Seasonal migrations of pregnant blue sharks *Prionace glauca* in the northwestern Pacific

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ABSTRACT: Information on the movements of highly migratory species is important to understand their ecology, including habitat use, population connectivity, and stock structure, to implement appropriate management and conservation measures. The blue shark *Prionace glauca* (Carcharhinidae) is highly migratory, has a global distribution, and is ecologically and economically important as one of the most abundant apex marine predators; however, the migration patterns of pregnant females are unknown. Here, we used pop-up satellite archival tags to elucidate seasonal migration of pregnant blue sharks in the northwestern Pacific. Of 24 tagged adult females, archival data were subsequently obtained for 21 individuals (141.1–243.3 cm precaudal length). Based on ultrasonography or analysis of sex steroid hormones, 17 of these females were confirmed to be pregnant at the time of release. Females with small embryos moved in a northeasterly direction, from subtropical (10–30° N) into temperate (30–40° N) waters during autumn and the following spring; 2 of these females returned to subtropical waters in spring and summer. In contrast, females with large embryos moved in a southwesterly direction, from temperate into subtropical waters during spring and autumn. Tagged sharks also showed regional differences in diving behaviors, reflecting thermal habitats in the ocean environment. Our findings indicate that pregnant blue sharks undergo a seasonal northeast–southwest migration within a year to give birth to pups in productive temperate waters. This is the first report on seasonal reproductive migration of pregnant blue sharks in the global ocean.

KEY WORDS: Latitudinal migration · Parturition · Reproduction · Spatiotemporal movements · Satellite tracking · Vertical distribution · Female blue shark · Kuroshio/Oyashio transition zone

1. INTRODUCTION

Knowledge of the movements of pelagic sharks is essential to understand their ecology, including habitat use, population connectivity, and stock structure, and to implement appropriate management and conservation measures (Kohler & Turner 2008, Harrison et al. 2018, Queiroz et al. 2019). In particular, knowledge of adult female movements contributes fundamental information about the reproductive events (e.g. mating and parturition grounds) of a species. However, such information is generally lacking for many shark species, especially highly migratory pelagic sharks, owing to the difficulty of determining the reproductive status of an individual prior to its release (Sulikowski et al. 2016, Reynolds et al. 2017). Assessing patterns of vertical movement is also essential from an ecological perspective, as it provides insights into vertical habitat use, thermal niche partitioning, and species interactions (e.g. Musyl et al. 2011, Vaudo et al. 2016).

The blue shark *Prionace glauca* (Carcharhinidae) is an ecologically and economically important species. It is one of the most abundant apex marine predators to occur worldwide in temperate to tropical waters from 60° N to 50° S (Nakano & Stevens 2008), where it plays a significant role in marine ecosystems. Blue sharks are caught commonly as bycatch in longline fisheries targeting swordfish (Campana 2016), in addition to being the target of commercial fisheries (Aires-da-Silva et al. 2008, Hiraoka et al. 2016). Their meat, liver (oil), cartilage, and fins are used in many countries (Clarke et al. 2006, Camhi et al. 2008). Stock assessments of this species have been conducted by several regional fisheries management organizations to assess stock status and to implement appropriate regional conservation and management measures.

Blue sharks exhibit complex movement patterns, with seasonal migrations coupled with spatial segregation by sex and life stage (Vandeperre et al. 2014, Ohshimo et al. 2016, Howey et al. 2017, Maxwell et al. 2019), and trans-Atlantic (Queiroz et al. 2005, Kohler & Turner 2008) and north–south migrations (Nakano 1994, Musyl et al. 2011, Vandeperre et al. 2014). Using fisheries data, Nakano (1994) defined a schematic sex-specific migration model for blue shark in the North Pacific (Fig. 1A), wherein (1) mating takes place in early summer (June–August) in subtropical waters, between approximately 20 and 30° N; (2) pregnant females move to temperate waters, between 30 and 40° N for parturition in spring (March–May); (3) nursery grounds are likewise located in temperate waters; (4) juvenile females generally move northward from parturition grounds, while juvenile males tend to occupy southern parturition grounds; and (5) adults mainly distribute in temperate to equatorial waters.

Recently, spatially explicit size and sex data were aggregated from 20 different fisheries (from Taiwan, China, the Republic of Korea, Japan, Mexico, and the USA) to improve understanding of size and stock structure of blue sharks in the entire North Pacific (Shippel et al. 2016). Results strongly support the sex-specific migration model proposed by Nakano (1994). Similar movement patterns of this species were reported for the North and South Atlantic, based on bycatch and tracking data (e.g. Montealegre-Quijano & Vooren 2010, Vandeperre et al. 2014).

Among pelagic shark species, the blue shark is highly productive because of its relatively fast growth and high numbers of offspring (Fujinami et al. 2017, 2019, Kai & Fujinami 2018). An annual reproductive cycle revealed using biological infor-

mation from females in the northwestern Pacific showed clear seasonality in ovulation, mating in summer, and parturition in spring (Fujinami et al. 2017). Based on current information about the annual reproductive cycle and migration model of this species, we hypothesized that pregnant blue sharks migrate from subtropical to temperate waters for parturition during autumn (September–November) to the following spring, and, postpartum, return to subtropical waters for subsequent reproduction. However, confirming this hypothesis requires direct and fisheries-independent information about the seasonal movements of adult female blue sharks in addition to verifying their reproductive status.

Developments in satellite tracking technology (e.g. pop-up satellite archival tags [PSATs]) allow us to investigate shark migrations in oceanic environments where direct observation is not possible. These tags have expanded our knowledge of horizontal and vertical movements, temperature preferences, and habitat use of several shark species (e.g. Weng et al. 2007, Campana et al. 2010, 2011, Coelho et al. 2015, Skomal et al. 2017). Several authors have reported information about blue sharks using electronic tags in the Atlantic (e.g. Queiroz et al. 2010, 2012, Campana et al. 2011, Vandeperre et al. 2014, Howey et al. 2017), Indian (Heard et al. 2018), and Pacific (Stevens et al. 2010, Musyl et al. 2011, Maxwell et al. 2019) oceans. These blue shark telemetry studies have revealed seasonal migration, clear diel vertical movements, and sex-based and ontogenetic segregation. However, information is lacking for the western and central North Pacific Ocean (Queiroz et al. 2019). Additionally, nothing has been reported regarding the habitat use, migration patterns, and vertical behavior of pregnant blue sharks anywhere in the world. Our main objectives were therefore to assess the effects of biological and environmental factors on the migration patterns and vertical distributions of pregnant blue sharks in the northwestern Pacific, which we determined using PSATs and a non-lethal approach to estimate shark pregnancy state at release.

