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Habitat use and movement patterns of small (age-0) juvenile Pacific bluefin tuna (*Thunnus orientalis*) relative to the Kuroshio

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Abstract

The habitat use of Pacific bluefin tuna (*Thunnus orientalis*; PBF) in nursery waters off the southern coast of Japan was investigated using archival tags over a 3 year study period (2012–2015), and the data were used to examine the free-ranging habitat preferences of PBF and the relationship between their horizontal movements and the path of the Kuroshio off the Pacific coast of Japan. The path of the Kuroshio fluctuated seasonally, leading to changes in water temperature that strongly influenced the habitat use of small PBF (2–3 months after hatching). Most PBF were present in coastal waters inshore of the path of the current, and their habitat use changed in response to the distance of the current from the coast. The Kuroshio typically flowed along the coast from summer to autumn, and PBF remained in the coastal waters off Kochi Prefecture during this period. In contrast, PBF quickly moved eastward in winter when the current moved away from the coast. Throughout the winter and spring, the area of habitat use extended widely from the eastern end of the southern coast of Japan (the Boso Peninsula) to the offshore Kuroshio-Oyashio transition region. These findings suggest that the seasonal habitat use and movement behavior of juvenile PBF are influenced by the distance of the Kuroshio axis from the coast, and the ultimate drivers are likely variations in oceanographic conditions and prey availability along the southern coast of Japan.

KEYWORDS
archival tag, coastal water, habitat preference, horizontal movement, nursery waters

1 | INTRODUCTION

The Pacific bluefin tuna (PBF, *Thunnus orientalis*) is a highly valuable resource for the Japanese fishery. The increased catch of young fish (age 0–2) over the past decade has raised sustainability concerns (Cyranoski, 2010). Age-0 PBF are advected into Japanese coastal waters by the Kuroshio, and estimating the abundance of recruited PBF is important for stock assessment (Ichinokawa, Okamura, Oshima, Yokawa, & Takeuchi, 2014; Yamada, Takagi, & Nishimura, 2006). Tuna undertake rapid, wide-ranging movements, making it difficult to accurately interpret fisheries catch and effort data for use in recruitment indices (Kurota et al., 2009). Thus, more research is needed to increase the understanding of the movement dynamics of early life-stage PBF to improve stock management.

Pacific bluefin tuna spawn in the region between the eastern Philippines and the Nansei Islands (Ryukyu archipelago) in the western Pacific Ocean from April to June and in the Sea of Japan from July to August (Ashida, Suzuki, Tanabe, Suzuki, & Aonuma, 2015;

Okiyama, 1974; Okochi, Abe, Tanaka, Ishihara, & Shimizu, 2016; Ueyanagi, 1969; Yabe, Ueyanagi, & Watanabe, 1966). Larval PBF that hatch in the North Pacific Ocean are primarily transported by the Kuroshio toward the East China Sea and the southern coast of Japan (off Kochi Prefecture; Kitagawa et al., 2010; Masujima, Kato, & Segawa, 2014). These coastal waters are a well known summer habitat for juvenile PBF, which age to 2–3 months and grow to a fork length (FL) of 17–32 cm during this period (Tanaka, Satoh, Iwahashi, & Yamada, 2006).

Past conventional tagging studies from the southern coast of Japan have indicated that 15–31 cm FL PBF move northeast along the Pacific coast of Japan during summer–autumn and that some juveniles move to the Eastern Pacific (Bayliff, 1994; Bayliff, Ishizuka, & Deriso, 1991). Ichinokawa et al. (2014), who analyzed commercial fishery data, also demonstrated that the distribution of the PBF catch shifted in a north-south direction with changes to the sea surface temperature in the East China Sea. However, little information is available regarding the movements of smaller, age-0 PBF (ca. 20 cm FL) in the nursery waters near Japan. Additionally, conventional tagging experiments and the analysis of fishery data cannot reveal continuous patterns of PBF habitat use. In particular, the distribution and movement patterns of juvenile PBF in offshore waters are unknown because fishing activities for young PBF have not been conducted in offshore regions.

Archival electronic tags have been applied to bluefin tuna since the early 1990s (Block et al., 1998, 2001; Itoh, Tsuji, & Nitta, 2003; Kitagawa, Kimura, Nakata, & Yamada, 2004; Kitagawa et al., 2000; Inagake et al., 2001) and have provided information on the migration and habitat use by the species in the open ocean. Archival tags record ambient light level measurements, which can be processed to reconstruct daily estimates of fish locations (Hill, 1994; Welch & Eveson, 1999). The accuracy of these location estimates can be improved by integrating sea surface temperatures and bathymetry parameters into position-estimation models (Galuardi et al., 2010; Lam, Nielsen, & Sibert, 2008; Teo et al., 2004). Kitagawa et al. (2000, 2004) and Itoh et al. (2003) applied these tags to age-1 PBF (45–78 cm FL at release), and other recent studies have deployed archival tags and accelerometers on small, juvenile PBF to describe their vertical movements in the wild (fish ranging from 20.5 to 26.5 cm FL) and swimming behaviors in an open-sea net cage (fish ranging from 21.0 to 24.5 cm FL) along the southern coast of Japan (Furukawa, Fujioka, Fukuda, Tei, & Ohshimo, 2017; Noda et al., 2016). However, these studies did not address horizontal habitat use by free-ranging individuals in natural waters.

Oceanographic features such as the Kuroshio can affect the larval transport (Kitagawa et al., 2010; Masujima et al., 2014), habitat use (Kitagawa, Sartimbul, et al., 2006), movement pathways (Itoh et al., 2003; Kitagawa et al., 2004), and foraging behavior (Kitagawa et al., 2004) of PBF at various life stages. The Kuroshio is a warm, low nutrient, western boundary current and is one of the strongest currents in the world. It flows northeastward along the continental shelf from Taiwan and the Pacific coast of Japan (Kawai, 1998; Mizuno & White, 1983; Figure 1). Fluctuations in the velocity of the current and path are thought to influence the biological productivity and distribution of small pelagic fish (Kimura et al., 1997; Nakata, Zenitani, & Inagake, 1995) on which juvenile PBF feed (Shimose, Watanabe, Tanabe, & Kubodera, 2013). Thus, variations in the Kuroshio system likely play a major role in influencing the habitat selection of juvenile PBF in important coastal nursery areas.

For 3 years (2012/2013, 2013/2014, and 2014/2015), we investigated the horizontal movements of juvenile PBF (age-0) along the southern coast of Japan from July to May using archival tags. Our primary objectives were to examine the patterns of spatial and temporal habitat use throughout the age-0 period, and to identify variations in their movement behavior in relation to fluctuations in the Kuroshio.

2 | MATERIALS AND METHODS

2.1 | Fish tagging

The movements of free-ranging juvenile PBF were determined using LAT2910 archival tags (7.8 mm in diameter, 26 mm in length, 2.3 g in weight; Lotek Wireless Inc, Newmarket, Ontario, Canada), which record swimming depth (at a resolution of 0.1 m from 0 to 500 m), ambient water temperature and internal temperature (at a resolution of 0.05°C), and relative ambient light levels at 30 s intervals over a predicted lifetime of 0.5–1 years (with 8 MB of memory). The miniaturization of this archival tag has enabled its application in smaller fishes, such as juvenile PBF, than was previously possible.

