waters, based on previous studies. Another new finding is that the mating ground appears to be broader than previously understood and seems to overlap with parturition and nursery grounds. From these new findings, we updated the schematic diagram of migration patterns for blue sharks in the northwestern Pacific (Fig. 8). We acknowledge that our understanding of the migration pattern based on satellite tracking includes uncertainties owing to limited sample sizes, especially for JF ( $n = 2$ ), and position estimation errors; therefore, it will be necessary to conduct further tracking research to confirm our conclusions through adequate satellite tracking data.

Importantly, the satellite tracking data and fisheries-dependent data revealed comparable movement and distribution patterns, suggesting that these data provide highly reliable movement patterns of this population. Using conventional tagging data, Sippel et al. (2011) showed that only a small percentage of blue sharks conduct trans-Pacific movements. Our satellite tracking data together with the results of Maxwell et al. (2019) indicate that blue sharks do not routinely perform trans-Pacific migrations, unlike the Pacific bluefin tuna *Thunnus orientalis* (Fujioka et al. 2018), and they also do not move beyond the Equator. Recent analysis of stable isotope ratios for both blue sharks and their prey items in the eastern and western North Pacific also revealed limited trans-Pacific movement by this species (Madigan et al. 2021). These insights into the stock structure of North Pacific blue sharks should benefit future stock assessments and fisheries management. Additional research on patterns of vertical movement in North Pacific blue sharks would help to verify fine-scale vertical segregation by sex and life-history stage.

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