2. MATERIALS AND METHODS

2.1. Tagging procedure and determination of pregnancy

The Japanese RV 'Shunyo-maru,' which was equipped with longline gear, operated in the northwestern Pacific in October 2015, 2016, and May 2017, to catch female blue sharks for tagging re-
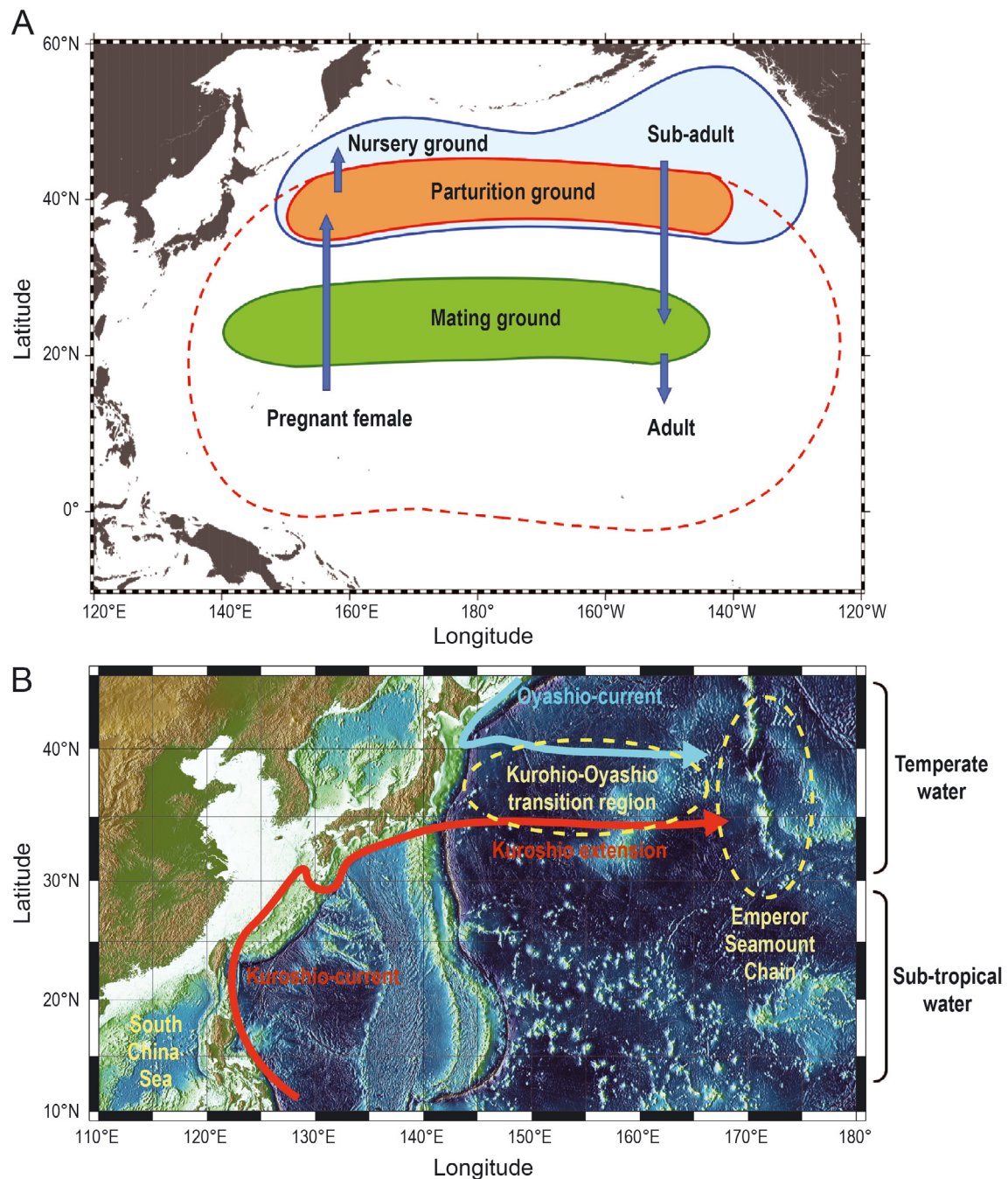
Fig. 1. (A) Modified schematic migration model for female blue sharks in the North Pacific proposed by Nakano (1994). (B) Kuroshio Current, Oyashio Current, and Kuroshio/Oyashio transition zone in the northwestern Pacific

search. The operational area in 2015 and 2016 was in waters off southern Japan (17–31° N, 129–145° E), and the area in 2017 was around the Kuroshio/ Oyashio transition zone (TZ) (32–37° N, 143–146° E). Live blue sharks (those exhibiting active, strong, or responsive movements) captured by longlines were retrieved from the water using a mechanism on the vessel designed to scoop up large-sized fish, and each individual was tagged while on the 'scooper.'

Each shark was physically restrained using 2 ropes around the body, the eyes were covered with a black, damp cloth to reduce stress, and a hose to pump seawater to oxygenate the gills was inserted into the mouth. Sex was visually determined by the presence or absence of male claspers. Dorsal length (DL, to the nearest cm) was measured as the distance from the origin of the first dorsal fin to the origin of the second dorsal fin. For data analysis, DL was converted to

precaudal length (PCL, distance from the tip of the snout to the precaudal pit) using the relation: PCL = 2.62DL + 7.48 (Fujinami et al. 2017).

During research effort in 2015, PSATs (MiniPAT, Wildlife Computers) were attached to adult female blue sharks by inserting a plastic umbrella dart (Domeier et al. 2005) approximately 7 cm into the dorsal musculature lateral to the first dorsal fin. The umbrella tip was attached to the PSAT with a fluorocarbon tether encased in silicone tubing (approximately 10 cm). The dart was positioned at a 40–45° angle to tightly affix the tag, and the applicator was inserted into the body lateral to the vertebral column to avoid injury to internal organs. A second plastic umbrella dart attached to a nylon ring was also inserted into the dorsal musculature just below the first dorsal fin, and the posterior part of that tag was fixed to prevent swinging of the PSAT. For tagging in 2016 and 2017, we improved the PSAT attachment method to reduce damage to the surface of the tag caused by the rough shark skin. We inserted the plastic umbrella dart of the PSAT into the dorsal musculature, near the anterior part of the first-dorsal-fin base, and fixed the posterior part of the tag near the anterior of the first dorsal fin using insulation lock. Otherwise, the specifications of the tether, the insertion angle, and the length of the dart were the same as used in 2015. In addition, a conventional tag was attached to the dorsal musculature behind the first dorsal fin.

To ascertain the pregnancy state (pregnant or not) of tagged female blue sharks, we applied 2 nonlethal approaches using sex steroid hormones and ultrasonography. During the 2015 survey, we collected blood samples (5 ml) from the caudal vein using plastic syringes. Plasma was collected after centrifugation at 504 × g for 5 min, and stored on board at −30°C. Concentrations of sex steroid hormones (progesterone [P_4] and 17β-estradiol [E_2] are suitable markers for determining pregnancy state for blue sharks; Fujinami & Semba 2020) in the plasma of Sharks 3 and 4 (Table 1) were measured at the Japan Institute for the Control of Aging (Shizuoka, Japan), utilizing ELISA. Although blood samples had been collected from 4 individuals (Sharks 2–4 and 6), hormone concentrations were not measured in Sharks 2 and 6 because the data for these specimens were excluded from tagging analyses (see

Table 1. Summary of pop-up satellite archival tag data for 24 adult female blue sharks in the northwestern Pacific. PCL: precaudal length; pregnant: pregnancy stage unknown; EP: early stage of pregnancy; LP: late stage of pregnancy; NA: not applicable

Shark	ID	PCL (cm)	Pregnancy state	Date tagged	Release latitude (°N)	Release longitude (°E)	Pop-up date	Pop-up latitude (°N)	Pop-up longitude (°E)	Days at liberty
1	152095	180.4	Unknown	4 Oct 2015	23.82	133.08	26 Mar 2016	32.66	145.86	174
2	152096	157.9	Unknown	4 Oct 2015	23.89	133.21	29 Oct 2015	21.31	127.12	25
3	152097	174.1	Pregnant	4 Oct 2015	23.82	133.06	3 Jun 2016	26.30	143.86	243
4	152098	160.5	Pregnant	4 Oct 2015	23.83	133.10	4 Jan 2016	31.67	147.96	92
5	152100	177.8	Unknown	4 Oct 2015	23.89	133.22	30 Dec 2015	31.49	142.03	87
6	152103	188.3	Unknown	14 Oct 2015	29.88	133.25	Not reported	NA	NA	NA
7	152104	151.6	Unknown	16 Oct 2015	29.62	133.34	Not reported	NA	NA	NA
8	152105	222.3	Unknown	13 Oct 2015	29.50	133.38	7 Feb 2016	29.72	134.75	117
9	152108	209.2	Unknown	15 Oct 2015	29.50	133.46	20 Oct 2015	27.97	132.15	5
10	162128	196.1	EP	8 Oct 2016	28.17	140.88	20 Nov 2016	35.13	142.38	43
11	162131	196.1	EP	7 Oct 2016	27.73	140.80	13 Nov 2016	31.40	148.50	38
12	162133	230.2	EP	11 Oct 2016	26.26	134.68	15 Jun 2017	21.98	121.61	247
13	162134	177.8	EP	5 Oct 2016	29.29	144.28	4 Jan 2017	33.87	161.81	91
14	162135	162.1	EP	7 Oct 2016	27.69	140.81	20 Mar 2017	32.75	142.38	164
15	162136	206.6	EP	7 Oct 2016	27.69	140.81	27 Nov 2016	31.92	140.22	51
16	162141	159.4	EP	7 Oct 2016	27.68	140.80	24 Feb 2017	27.05	144.56	141
17	162144	141.1	EP	7 Oct 2016	27.76	140.82	3 Dec 2016	29.28	144.87	58
18	162146	188.3	EP	7 Oct 2016	27.71	140.79	25 Nov 2016	28.51	132.43	50
19	170052	224.9	LP	19 May 2017	33.25	144.30	06 Sep 2017	14.58	111.61	111
20	170055	169.9	LP	20 May 2017	33.66	145.51	19 Jun 2017	28.73	133.01	30
21	170057	172.5	LP	28 May 2017	35.57	146.04	2 Oct 2017	25.16	144.85	127
22	170059	243.3	LP	20 May 2017	33.59	145.52	27 Aug 2017	13.82	113.73	100
23	170062	224.9	LP	26 May 2017	36.65	146.43	25 Aug 2017	26.73	132.75	92
24	170065	164.7	LP	26 May 2017	36.55	146.43	Not reported	NA	NA	NA

Section 3.1). All female sharks in 2015 were of unknown pregnancy state except for Sharks 3 and 4, which was determined based on their hormone concentrations (Table 1). Pregnancy state was statistically identified using a machine learning algorithm, an approach that can estimate the pregnancy state of blue shark with high accuracy (86.1%, Fujinami & Semba 2020). In addition, ultrasonography has proven useful to accurately determine the pregnancy of some elasmobranchs (e.g. Sulikowski et al. 2016, Anderson et al. 2018). Therefore, the pregnancy state of all tagged females in the 2016 and 2017 surveys was directly determined via ultrasonography (Sono Scape A6V, SonoScape Medical) by scanning the ventral body from the pectoral to pelvic fins in transverse and longitudinal directions (Table 1). Sharks were retained on the scooper for 3–6 min for tagging and measurements.