Juvenile PBF were caught by hook-and-line trolling from the stern of a fishing vessel and then placed in a live-well for transport to a net pen (12 × 12 × 6 m) anchored off the port of Kaminokae (33.282°N, 133.246°E) in Kochi Prefecture. The time from capture on the fishing grounds to arrival at the net pen was approximately 0.5–2 hours. The fishing grounds are primarily restricted to the continental shelf located 8–24 km from the port with depths ranging from 50 to 200 m.

Archival tags were surgically implanted into the peritoneal cavity of each fish, and the fork lengths (FLs) were measured to the nearest 0.5 cm. A 1.0 cm horizontal incision was made approximately 0.5 cm off the midline and 2.0 cm anterior to the anus. The fish were also tagged with conventional plastic dart tags placed at the base of the second dorsal fin. The implantation procedure generally took <30 s, and all procedures were performed by a single experienced operator. To ensure the vitality of the fish after the capture and tagging process, they were held in the net pen for an average of 4 days (range: 0–13 days), and daily underwater observations were made to confirm that the tagged fish were swimming normally. The survival rate in the net pen post-surgery was 84.2%. The tagged fish were released directly to the open ocean after this recovery period.

A total of 214 PBF ranging from 18.0 to 33.0 cm FL (mean ± SD: 23.8 ± 2.5) were released in the coastal waters off Kochi (Figure 1) from 28 July to 23 August in 2012, 17 July to 15 August in 2013 and 19 July to 20 August in 2014 after being held in a net pen. Of these fish, 51 (23.8% of the total) were recovered,

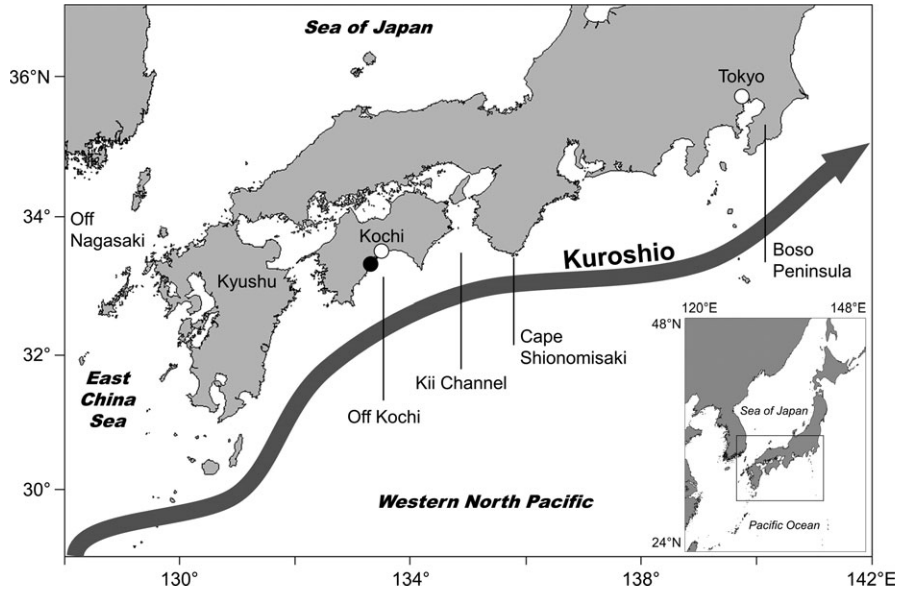


FIGURE 1 The study area along the southern coast of Japan. The black circle indicates the release location of tagged Pacific bluefin tuna, and the grey arrow represents the path of the Kuroshio

and the data from 30 of these tags (10, 4, and 16 fish each year) were successfully downloaded. We were unable to successfully download data from 10 of the recovered tags due to mechanical problems, and in 11 recovered fish, only the conventional tags remained. In this study, we examined the archival tag data from July to the following May (the age-0 period) for each tagging year. The release and recovery details for each fish are shown in Table 1.

2.2 | Analyses of fish locations

Archival tags have been used for over a decade to estimate the daily positions of animals in the open ocean using a light sensor to detect the time of sunrise and sunset (e.g., Block et al., 1998). Welch and Eveson (1999) noted that the errors associated with such geolocation estimates can be considerable, with standard deviations of 0.9° in longitude and 1.2° in latitude. The accuracy and precision of movement estimates have recently been improved by integrating the sea surface temperature and depth data recorded by the tags (Galuardi et al., 2010; Lam et al., 2008; Teo et al., 2004). Lam et al. (2008) provided a detailed explanation and a state-space model analysis with a sea surface temperature matching algorithm. In this study, to assess the horizontal movements of tagged PBF, the state-space extended Kalman filter statistical model was used to estimate geolocation errors, movement parameters, and most probable tracks (Galuardi et al., 2010; Lam et al., 2008; Sibert, Musyl, & Brill, 2003). The 8 day composite 0.1° gridded sea surface temperature (SST) products of the satellite derived Pathfinder Advanced Very High Resolution Radiometer (AVHRR) were used for this analysis and are available from the NOAA BloomWatch 360 website (http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW360.jsp). We also made bathymetric corrections for location estimations based on the daily maximum depth reached by the fish (Galuardi et al., 2010; Teo, Boustany, & Block, 2007). Bathymetric data from the ETOPO1 model (1 arc-minute by 1 arc-minute) were obtained from the NOAA website (http://www.ngdc.noaa.gov/mgg/global/global.html). These most probable track estimates were performed using an unscented Kalman filter (implemented with the *ukfsst* package of R software, Lam et al., 2008).

The *ukfsst* model, described in detail in Lam, Nielsen, and Sibert (2010) and Lam et al. (2008), was used to increase the reliability of the geolocation estimate. We ran a 128 scenario model by changing the initial values of the measured parameters for each individual tag record, and the highest likelihood scenario was ultimately selected as the most probable track. We defined the range in the model parameters quantifying the northward and eastward movement components as 3–7 nautical miles/day. Random errors in the longitude and latitude position estimates were set from 0.5° to 1.0° and from 1° to 5°, respectively. The smoothing radius of the SST data parameter ranged from 30 to 90 nautical miles. Other parameters were set at the default values of the package (https://github.com/positioning/kalmanfilter/wiki/ArticleParUkfsst).

2.3 | Habitat estimation and seasonal changes in fish movements

Daily distributions of all tags were estimated using the Kalman filter model (n = 2,461). Habitat preferences throughout the investigation period were examined using the fixed kernel density of the daily distribution with non-parametric estimates, in accordance with previous studies (Block et al., 2005; Boustany, Matteson, Castleton, Farwell, & Block, 2010; Kitagawa, Sartimbul, et al., 2006). The search radius was fixed at 1° for the kernel density analysis, and the smoothing parameters were estimated using the least squares method. The kernel density estimates by season were performed using R software (The R Project for Statistical Computing: http://www.r-project.org/).