PSATs archived data for ambient seawater temperature (±0.1°C) and depth (±0.5 m) at 10 min intervals, and light intensity (5×10^{-12} to 5×10^{-2} W cm^{-2}) after the tagged sharks were released. All tags were programed to start transmitting data via the Argos satellite system and to detach from the shark after 180 or 240 d. PSATs were also programed to automatically detach under the condition of a constant depth (within a range of ±2.5 m) recorded over a specific duration (5 d, indicating the shark was dead) or after exceeding a depth of 1700 m to prevent the tag from being crushed. For tagging-data analyses, transmitted data were first decoded with manufacturer software (see Wildlife Computer — Data Portal, https://wildlifecomputers.com).

2.2. Horizontal movements

We estimated the geolocation between the release and pop-up locations using the tag manufacturer's proprietary geolocation processing estimator, Global Position Estimator version 3 (GPE3), based on a hidden Markov state-space model with 0.25×0.25 grid spacing. GPE3 utilizes the corresponding reference data on the satellite-based sea surface temperature (NOAA Optimum Interpolation [OI] Sea Surface Temperature [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's ETOPO Global Relief Model version Bedrock, https://www.ngdc.noaa.gov/mgg/global/) along with the recorded depth, water temperature, and dawn and dusk light readings, at both the tagging and pop-up locations. In addition, we estimated

kernel density with 1×1 grid spacing using the package 'MASS' in R version 3.3.0 (R Core Team 2016) to investigate seasonal changes in relatively high-density areas of pregnant blue sharks (i.e. hotspots: Yasuda et al. 2014). In this analysis, the bandwidth of the x–y-axis for the estimates of kernel density was determined using the 'bandwidth.nrd' function in R.

2.3. Vertical movements

To examine the diel depth and temperature preference of pregnant blue sharks, we analyzed time-series data for depth and temperature. Time-series data were classified into day (dawn to dusk) and night (dusk to dawn) categories, using values of light intensity obtained from the light sensor of each tag. Dawn was defined as the start of civil twilight, and dusk as the end of civil twilight. Pooled data obtained from all transmitters were used to compile histograms of the diel depth and temperature preference of pregnant blue sharks. Depth and temperature bins were aggregated into time-at-depth distributions of 0–10, 10–50, 50–100, 100–150, 150–200, 200–300, 300–400, 400–600, 600–800, and >800 m, and time-at-temperature distributions of <8, 8–10, 10–12, 12–14, 14–16, 16–18, 18–20, 20–22, 22–24, 24–26, 26–28, 28–30, and >30°C.

Since pregnant blue sharks were tagged in different seasons and years (October in 2015 and 2016, and May in 2017) and tracked for long periods, we considered that the environmental conditions experienced by individual sharks would change significantly on a daily basis, between and within individual tracking data. To account for daily differences in the water column encountered by sharks, we performed a cluster analysis based on daily temperature–depth profiles (Vaudo et al. 2018). Before analysis, temperature–depth profiles were interpolated to 1 m intervals using a smoothing spline to account for differences in the sampling intervals between profiles. Next, the sharks' thermal habitats were created via divisive hierarchical cluster analysis on the matrix of Euclidean distances between the temperature–depth profiles, using the package 'cluster' in the R environment (Mächler et al. 2016). For each cluster, we calculated the proportion of time spent in each bin, during the day and night, for depth and temperature. Finally, we tested differences in the depth and vertical thermal distributions between day and night, using the Wilcoxon rank-sum test. All analyses and statistical approaches were conducted using R.

2.4. Generalized additive mixed models

The effects of biological and environmental factors on the vertical habitat use of pregnant blue sharks were investigated using generalized additive mixed models (GAMMs) based on Coffey et al. (2017). Mean diving depth was defined as the response variable assuming that vertical behavior was affected by various environmental factors. We used the following explanatory variables as fixed effects: PCL; location as the interaction term between latitude and longitude; daily mean water temperature at 100 m; log-transformed chlorophyll *a* (chl *a*) concentration; bathymetry; and diel period (day or night). Explanatory variables of PCL, water temperature at 100 m, log-transformed chl *a* concentration, and bathymetry were modeled as continuous and smoothed, and the variable of diel period was included as a categorical function. The smooth terms were estimated using thin-plate regression splines. To account for repeated observations of the same individuals, a variable of each individual was modeled as a random effect. Correlations among variables (i.e. multicollinearity) were assessed based on the variance inflation factor (VIF), which was calculated using the R package 'car.' In the modeling, we assumed that the response variable (mean diving depth) followed a gamma distribution with a log link function. Parameters were estimated using the R package 'gamm4' (Wood & Scheipl 2017). The most parsimonious model was selected from those including all possible combinations of explanatory variables using Akaike's information criterion corrected for small sample size (AICc) (Burnham & Anderson 2002). This process was performed using the R package 'MuMIn' (Bartoń 2019). The model with the lowest AICc value was considered the best. The delta AIC (ΔAIC) was calculated to determine the extent to which variables contributed to the most parsimonious model. A single best model was used for graphical representation of smoothed and parametric terms, and evaluation of model fitting.

Mean diving depth and water temperature at 100 m were derived from PSATs. The monthly composite chl *a* concentration was extracted from the ESA CCI Ocean Colour product (1/24° resolution). Bathymetry was extracted from the ETOPO1 Global Relief Model (1/60° resolution). These satellite oceanography data were downloaded from the NOAA Coast Watch, Environmental Research Division Data Access Program (https://coastwatch.pfeg.noaa.gov/data.html).

3. RESULTS

3.1. Tracking data and pregnancy state of blue sharks

Of the 24 PSATs deployed on female blue sharks, 21 tags (88%) successfully transmitted data via the Argos system, whereas 3 tags (Sharks 6, 7, and 24) did not report (Table 1). Among the 21 individuals tracked, 2 females (Sharks 2 and 9) suddenly sank to a depth of over 1700 m (1756.0 and 1812.0 m) within a short period after tagging (5 and 25 d), suggesting their death, and thus data for these sharks were excluded from subsequent analysis. In addition, Shark 18 was considered to have been preyed upon because the experienced temperature of this individual increased suddenly 1 mo after tagging, with high temperatures (25.0–30.0°C) recorded regardless of the water depth (1.5–800.0 m, average 109.8 m); therefore, Shark 18 was also excluded from subsequent analysis. Tracking periods of the remaining 18 tags ranged from 30 to 247 d (total 2006 d, mean 111 d). Tagged females measured 50.0–82.0 cm DL, and PCL (converted from DL) was 141.1–243.3 cm (mean 191.2 cm PCL).

The machine-learning method (Fujinami & Semba 2020) identified 2 females (Sharks 3 and 4) tagged in 2015 as pregnant based on their sex steroid hormone concentrations (Shark 3, P_4: 10.6 ng ml^{-1}, E_2: 439.0 pg ml^{-1}; Shark 4, P_4: 46.4 ng ml^{-1}, E_2: 774.0 pg ml^{-1}). Using ultrasonography during 2016–2017, we determined that 8 females tagged in autumn (Sharks 10–17) had small embryos (see Fig. S1A in the Supplement at www.int-res.com/articles/suppl/m658p163_supp.pdf), and 5 females tagged in May (Sharks 19–23) had large embryos (Fig. S1B). Although the pregnancy state at the time of release can be determined as above, development of embryos during the tracking period cannot be observed. Therefore, we assumed that 'season' represents pregnancy state as follows: autumn, early pregnancy; winter (December–February), middle pregnancy; spring, late pregnancy; and summer, postpartum, based on an annual reproductive cycle (Fujinami et al. 2017). Additionally, the pregnancy state at the time of release agreed with what was known of the annual reproductive cycle. We considered the remaining 3 individuals (Sharks 1, 5, and 8) to be adults (their pregnancy state was unknown) based on their body lengths (177.8–222.3 cm PCL; Table 1) being greater than the size at 50% maturity for female blue sharks in the North Pacific (149.1–156.6 cm PCL: Carrera-Fernández et al. 2010, Fujinami et al. 2017).

3.2. Seasonal migrations

Sharks in early pregnancy tagged in October (Sharks 3, 4, and 10–17) tended to move in a northeasterly direction, from subtropical to temperate waters, during autumn and the following spring (Fig. 2A,C,D). Of these 13 sharks, 2 (Sharks 3 and 12) traveled farther offshore along the Kuroshio Current from late winter to early spring, before immediately returning to subtropical waters during spring and early summer. Late-pregnancy individuals tagged in May (Sharks 19–23) moved in a southwesterly direction, from temperate waters of the TZ to subtropical waters during spring and summer (Fig. 2A,B). Two individuals (Sharks 19 and 22) moved long distances from the temperate waters around the TZ (33–34° N) into the South China Sea (13–14° N). The 3 adult sharks (Sharks 1, 5, and 8) for which the pregnancy state could not be determined and that were tagged in October, showed movement patterns similar to those of pregnant sharks released in the same

month (Fig. S2). All blue sharks were distributed at higher latitudes (>30° N) between February and April (i.e. middle–late pregnancy), and at lower latitudes (<25° N) between June and September (i.e. postpartum) (Fig. S3A); females were also found in more eastern waters (around 140–180° E) between January and April, and in more western waters (around 110–140° E) between June and August (Fig. S3B).

Kernel-density analysis of pregnant blue sharks revealed seasonal differences in their hotspots (Fig. 3). In spring (i.e. late pregnancy), hotspots appeared in temperate waters along the Kuroshio Current (30–35° N, 140–150° E and 30–35° N, 160–170° E; Fig. 3A). In summer (i.e. postpartum), a hotspot appeared in the South China Sea (18–22° N, 117–122° E; Fig. 3B). In autumn (i.e. early pregnancy), a hotspot appeared in subtropical waters (26–28° N, 138–141° E; Fig. 3C). In winter (i.e. middle pregnancy), a hotspot appeared in a coastal area off Japan (33–35° N, 140–144° E; Fig. 3D).
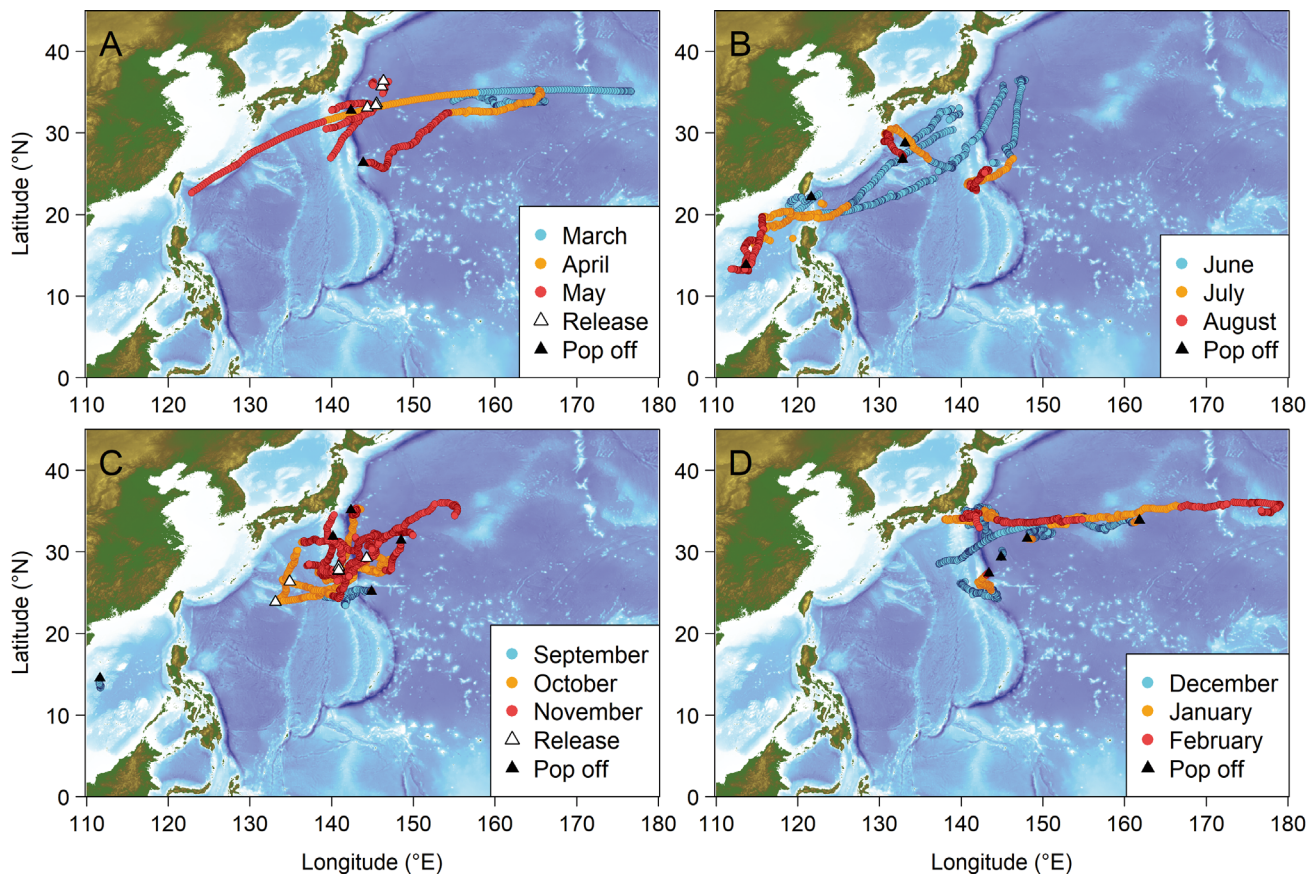

Fig. 2. Migration paths of pregnant blue sharks in the northwestern Pacific by season: (A) spring; (B) summer; (C) autumn; and (D) winter. Open triangles denote locations of sharks released with a tag in May or October; solid triangles denote pop-off locations of the pop-up satellite archival tags
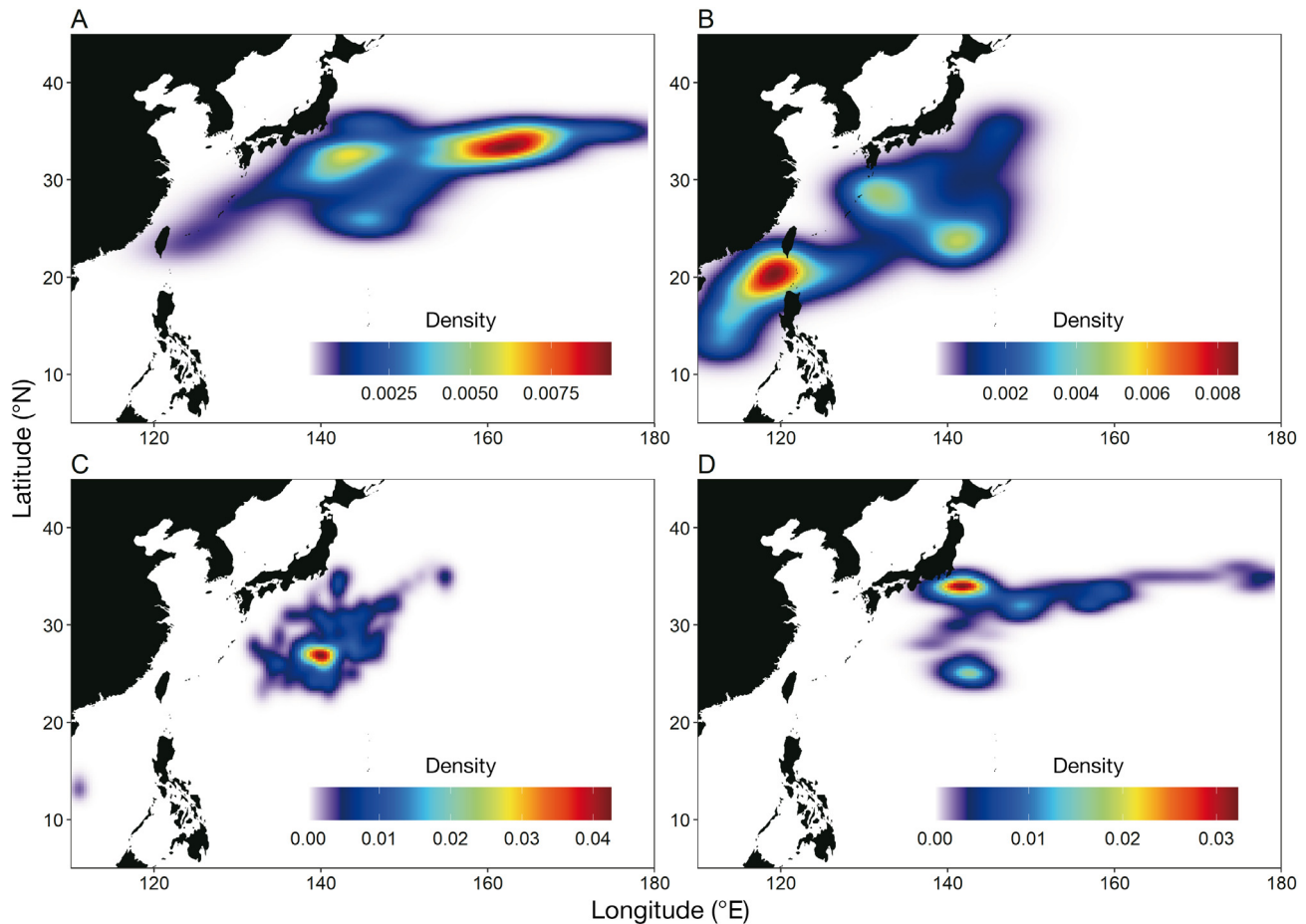
Fig. 3. Kernel-density plots of all data, collected in 2015, 2016, and 2017, for pregnant blue sharks by season: (A) spring, March–May; (B) summer, June–August; (C) autumn, September–November; and (D) winter, December–February. Warmer colors indicate higher densities (hotspots) of pregnant blue sharks (note different scales on the density bars)