To examine the movement patterns of the tagged PBF along the southern coast of Japan, the daily distributions were compared with satellite-derived images of sea surface temperature in each season (summer, June–August; autumn, September–November; winter,

TABLE 1 Data periods, dates of tag recovery, fork lengths at release and at recovery, travel distances per day (km) and daytime and nighttime swimming depths (m) of tagged Pacific bluefin tuna

			Fork length (cm)		Travel distance per	Swimming depth (mean ± *SD*, m)		Mann-Whitney
Fish no.	Data period (days)	Date of tag recovery	At release	At recovery	day (mean ± *SD*, km)	Daytime	Nighttime	*U*-test *p*-value
922	12 August 2012 to 2 September 2012 (22)[a]	6 July 2014	26.0	110.0[c]	14.6 ± 10.6	25.5 ± 20.0	17.3 ± 11.2	<.01
925	28 July 2012 to 13 February 2013 (201)	25 August 2014	24.0		6.1 ± 7.9	41.1 ± 28.2	19.2 ± 20.2	<.01
932	3 August 2012 to 12 December 2012 (132)	12 December 2012	28.0	53.5	15.3 ± 14.5	48.2 ± 30.8	31.9 ± 25.2	<.01
945	3 August 2012 to 2 February 2013 (184)	9 June 2014	24.5	85.0[c]	17.9 ± 19.4	51.2 ± 48.2	21.9 ± 29.8	<.01
948	3 August 2012 to 21 October 2012 (80)	21 October 2012	24.5	50.0	4.2 ± 3.3	37.9 ± 25.7	20.6 ± 18.8	<.01
1092	3 August 2012 to 14 August 2012 (12)	14 August 2012	29.0	30.0	13.8 ± 5.9	33.0 ± 29.8	15.5 ± 9.0	<.01
1117	15 August 2012 to 9 September 2012 (26)[b]	8 September 2014	30.0		18.4 ± 19.1	34.5 ± 22.9	19.8 ± 15.9	<.01
1127	23 August 2012 to 28 July 2013 (340)	28 July 2013	26.5		46.8 ± 71.0	39.2 ± 53.8	20.6 ± 28.9	<.01
1128	23 August 2012 to 3 September 2013 (377)	3 August 2014	27.0		51.7 ± 67.9	55.6 ± 32.4	27.1 ± 27.5	<.01
1139	23 August 2012 to 2 September 2012 (11)	2 September 2012	26.0	29.0	21.5 ± 13.0	27.6 ± 18.8	19.7 ± 10.1	<.01
1696	22 July 2013 to 19 August 2013 (29)	19 August 2013	24.0	34.5	3.1 ± 4.3	12.3 ± 14.1	5.0 ± 6.8	<.01
1700	28 July 2013 to 15 August 2013 (19)[a]	12 September 2013	20.0	36.0	8.1 ± 5.4	10.7 ± 11.1	4.7 ± 5.6	<.01
1736	15 August 2013 to 22 August 2013 (8)[a]	26 January 2014	22.5	52.0	17.8 ± 9.1	15.5 ± 15.4	6.7 ± 4.6	<.01
1766	15 August 2013 to 13 May 2014 (272)	19 September 2014	23.0		29.0 ± 35.8	34.5 ± 35.4	18.5 ± 25.6	<.01
1773	24 July 2014 to 27 August 2014 (35)	27 August 2014	25.5	36.0	11.9 ± 10.6	12.2 ± 16.7	8.7 ± 11.1	<.01
2852	24 July 2014 to 7 September 2014 (46)	7 September 2014	23.5	35.0	8.8 ± 6.6	18.0 ± 18.8	12.6 ± 12.2	<.01
2845	28 July 2014 to 10 November 2014 (106)	10 November 2014	22.0	45.0	8.9 ± 5.5	45.3 ± 38.5	31.0 ± 26.9	<.01
2850	31 July 2014 to 29 August 2014 (30)	29 August 2014	22.5	34.0	6.4 ± 4.6	19.0 ± 17.5	13.3 ± 12.7	<.01
2876	31 July 2014 to 26 August 2014 (27)	26 August 2014	22.0		3.4 ± 2.3	16.5 ± 16.6	10.6 ± 9.5	<.01
2878	31 July 2014 to 26 August 2014 (27)	26 August 2014	22.0	26.0	6.1 ± 3.4	20.9 ± 19.2	13.5 ± 11.3	<.01
2891	31 July 2014 to 12 September 2014 (44)	12 September 2014	20.5	29.5	3.0 ± 1.8	22.6 ± 24.3	11.5 ± 12.3	<.01
2880	21 August 2014 to 18 November 2014 (90)	18 November 2014	21.5	47.0	2.3 ± 3.5	53.3 ± 35.0	22.1 ± 24.2	<.01
2903	21 August 2014 to 30 August 2014 (10)	30 August 2014	23.0		18.7 ± 14.8	27.2 ± 20.9	10.5 ± 12.2	<.01
2914	21 August 2014 to 17 November 2014 (89)	17 November 2014	20.5		6.9 ± 6.9	57.6 ± 31.5	28.7 ± 27.4	<.01
2921	21 August 2014 to 21 February 2015 (185)	16 June 2015	23.0	64.0	11.0 ± 11.4	50.1 ± 35.4	24.8 ± 30.6	<.01
2922	21 August 2014 to 14 November 2014 (86)	14 November 2014	23.0	49.0	6.3 ± 6.6	52.8 ± 35.7	27.2 ± 25.7	<.01
2929	21 August 2014 to 13 September 2014 (24)	13 September 2014	25.0	34.0	6.6 ± 4.5	39.1 ± 25.4	14.0 ± 14.6	<.01
2933	21 August 2014 to 1 September 2014 (12)	1 September 2014	23.5		11.3 ± 7.7	16.8 ± 18.2	6.7 ± 7.6	<.01
2940	21 August 2014 to 8 November 2014 (80)	8 November 2014	23.5	40.0	3.0 ± 3.9	59.7 ± 31.7	27.4 ± 27.4	<.01
2952	21 August 2014 to 14 November 2014 (86)	14 November 2014	25.0	46.5	2.8 ± 3.6	55.6 ± 32.4	27.1 ± 27.5	<.01

The Mann-Whitney *U* test was used to determine the statistical significance of the differences between daytime and nighttime.
[a]Stopped recording during deployment.
[b]Excludes monitoring during the period of being farmed in the tuna net pen.
[c]Measurement after a period of being farmed in the tuna net pen.

December-February; spring, March–May) for 3 years. The temperature images were composite 3 month averages obtained from the FRA-ROMS (http://fm.dc.affrc.go.jp/fra-roms/), which is a high resolution ocean data assimilation and forecast system for the North-western Pacific developed by the Fisheries Research Agency. To examine the spatial distribution of tagged PBF with respect to the path of the Kuroshio, we used a satellite-derived subsurface temperature product (50 m depth) of the FRA-ROMS to clearly visualize temperature and to reduce the effects of surface heating and evaporation, which can be particularly strong in the region during summer.

The distance (km) traveled per day by tagged PBF was calculated by examining the daily distribution of the most probable track within each season throughout the 3 year period. The observed variation in travel distance was used to estimate the spatial usage and movement patterns of tagged PBF. The Steel-Dwass test was used to identify seasonal differences in spatial use, and the significance level was set at 0.05.