3.3. Vertical movements

Tagging data of pregnant blue sharks revealed different patterns in their diel vertical movements by season (i.e. pregnancy stage) and by time of day: during the day the sharks frequented depths from the surface to 1517 m (mean 230.5 m), and at night from the surface to 1427 m (mean 78.5 m). Ambient water temperatures experienced ranged from 3.1 to 32.6°C (mean 18.0°C) during the day, and from 3.3 to 31.0°C (mean 22.4°C) at night. For all individuals, the depths and temperatures experienced during the day were significantly deeper and cooler than those experienced at night (Wilcoxon rank-sum test, p < 0.001). Diving behavior of pregnant blue sharks differed by season (i.e. pregnancy stage) (Fig. 4; Fig. S3C,D). During summer and winter (i.e. postpartum and early to middle pregnancy), sharks showed clear diel vertical movements, but movements tended to be relatively weak in spring (i.e. late pregnancy). In addition, pregnant sharks in spring experienced sig-

nificantly cooler water temperatures (mean 15.5°C during the day and 18.8°C at night) compared with other seasons (mean 17.6–19.6°C during the day and 20.3–23.9°C at night) (Fig. 4A).

Cluster analysis separated the 995 daily temperature–depth profiles into 3 thermal habitats (Habitats A, B, and C) in the northwestern Pacific (Table 2, Fig. 5). Most data (87.8%) were classified as Habitat A, which was widely observed outside the Kuroshio Current (Figs. 1B & 5A). Mean ambient water temperature in Habitat A was high (20.6°C) and decreased gradually with depth to 16.9°C at 300 m (Fig. 5B). Habitat B also had a high mean ambient water temperature (20.0°C), but temperature decreased quickly with depth to reach 15.2°C at 200 m (Fig. 5B); Habitat B occurred mainly in the South China Sea and the Kuroshio Current (Fig. 5A). The mean water temperature in Habitat C was 15.2°C, and temperature decreased continuously with depth to reach 11.5°C at 200 m (Fig. 5B). This cold thermal habitat was observed in the TZ or cold-water mass
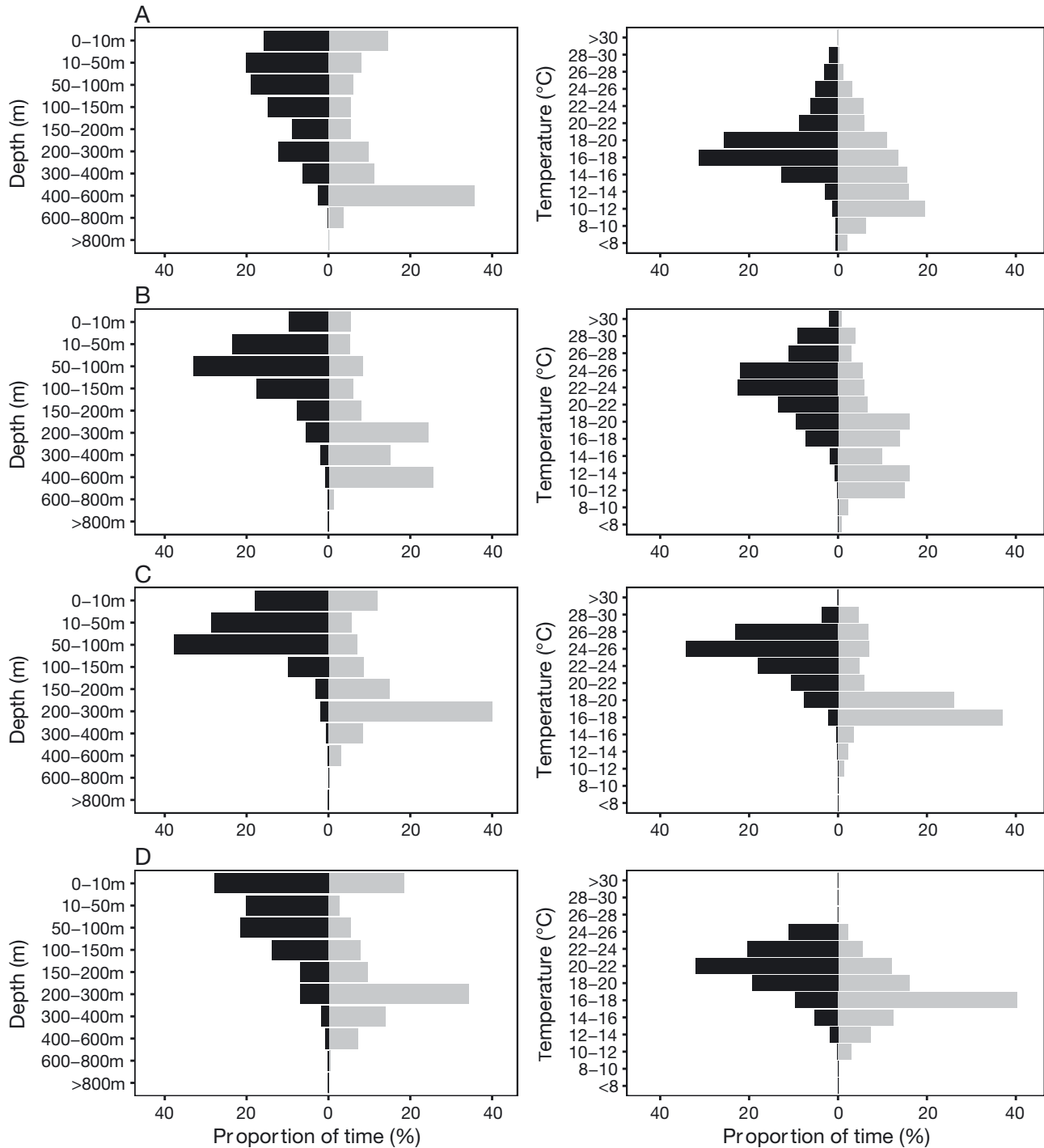
Fig. 4. Proportion of time-at-depth (left column) and time-at-temperature (right column) for pregnant blue sharks by season: (A) spring, March–May; (B) summer, June–August; (C) autumn, September–November; and (D) winter, December–February. Black and grey histograms denote data for nighttime and daytime, respectively

related to the Kuroshio meandering (Figs. 1B & 5A), during November and June. It is worth noting that compared with seasonal differences in thermal habitat use, pregnant blue sharks more frequently utilized Habitat C (15.2%) in spring (i.e. late pregnancy) than in other seasons (<4.0%) (Table S1).

Pregnant sharks in Habitats A and B had clear diel vertical movements (Table 2, Fig. 5C). At nighttime, they were distributed mainly from the surface to 100 m, at temperatures ranging from 24.0 to 26.0°C; in the daytime, they were distributed around 200–300 m in temperatures of 16.0–18.0°C in Habitat A, and 12.0–
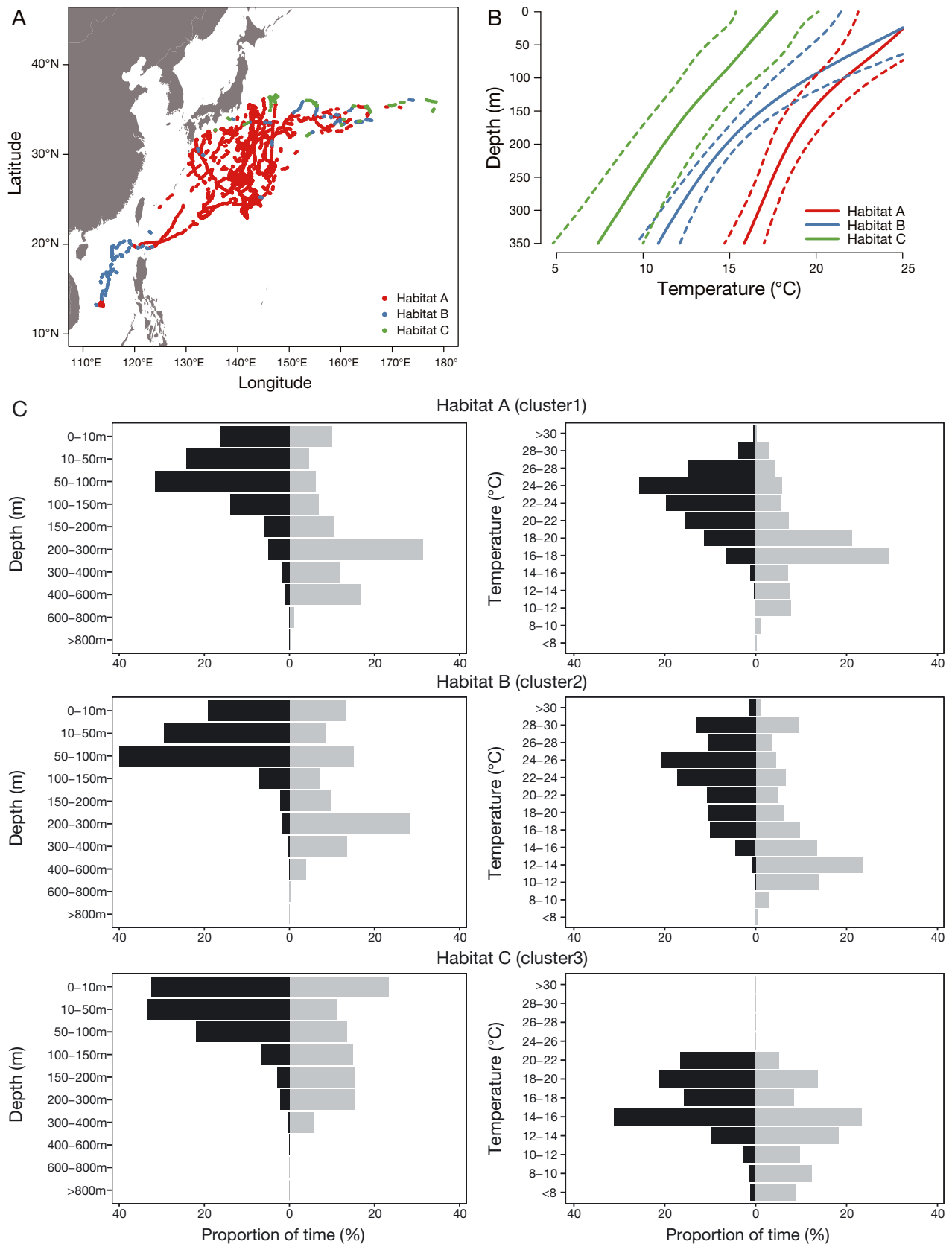
Fig. 5. Outputs of cluster analysis: (A) spatial distributions of the 3 thermal habitats; (B) aggregated mean values of temperature–depth profiles (±SD) of the 3 thermal habitats; and (C) proportion of time-at-depth (left column) and time-at temperature (right column) in relation to the 3 thermal habitats, as determined for pregnant blue sharks in the northwestern Pacific. Black and grey histograms denote data for nighttime and daytime, respectively

Table 2. Frequency and mean ± SD of dive depth and temperatures experienced in 3 thermal habitats (Habitats A, B, and C) for pregnant blue sharks in the northwestern Pacific

Cluster	Frequency (%)	Dive depth (m)		Experienced temp. (°C)	
		Day	Night	Day	Night
A	87.8	246.9 ± 165.1	80.9 ± 81.2	18.2 ± 4.4	23.0 ± 3.3
B	8.5	177.9 ± 132.2	55.6 ± 48.0	17.4 ± 6.1	23.0 ± 4.1
C	3.7	119.0 ± 104.5	46.5 ± 53.8	13.7 ± 3.9	16.6 ± 2.9

14.0°C in Habitat B. Sharks in Habitat C (cold thermal habitat) had a weak tendency for diel vertical movement compared with those in Habitats A and B, and were mainly distributed in surface layers at any time of the day (mean 119.0 m) or night (mean: 46.5 m).

Focusing on the vertical movements of 4 pregnant sharks (Sharks 3, 12, 21, and 23), females appeared to stay in the TZ for a short period of time before moving from temperate to subtropical waters (Fig. 6; Table S1). These 4 females clearly changed their vertical distributions before and after frequenting the TZ during late winter and spring (Fig. 6); they stayed in the cooler epipelagic zone of Habitat C from February to March (Sharks 3 and 12) and in May (Sharks 21 and 23), but dived deeper in other areas identified as Habitat A and B.

3.4. Effects of environmental and biological factors

VIF values among explanatory variables were <3.4, suggesting low collinearity. One model (Model 1) that included location (latitude, longitude), daily water temperature at 100 m, PCL, and diel period
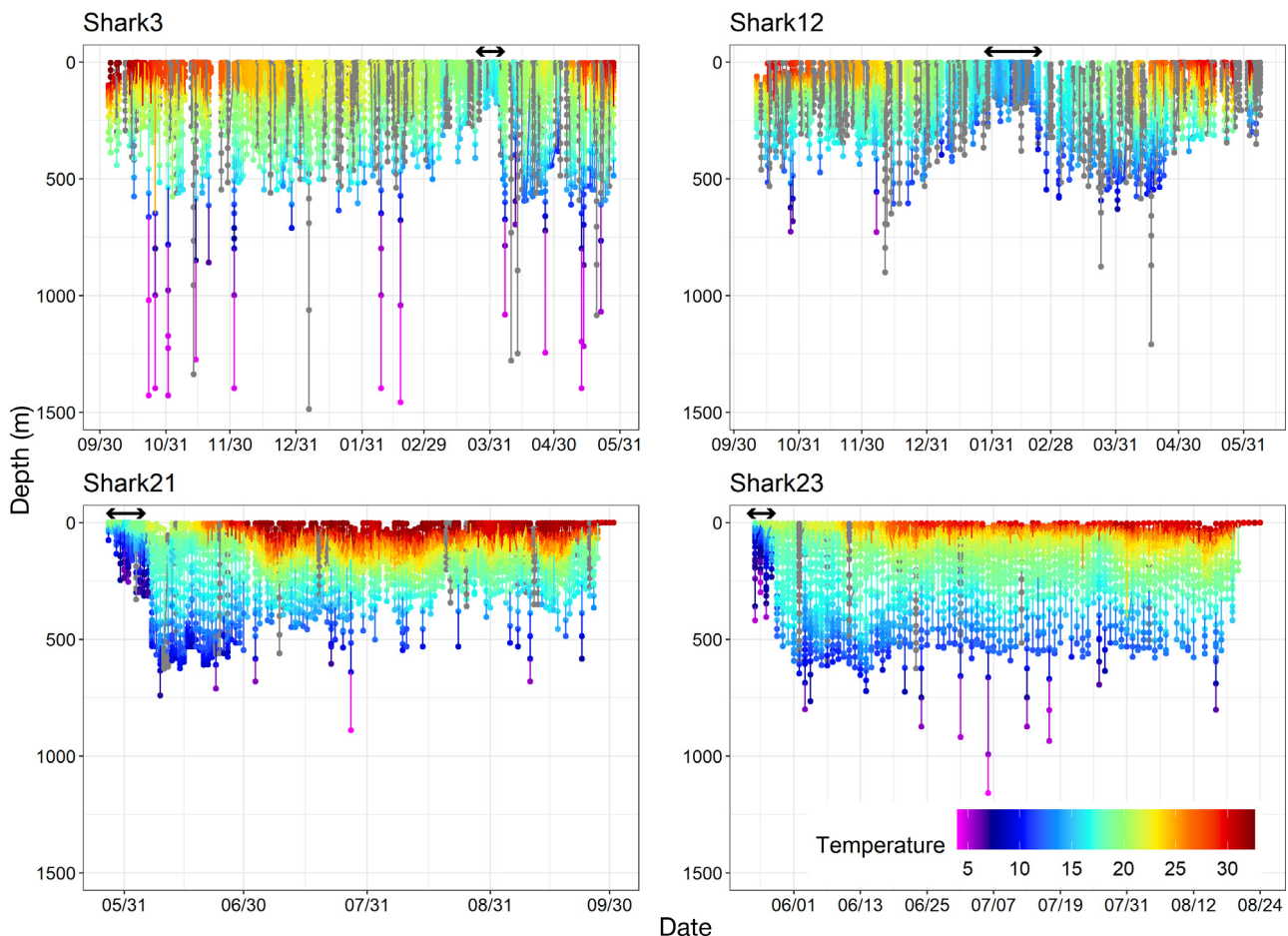