2.4 | Fish distribution in relation to the path of the Kuroshio

The distance of the axis of the Kuroshio from Cape Shionomisaki (Figure 1) at the southern end of Honshu was used to quantify the location of the current relative to the coast. The distance between Cape Shionomisaki and the Kuroshio axis was measured every 7 days from the Marine Information Research Center (MIRC; http://www.mirc.jha.jp/en/index.html) as a proxy of the path of the current. The position of the Kuroshio was estimated based on a comprehensive analysis of temperature, surface velocity, and sea surface height data from field observations. Monthly means, based on 7 day average distances of the Kuroshio axis from the coast calculated over the 3 year study, were used to determine the seasonal variation in the path of the current.

To evaluate the spatial distribution of the tagged PBF relative to the seasonal variation of the path of the current along the south coast of Japan, the latitudinal distance of the tagged PBF, measured perpendicularly to the nearest point on land, and the distance of the Kuroshio axis from the coast between Kochi and the Boso Peninsula (ranging from 132.236°E to 139.859°E) were calculated for the same period (Figure 1). Figure 2 shows a schematic diagram of the distance calculations. The distance of tagged PBF from the coast is a good indicator of whether juvenile PBF prefer the inshore coastal habitat or the oceanic region offshore of the Kuroshio. For example, if the distribution of tagged PBF is further offshore than the Kuroshio axis, then the distance between the tagged PBF and the coast is greater than the distance between the axis and the coast (Figure 2). We plotted the daily latitudinal distance of all tagged PBF along the south coast of Japan (n = 2,051) and the Kuroshio axis from the coast to assess temporal differences in the habitat coverage of PBF in the region.

Finally, to explore the thermal preferences of the PBF, we estimated the monthly median and the range of the 50–90th percentile values obtained for ambient water temperatures recorded by all individuals throughout the age-0 period.

3 | RESULTS

3.1 | Habitat usage

Kernel density analysis of all tagged PBF revealed their habitat use and its seasonal variability along the southern coast of Japan from July to the following May (Figure 3). During the summer and autumn (n = 590 and 1,110 days, respectively), the areas of highest density were found in the coastal waters off Kochi near the tagging area, and the eastern boundary of the habitat was mostly restricted by Cape Shionomisaki (Figure 3a,b). In winter (n = 503 days), the area with the highest occurrence of PBF shifted to the east of the Kii Channel and extended across Cape Shionomisaki and the eastern edge of the south coast of Japan (Figure 3c). Additionally, the offshore range east of Cape Shionomisaki expanded more broadly

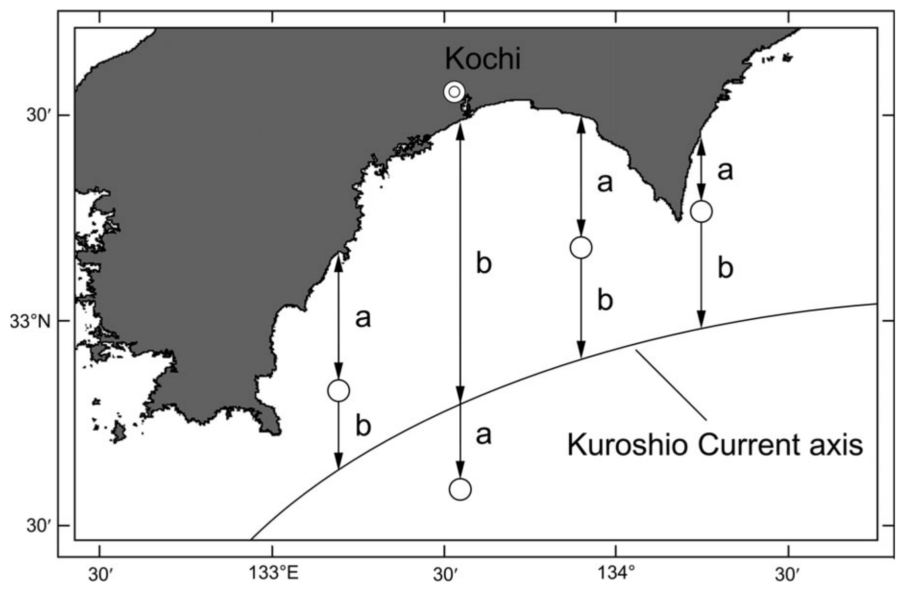


FIGURE 2 An example of the method used to calculate the latitudinal distances of tagged Pacific bluefin tuna (a) and the Kuroshio axis (b) from the coast. White circles indicate the estimated positions of bluefin tuna

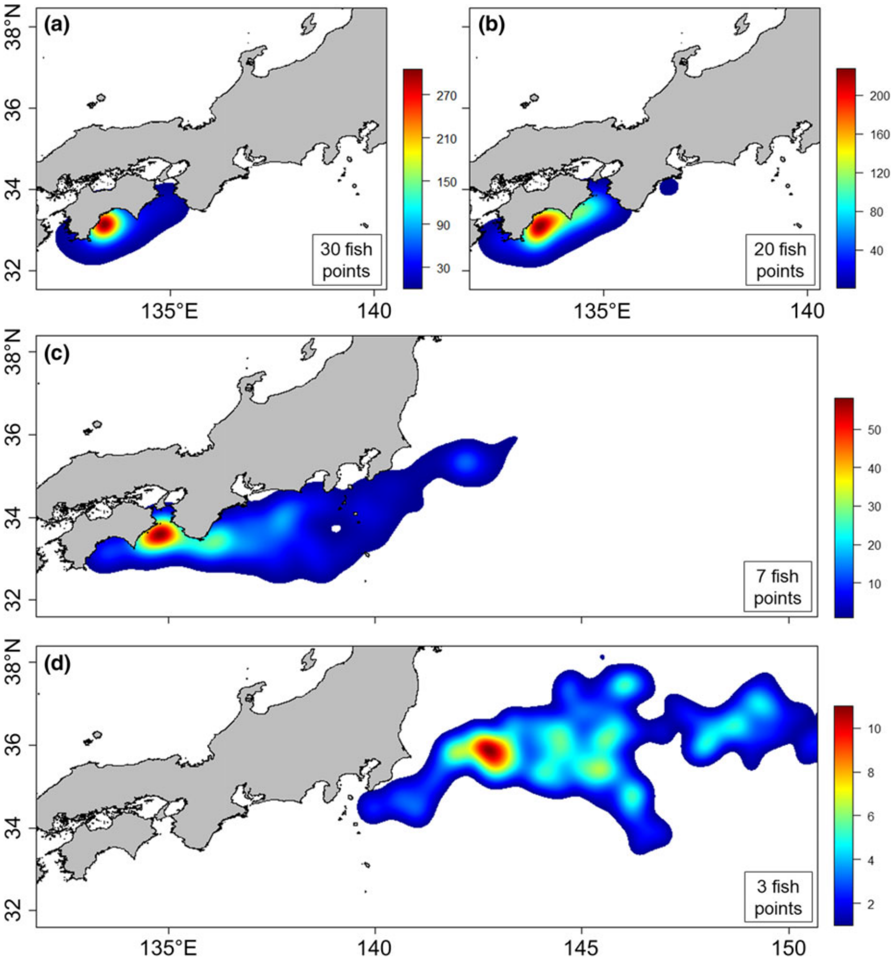


FIGURE 3 Kernel density plots of tagged Pacific bluefin tuna by season: summer (a), autumn (b), winter (c), and spring (d) with the data combined for the 3 years (2012/2013, 2013/2014, 2014/2015). Warmer colors indicate higher densities. The number of points representing fish indicates the number of tags remaining in each season

offshore to a lower-latitude area. In the spring (n = 258 days), the highest density of tagged PBF occurred further offshore, east of the Kuroshio-Oyashio transition region, and other PBF were dispersed near 145°E (Figure 3d). These results indicated that tagged PBF frequently occupied coastal waters until the autumn and that the habitat use by PBF expanded eastward from Kochi along the southern coast of Japan in the winter.

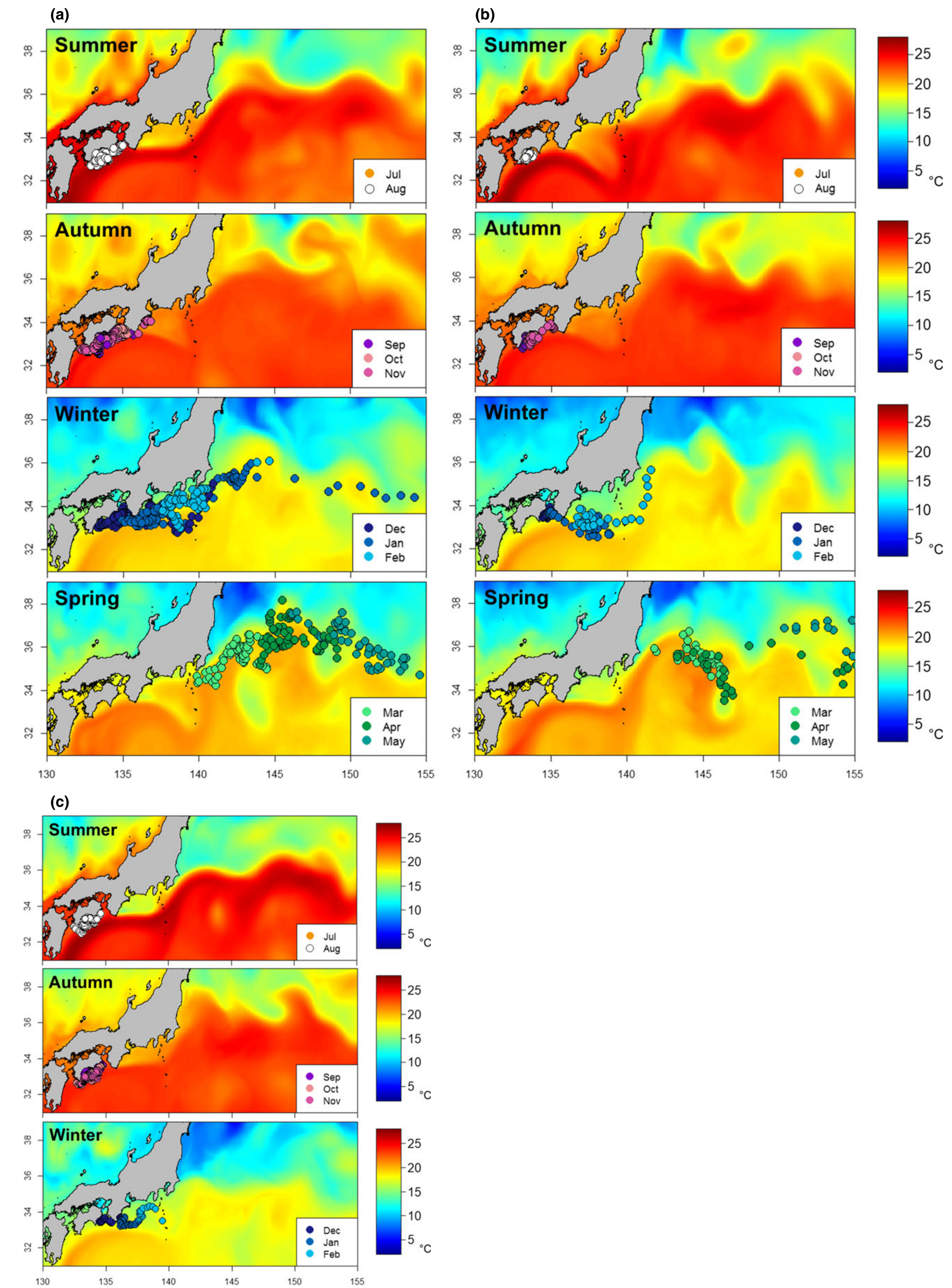
3.2 | Movement patterns of tagged fish

The daily locations of all tagged individuals, estimated using the geolocation model described above, are shown in Figure 4. These results demonstrate that all PBF tagged throughout the 3 year study period remained near the release location between Kochi and the Kii Channel from summer–autumn (Figure 4).

Seasonal differences in the daily distance travelled by tagged PBF are shown in Figure 5. The travel distance across the three summer periods was 8.8 km/day (n = 188) in 2012, 5.6/km day (n = 69) in 2013, and 5.1 km/day (n = 303) in 2014. In the autumn, the distances travelled were 6.7 (n = 519), 6.1 (n = 91) and 3.3 (n = 500) km/day, respectively. No significant difference in the distance travelled was observed between the summer and autumn periods within each tagging year (Steel-Dwass test, $p < .05$).

The tagged PBF moved eastward across Cape Shionomisaki at the same time each year beginning in the winter in all 3 years (Figure 4). The distribution of tagged PBF expanded widely to the offshore Kuroshio-Oyashio transition region in the spring of two tagging years (2012/2013, 2013/2014), and the daily distance travelled by tagged PBF increased markedly after they shifted to the eastern area off Cape Shionomisaki during the winters of 2012 and 2013. The daily distance travelled in the winter was 19.6 km/day (n = 330) in 2012/2013, 18.0 km/day (n = 90) in 2013/2014, and 9.7 km/day (n = 83) in 2014/2015 (Figure 5). Tagged PBF were distributed farther to the west during the winter of 2014/2015 than in the other 2 years, although this is likely because tagged PBF were

FIGURE 4 Estimated daily distributions of tagged Pacific bluefin tuna plotted over subsurface (50 m) temperature images for each season (from the top, summer, autumn, winter and spring) throughout the three study years (a) 2012, (b) 2013, and (c) 2014. Data were not available for the spring of 2014 due to the early recapture of tagged fish in that year. The high resolution monthly SST images (0.1° × 0.1°) were obtained from the ocean general circulation model (FRA-ROMS, Fisheries Research Agency of Japan)


(a)
Summer
Jul
Aug
Autumn
Sep
Oct
Nov
Winter
Dec
Jan
Feb
Spring
Mar
Apr
May
(b)
Summer
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Aug
Autumn
Sep
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130
135
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145
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155
32
34
36
38

recaptured early in the winter of this year before they could move farther offshore (Table 1).

In the spring, the daily distance travelled increased to 32.4 (n = 184) km/day in 2012/2013 and 48.9 (n = 74) km/day in 2013/2014. The Steel-Dwass test revealed statistically significant differences in movement patterns between winter and spring, but no significant differences were observed after the winter of 2014/2015. Additionally, no westward movements were made from the release location off Kochi into the East China Sea throughout the survey period.