Fig. 6. Ambient water temperature−depth profiles against tracking dates for 4 pregnant blue sharks (Sharks 3, 12, 21, and 23). Sharks 3 and 12 were released in October, and Sharks 21 and 23 were released in May. Gray points denote missing temperature data. Arrows demarcate the periods when sharks stayed in Habitat C (i.e. Kuroshio/Oyashio transition zone)

(daytime and nighttime) was selected as the best model to account for mean diving depth of pregnant blue sharks (Table S2). The variables of log-transformed chl *a* concentration and bathymetry were not selected in the model. Diagnostic plots indicate both normality and homoscedasticity of model residuals, suggesting GAMM use was appropriate (Fig. S4). The best-fit model explained (adjusted R^2) 60.7 % of deviance in shark mean diving depth. The diel period was the most important variable, followed by location, water temperature at 100 m, and PCL (Table 3). The mean diving depth of sharks increased with increasing PCL, when the water temperature at 100 m was >18.0°C, and during daytime (Fig. 7A,B,D). In addition, shallower mean diving depths occurred in the South China Sea and around the TZ, related to spatial differences in other variables, including water temperature at 100 m depth (Fig. 7C).

4. DISCUSSION

We determined that pregnant blue sharks in the northwestern Pacific make seasonal northeast–southwest migrations between temperate and subtropical waters over the course of a year. Although our tracking data did not cover whole years, 2 females (Sharks 3 and 12) tagged in subtropical waters clearly migrated seasonally according to their pregnancy state, as they moved to temperate waters from autumn to spring and stayed in the TZ for only a short time before returning to subtropical waters. The hotspots for early-stage pregnant sharks appeared in subtropical waters during autumn, and those of late-stage pregnancy in temperate waters during spring. Blue sharks in the North Pacific are well known to mate in subtropical waters (20–30° N) in summer and then give birth to pups in temperate waters (30–40° N) in spring (Nakano 1994). We also found that pregnant blue sharks with early-stage embryos (mean 12.0 cm PCL) occurred in subtropical waters (15–30° N) with a higher SST (mean 27.3°C), while those possessing more developed embryos (mean 26.3 cm PCL) occurred in temperate waters (30–40° N) with a lower SST (mean 19.5°C) (Figs. S5 & S6). Our findings strongly support the migration model for adult female blue sharks proposed by Nakano (1994).

Similar seasonal migration patterns by adult female blue sharks have been reported in both the Northern and Southern Hemispheres. Female blue sharks in the eastern North Pacific Ocean showed seasonal north–south migration patterns (8–31° N) from waters near Hawaii into the Subtropical Convergence Zone (Musyl et al. 2011). In the South Atlantic, clockwise migration patterns were suggested for adult female blue sharks based on fishery-dependent information (Hazin et al. 1994, 2000). In the North Atlantic, adult female blue sharks with fresh mating wounds captured in the Bahamas (24° N, 75° W) migrated to the mid-Atlantic ridge (32° N, 38° W) from May to November; it has been suggested that females may move to the eastern Atlantic adult female aggregation site near the Azores (Howey et al. 2017). Vandeperre et al. (2014) reported that pregnant blue sharks with fully developed embryos at time of capture moved in a southward direction (from approximately 38 to 29° N) during May and June. Additionally, adult females moved to tropical waters (3–12° N) in the North Atlantic from spring to autumn, and some possessed embryos at the time of recapture in autumn (Vandeperre et al. 2014), demonstrating a movement pattern hypothesized to facilitate fertilization and embryonic development (Hazin et al. 1994).

Evidence shows that adult females of some sharks perform return migrations to their places of birth for mating or parturition. Although evidence of parturition site fidelity is rare for sharks, females of several coastal species, such as lemon shark *Negaprion brevirostris*, blacktip shark *Carcharhinus melanopterus*, and bull shark *Carcharhinus leucas* returned to the same nursery sites for parturition (Chapman et al. 2015, Lea et al. 2015). For wide-ranging pelagic shark species, it is difficult to demonstrate parturition site fidelity. However, adult female porbeagle sharks *Lamna nasus* migrate to a specific area for parturition, and adult female porbeagle sharks in the North

Table 3. Summary statistics for the best fitting generalized additive mixed model for mean diving depth of pregnant blue sharks in the northwestern Pacific. ΔAIC indicates the magnitude of the effects on Akaike's information criterion (AIC) when the variable is excluded from the model, and a larger ΔAIC means that the variable is more important. edf: estimated degrees of freedom

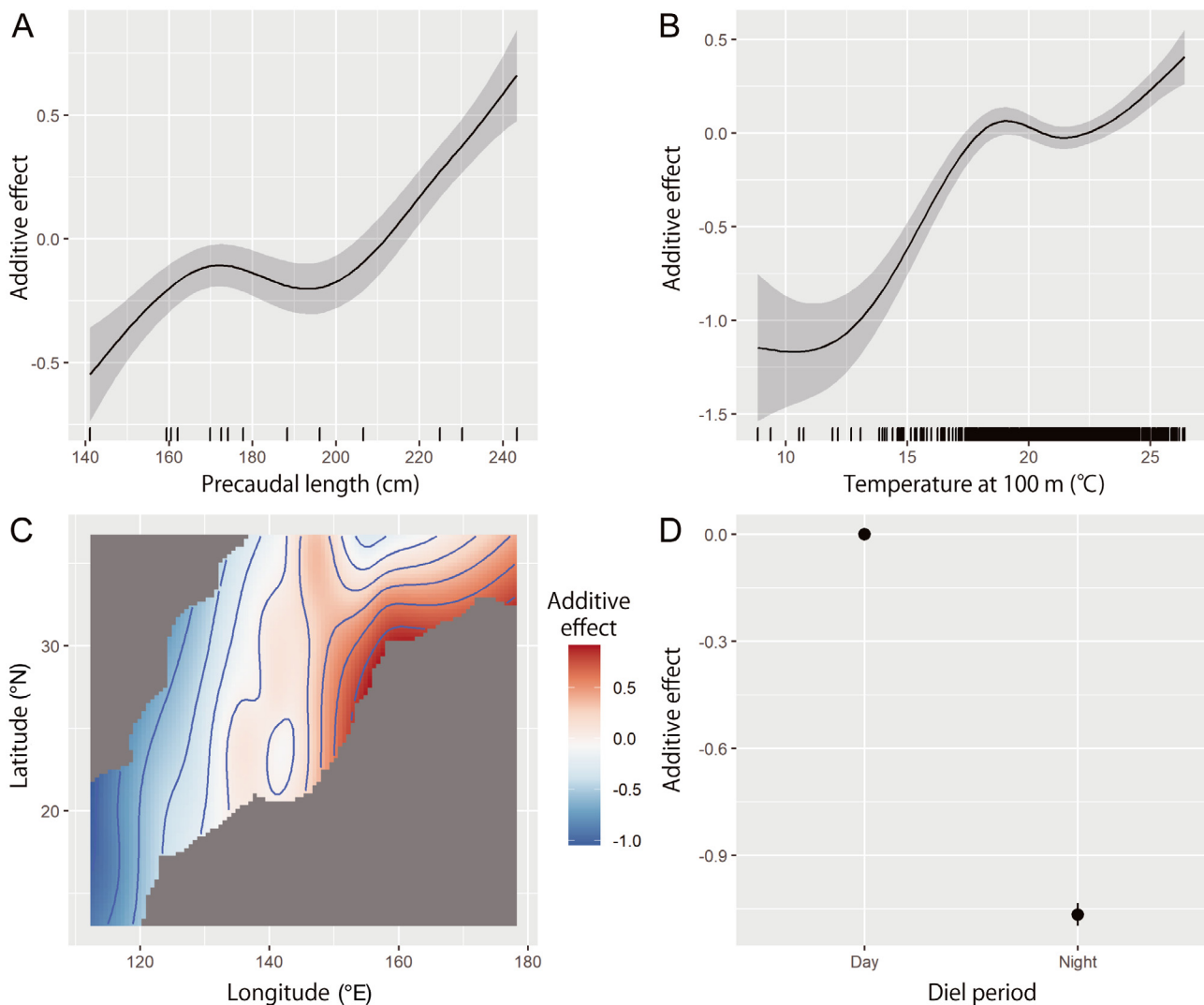| Smooth terms	edf	*F*-ratio	p	ΔAIC
Longitude, latitude	22.15	27.04	<0.00001	471.4
Temperature at 100 m (°C)	5.93	34.19	<0.00001	178.9
Precaudal length (cm)	3.39	30.98	<0.00001	4.5
Parametric term	df	*F*-ratio	p	ΔAIC
Diel period (day, night)	1	4398.0	<0.00001	2213.2