3.3 | Habitat preference of tagged fish in relation to the Kuroshio

The Kuroshio axis flowed within 32.0–46.1 km of the coast during July–November, as determined from the satellite-derived SST composites analyzed over the 3 year period (Figure 6). During the summer and autumn, the path of the current was generally closer to the coastal area with little offshore meandering. In contrast, during the winter, the axis of the current ranged between 29.9 and 54.5 km from the coast and tended to meander widely. We found that the Kuroshio flowed close to the shore with less meandering during summer–autumn, subsequently shifting offshore and exhibiting greater spatial variability in the winter.

To determine the latitudinal distance between the daily distributions of tagged PBF and the axis of the Kuroshio along the southern coast of Japan, we calculated 2,051 geolocation estimates for the region between Kochi and the Boso Peninsula. Nearly all these location estimates were distributed inshore of the Kuroshio during the summer and winter in each of the three tagging years (99.9%; Figure 7). When the current was restricted to nearshore waters in the summer–autumn period, the PBF were highly resident in this coastal region, but in the winter, they began to move along the inshore side of the current and/or along the current front. Thus, the

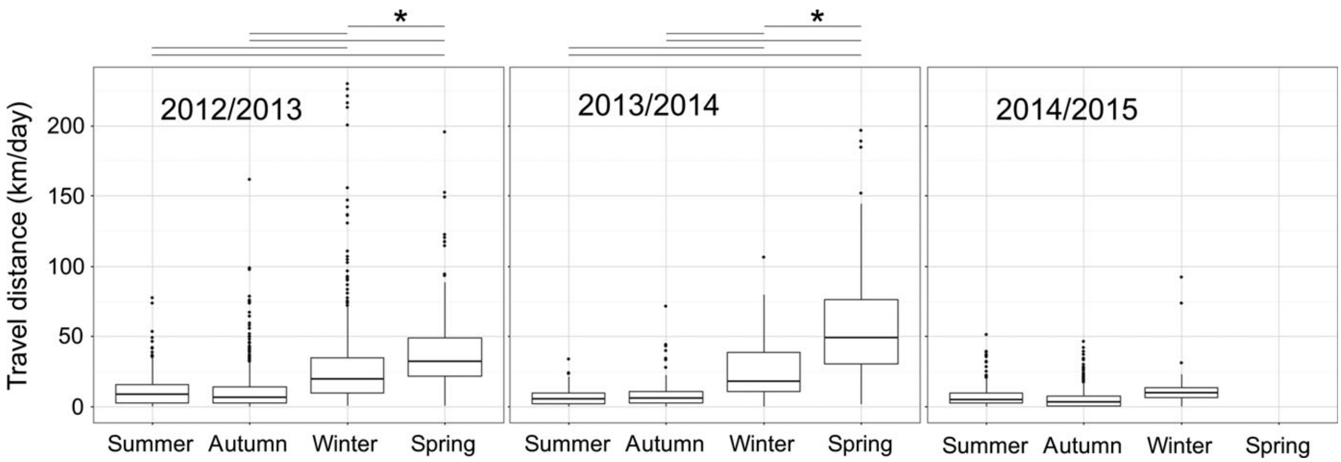

FIGURE 5 Seasonal differences in the daily travel distance of tagged Pacific bluefin tuna throughout the 3-year study period calculated from the daily locations of each individual. Different superscript lines on the box plots denote statistically significant differences (*p < .05, Steel-Dwass test for multiple comparisons)

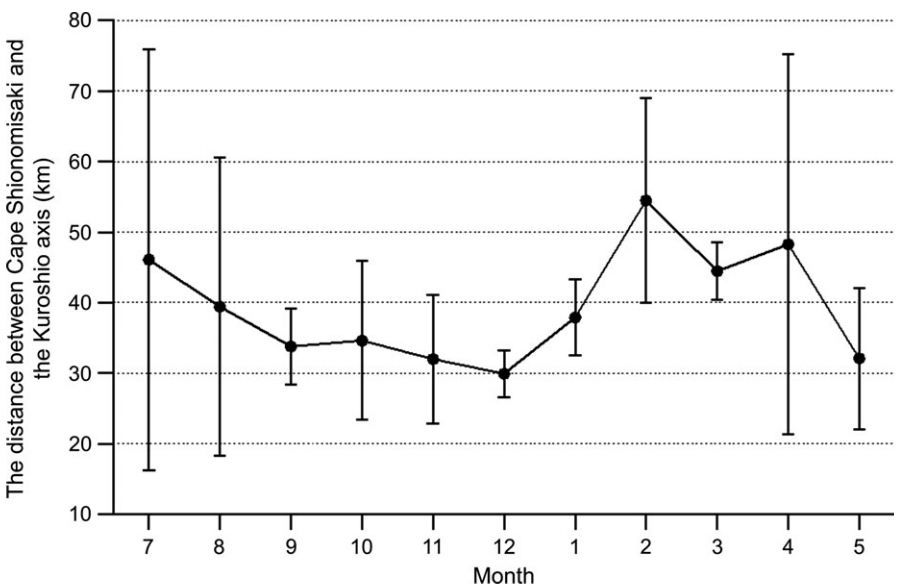

FIGURE 6 Monthly changes in the distance between Cape Shionomisaki and the Kuroshio axis (2012–2015). Each datapoint represents the monthly average distance as calculated from 7 day periods throughout the 3 years study. Black circles and bars represent averages and standard deviations, respectively