Fig. 7. Response plots from the best-fitting generalized additive mixed model on mean diving depth of pregnant blue sharks in the northwestern Pacific. (A) Precaudal length, (B) daily mean temperature at 100 m, (C) location (interaction of latitude and longitude) in the movement range, and (D) diel period (daytime or nighttime). Shaded areas in A and B represent the 95% confidence intervals. Positive values on the *y*-axes in A, B, and D and the warmer colors in C indicate increased mean diving depths

Atlantic Ocean migrate up to 2356 km through the winter, from off eastern Canada to the subtropical Sargasso Sea for parturition (Campana et al. 2010). Therefore, pregnant blue sharks in the northwestern Pacific might utilize specific water regions (e.g. subarctic waters: TZ) as parturition grounds.

Pregnant blue sharks (except those at a late stage) showed wide and clear diel vertical movements, as reported for several pelagic shark species, including blue sharks (e.g. Campana et al. 2011, Queiroz et al. 2012, Francis et al. 2015, Vaudo et al. 2016, Howey et al. 2017). We also identified different vertical movement patterns for pregnant blue sharks between subtropical and temperate waters in the northwestern

Pacific, reflecting differences in the oceanic environment. Results of GAMMs statistically clarified that the mean diving depth of pregnant blue sharks was influenced by diel period, location, water temperature (i.e. temperatures at 100 m), and body length, and was deeper (1) during the daytime, (2) outside of the Kuroshio Current, (3) in higher temperatures at 100 m (>18.0°C), and (4) with larger body length (Table 3, Fig. 7). For ectothermic sharks (including blue sharks), ambient water temperature is a physiological regulator, and they typically seek physiologically optimal temperatures (e.g. Carey & Scharold 1990). Blue sharks prefer waters between 12 and 20°C (Nakano & Stevens 2008), and in the tropics,

they move to greater depths to seek cooler water (Hazin et al. 1994, Nakano & Stevens 2008, Vandeperre et al. 2016). The vertical distribution of pregnant sharks was shallower in the water column as they moved into the TZ (Figs. 5C & 7C).

In summary, deeper-diving behavior was observed where surface waters were warm (i.e. Habitats A and B) than where they were cold (i.e. Habitat C). In a similar case, the diving behavior of North Atlantic blue sharks varied significantly within and outside the warm Gulf Stream (Campana et al. 2011). Campana et al. (2011) reported blue sharks feeding on squid and fish prey near the surface at night, and then diving deeper to follow them during the day in warm waters, which might reduce metabolic losses through thermoregulation and increase foraging efficiency. For pregnant blue sharks, this may be a strategy to preserve energy for embryonic development and broad-scale seasonal migration.

In the TZ, pregnant blue sharks mainly occurred in the epipelagic zone (<200 m) at any time of the day or night (Fig. 5C). Additionally, pregnant sharks changed their vertical distributions before and after staying in the TZ in spring (Fig. 6). As several conditions, namely, season, location, and pregnancy state of these females, are consistent with the parturition conditions reported by Nakano (1994), pregnant blue sharks are likely to give birth in the epipelagic zone of the TZ in spring. Four pregnant individuals (Sharks 3, 12, 21, and 23) utilized the cooler epipelagic zone during their short stay in the TZ (Fig. 6); they did not dive to deep water with regular diel vertical movement during this period. In general, the diving ability of sharks increases as the individual grows, with individuals becoming more buoyant with age (Iosilevskii & Papastamatiou 2016, Vaudo et al. 2016). Accordingly, compared with adults, blue shark neonates will have reduced ability to control their buoyancy and are less likely to dive deep (i.e. blue shark neonates cannot seek physiologically optimal temperatures by diving to depth). Young-of the-year blue sharks in the northeastern Pacific spent 96.4% of their time at depths shallower than 40 m (Nosal et al. 2019), further suggesting that sharks are likely to give birth to pups in epipelagic waters that provide a physiologically optimal temperature for their neonates.

Blue sharks show spatiotemporal segregation by sex and life stage, and juveniles occur mainly in temperate waters (Nakano 1994, McKinnell & Seki 1998, Vandeperre et al. 2014). Juvenile females occur mainly north of 33° N throughout the year in the northeastern Pacific (Maxwell et al. 2019, Nosal et al. 2019). In the North Atlantic, juvenile females are also distributed in temperate waters between 31 and 59° N throughout the year (Vandeperre et al. 2014). These findings contrast with a north–south migration pattern for adult female blue sharks in relation to reproduction, but they support ontogenetic segregation between adults and juveniles.

Juvenile blue sharks may experience some advantages in utilizing the TZ as a nursery ground. Unlike characteristically oligotrophic subtropical waters (Morel et al. 2010), the temperate waters of the TZ are a highly productive and important fishing ground in the North Pacific (Zainuddin et al. 2008, Ohshimo et al. 2016). The TZ is an important habitat for numerous pelagic fishes, particularly Japanese anchovy *Engraulis japonicus* and Japanese sardine *Sardinops melanostictus* (Murase et al. 2012), as well as squid (Kubodera et al. 1983). The area is also a feeding ground for several highly migratory species, including albacore *Thunnus alalunga* (Zainuddin et al. 2008), bigeye tuna *T. obesus* (Ohshimo et al. 2018), and Pacific bluefin tuna *T. orientalis* (Fujioka et al. 2018), as well as blue sharks (Block et al. 2011). In fact, hotspots of blue sharks were observed in temperate waters, from the TZ to the Emperor Seamount Chain (Kai et al. 2017, Kai 2019; Fig. 1B). The diet of blue sharks in the northwestern Pacific mainly comprises oceanic squids and small pelagic teleost fishes, such as anchovy and lanternfish (Kubodera et al. 2007, Fujinami et al. 2018).

Harris (1952) suggested that water temperature plays a vital role in the embryonic growth of small-spotted catshark *Scyliorhinus canicula*, as embryos developed 1.64 times faster at higher temperatures than at lower temperatures. A similar trend in which pregnant sharks prefer warmer water temperatures than non-pregnant sharks was reported for other shark species, such as grey reef shark *Carcharhinus amblyrhynchos* (Economakis & Lobel 1998) and shortfin mako *Isurus oxyrinchus* (Semba et al. 2011). Given these findings, we may surmise that the movement to subtropical waters by pregnant blue sharks in the northwestern Pacific serves to aid fertilization and embryonic growth at the early development stage as hypothesized by Hazin et al. (1994).

5. CONCLUSIONS

This study reports seasonal reproductive migration of pregnant blue sharks for the first time in any ocean. Pregnant blue sharks tagged in the northwestern Pacific showed a seasonal northeast–southwest migration pattern over a year, and their

horizontal movements and vertical distributions were influenced by the oceanic environment, specifically water temperature. Females at an early stage of pregnancy occurred in subtropical waters and moved northward as their embryos developed; females at a late stage of pregnancy occurred in temperate waters (the TZ) and then returned to subtropical waters. Sharks at a late stage of pregnancy mainly utilized the epipelagic zone, and stayed in the TZ for a short period of time. Our results suggest that pregnant blue sharks in the northwestern Pacific likely visit the TZ and give birth to pups in the epipelagic zone; our results also support the schematic sex-specific migration model for female blue sharks in the North Pacific proposed by Nakano (1994). Our tracking data revealed that pregnant blue sharks passed through multiple national jurisdictions and international waters in the northwestern Pacific. This means that their effective management and conservation requires multinational cooperative plans. Although we revealed that pregnant blue sharks utilize a wide range of pelagic areas in the northwestern Pacific, they did not cross the International Date Line—inconsistent with results of previous population structure of this species in the North Pacific (King et al. 2015). Therefore, further study on blue sharks throughout the North Pacific is required using electronic tags. Other approaches, such as stable isotope ratios (e.g. Ohshimo et al. 2019), would likewise be useful to verify the comprehensive movements of this species.

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