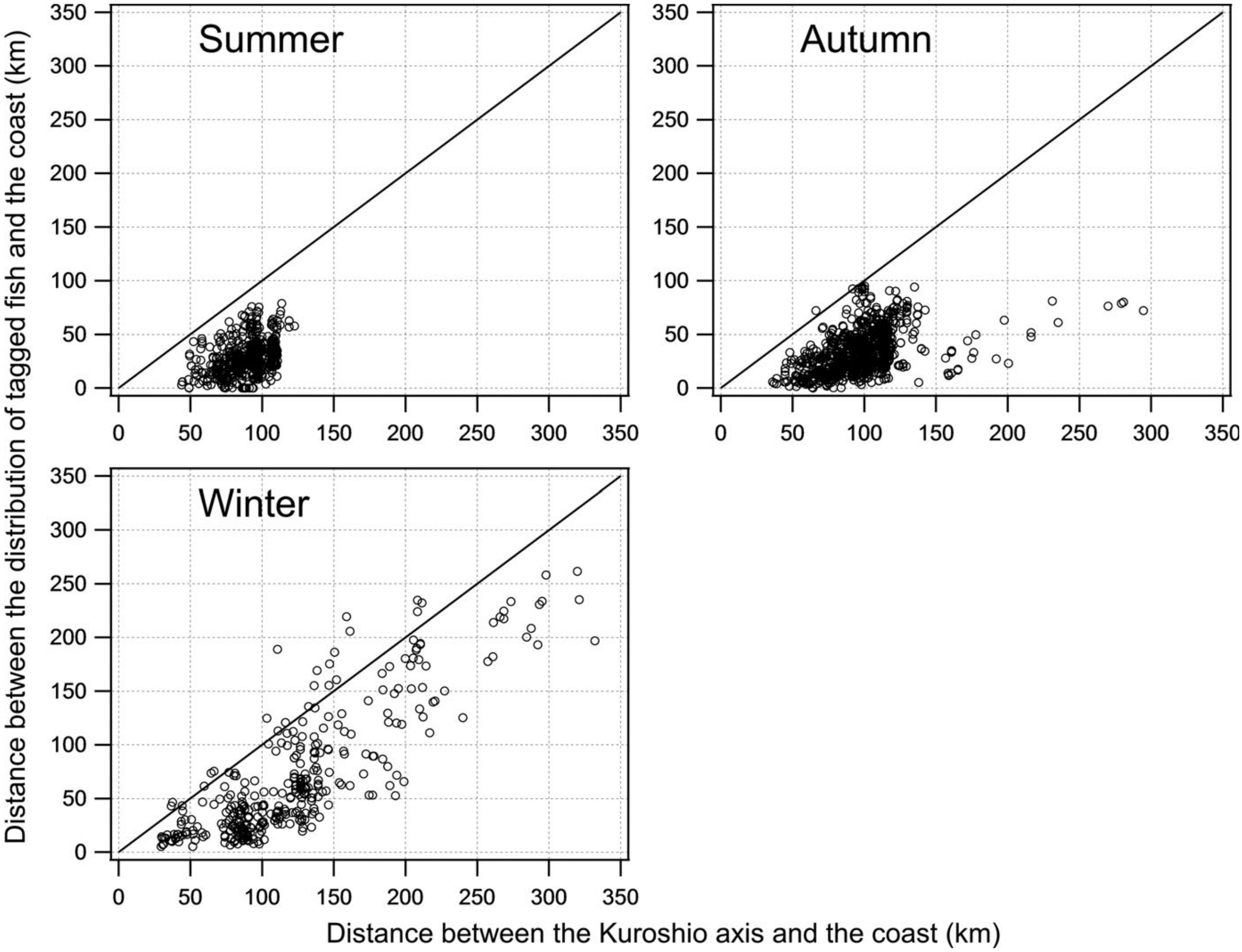

FIGURE 7 Relationship between the daily distribution of tagged Pacific bluefin tuna and the latitudinal distance of the axis of the Kuroshio along the southern coast of Japan. Diagonal lines indicate cases where the latitudinal distance of the Kuroshio axis equals the latitudinal distance of tagged fish from the coast

spatial range of PBF movement varied significantly depending on the path of the Kuroshio, with a clear pattern of habitat expansion as the current shifted offshore.

The monthly median and the 50th–90th percentile contours of ambient water temperature from July to the following May for all the tagged PBF are shown in Figure 8. Monthly median temperature in all 3 years gradually decreased from the summer to the winter with values from 27.6 to 17.0°C from July to May, respectively. In August, the tagged PBF experienced high ambient water temperatures with a maximum median value and upper 90th percentiles of 27.6 and 28.8°C, respectively. The relatively high temperatures measured from the Kuroshio were observed in offshore waters outside the coastal habitat of tagged PBF (Figure 4). During the summer-autumn period, when the Kuroshio flowed through inshore waters, the tagged PBF were narrowly distributed in relatively cool waters near the coast (Figures 4, 6 and 7). In contrast, when the current followed a more gradual offshore path during the winter, the tagged PBF were widely distributed in cool waters between the coast and the Kuroshio axis and along the front of the current.

The swimming depths of tagged PBF at different times are shown in Table 1. The mean swimming depth of all individuals throughout the survey period ranged from 10.7 to 59.7 m in the daytime and from 4.7 to 31.9 m during the night. The difference between the daytime and nighttime depths was significant (Mann-Whitney *U* test, $p < .01$), with shallower swimming depths observed during the day.

4 | DISCUSSION

Our tagging data indicated that the southern coast of Japan represents an important habitat for age-0 PBF throughout the summer and into the winter (Figure 3), and this result is supported by historical catch data from the coastal troll fishery operating in this region (Bayliff et al., 1991; Bayliff, 1994; Fukuda & Oshima, 2012; Ichinokawa et al., 2014; Kitagawa et al., 2010). Therefore, the habitat patterns exhibited by these tagged PBF are likely to be descriptive of the movements of most surviving PBF recruits to the southern

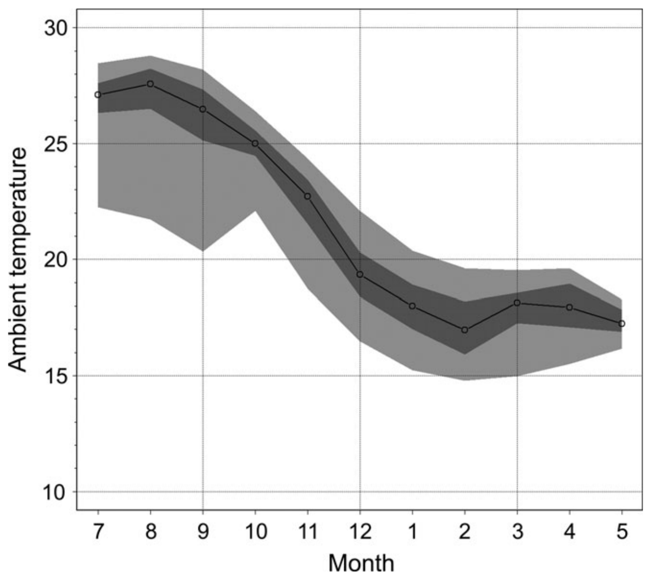

FIGURE 8 Monthly changes in ambient water temperature experienced by tagged Pacific bluefin tuna (n = 30). Dark grey and light grey symbols indicate the medians and the ranges of the 50% and 90% contours, respectively, of the ambient water temperature

coast of Japan from the main spawning region in the Ryukyu Archipelago (Kitagawa et al., 2010; Tanaka et al., 2006).

Kitagawa, Sartimbul, et al. (2006) described the overwintering habitats of young PBF in the East China Sea. However, in the present study, juvenile PBF that were released off Kochi did not undertake westward movements into the East China Sea. This difference may be explained by the seasonal shifts in water temperature in both nursery regions. Young PBF in the Sea of Japan, where SSTs range from 12 to 28°C (Ichinokawa et al., 2014), migrate to overwinter in the warm East China Sea (Ichinokawa et al., 2014; Itoh et al., 2003; Kitagawa et al., 2004; Kitagawa, Sartimbul, et al. 2006). In contrast, the warm Kuroshio flows near the southern coast of Japan throughout the year (SSTs ranging from 17 to 28°C; Figure 4; Ichinokawa et al., 2014), enabling juvenile PBF to remain in a stable 18°C environment through the winter (Figure 8).

The southern coast of Japan and the East China Sea (both of which are between 32°N and 35°N) are both important winter habitats for juvenile PBF, but the level of recruitment to each nursey likely varies interannually depending on the path and behavior of the Kuroshio during the larval transport phase of the PBF lifecycle (Fujioka, Masujima, Boustany, & Kitagawa, 2015; Kitagawa et al., 2010).

The summer–autumn period in all three study years was characterized by the persistent distribution of all tagged PBF in the coastal waters between Kochi and the Kii Channel (Figure 4); at this time, the Kuroshio tends to flow close to Cape Shionomisaki (Figure 6). During the winter, the tagged PBF moved northeastward to the waters off the Boso Peninsula, and they remained in the Kuroshio-Oyashio transition region until the spring (Figure 4). The daily travel distances estimated for the tagged PBF increased during the winter-spring period relative to those recorded during summer–autumn (Figure 5). The distance of the Kuroshio axis from the coast was greater in the winter months than in the other seasons (Figure 6), which is consistent with the results of a previous study (Sakamoto, 1971). Accordingly, the area of PBF habitat use shifted eastward into the coastal area between Cape Shionomisaki and the Kuroshio (Figure 4). The limited coastal paths of PBF movements likely reflect the high velocity of the offshore Kuroshio. In the East China Sea, young PBF were found to prefer frontal regions of the Kuroshio, but never entered the fast-moving current (1.3–1.7 m/s), which moved faster than the swimming speed of the PBF (1.1–1.4 m/s^{ß}) (Kitagawa, Sartimbul, et al., 2006). Juvenile PBF have been found to swim slower (0.6–0.7 m/s) (Noda et al., 2016) than the current velocity along the southern coast of Japan (1.0–1.5 m/s) (Nitani, 1975). Tagged PBF likely preferred the stable environment of the coastal waters over the offshore Kuroshio because of the reduced energetic costs of swimming in the former. The proximity of the Kuroshio to the coast likely restricts the movements of PBF beyond Cape Shionomisaki.

The path of the Kuroshio changes interannually (Kawai, 1998) as it meanders along the southern coast of Japan (Kasai, Kimura, & Sugimoto, 1993; Nitani, 1969). During the study period, the path changed from being straight (N-type) in the summer to being small and meandering (B- and C-type) in the winter and spring (FRA-ROMS website). However, the summer of 2013 was an exception, as the Kuroshio exhibited some offshore meandering, and this anomalous behavior may explain the relatively low recapture rate of tagged PBF in that year because the fishery catch per unit effort (CPUE) would have been reduced due to the offshore expansion of the area of PBF habitat. Furthermore, although large fluctuations in the path of the Kuroshio were not observed during this investigation period, the Kuroshio countercurrent runs near the coast, and its path and velocity are strongly influenced by the high degree of meandering by the Kuroshio (Kagimoto & Yamagata, 1997; Usui, Tsujino, Nakano, Fujii, & Kamachi, 2011). Further research based on a large number of individuals is needed to examine the effects of the Kuroshio countercurrent via the main current on habitat selection by juvenile PBF.

Ichinokawa et al. (2014) indicated that seasonal variation in the fisheries catch pattern of juvenile PBF in the Kuroshio region was not associated with changes in sea surface temperature. This finding is likely attributable to the low temperature gradient within the coastal fishing grounds off the south coast of Japan, which are all located at similar latitudes. Our results suggest that tagged PBF continuously select coastal waters with low temperature gradients and avoid the offshore Kuroshio area (Figures 4 and 7). The Kuroshio is likely to significantly influence habitat utilization in the inshore-offshore direction (Figure 7).

An important factor for understanding the habitat usage of juvenile PBF is likely the availability of appropriate food resources during this high-growth life stage. During the juvenile stage, the consumption of prey items of high mass and caloric content is essential to the development of PBF swimming ability and endothermy (Kitagawa & Fujioka, 2017; Kubo, Sakamoto, Murata, & Kumai, 2008; Shimose et al., 2013; Tamura & Takagi, 2009). Shimose et al. (2013)

reported that the diets of juvenile PBF ranging from 20 to 60 cm FL predominantly consisted of small zooplankton and epipelagic fishes, such as anchovy, *Engraulis japonicas*, sardine, *Sardinops melanostictus*, and round herring, *Etrumeus teres*, during August–December in the study region. The primary productivity is significantly higher in the coastal waters than offshore of the Kuroshio (Nakata et al., 1995; Okazaki, Nakata, Kimura, & Kasai, 2003), and adult anchovies are likely an important prey item for juvenile PBF during the spring–autumn (Yasue, 2010).

Furthermore, stocks of anchovy and sardine exhibit large fluctuations in the Pacific (Takasuka & Aoki, 2006; Yatsu, Watanabe, Ishida, Sugisaki, & Jacobson, 2005), the East China Sea, and the Sea of Japan (Ohshimo, Tanaka, & Hiyama, 2009). Anchovy and sardine stocks off the Pacific coast of Japan were high and low in the 2000s, respectively, but sardine stocks have drastically increased in this area since the late 2000s (Yasuda, Kurota, Hayashi, Yoda, & Takahashi, 2017; Yukami et al., 2017). The habitat selection patterns of juvenile PBF are likely affected by shifts in the abundance of these important prey species. In fact, decadal changes in prey abundance are probably related to the movement patterns of juvenile PBF (Polovina, 1996).

The tagged PBF proceeded offshore to the Kuroshio-Oyashio frontal region in the spring at the end of the age-0 period (Figure 4), presenting a similar distribution to that observed in a previous study (Kitagawa et al., 2004). Kitagawa et al. (2004) found that young PBF in the Kuroshio-Oyashio transition region were primarily distributed along the Kuroshio front during the spring, where they were likely foraging. During this period, juvenile PBF are dispersed widely in the frontal region (Figure 3) where they move quickly in and out of local foraging habitats. During the winter, the prey environment along the southern coast of Japan is poor (Nakata, Kimura, & Okazaki, 2000; Yasue, 2010), whereas high primary production and abundant anchovy are typical in the spring in the Kuroshio-Oyashio transition region (Shiozaki et al., 2014; Takahashi & Watanabe, 2004; Tameishi, Shinomiya, Aoki, & Sugimoto, 1996). Thus, the main driver of juvenile PBF movement to the highly productive waters of the Kuroshio-Oyashio transition region may be the increased food availability in the spring months.

Bayliff (1994) examined catch data from the summer troll fishery off Kochi and reported that juvenile PBF prefer temperatures between 24 and 29°C. Our observations showed median temperatures of 27.1–27.6°C (ranging from 21.7 to 28.8°C) during July–August (Figure 8). The swimming depth of the tagged PBF was shallower than 60 m throughout the age-0 period (Table 1). These results indicate that the fish were restricted to the surface layer, and the observed higher temperatures in this layer are within the preferred range for juvenile PBF. Notably, the difference between the peritoneal cavity temperature and ambient temperature of tagged PBF gradually increased from <1 to 3°C (Furukawa et al., 2017) as ambient water temperatures decreased from 27.6 to 19.3°C during August–December (Figure 8). PBF may have a limited physiological tolerance for ambient temperatures above 30°C (Kitagawa, Kimura, Nakata, & Yamada, 2006; Neill, Chang, & Dizon, 1976). Consequently, juvenile PBF are constrained between the upward extent of their thermal range and the metabolic benefits (higher energy absorption and faster digestion) of higher ambient water temperatures that facilitate faster growth rates at both the larval and juvenile life stages (Tanaka, Kaji, Nakamura, & Takahashi, 1996).

An important, yet poorly understood, factor in defining the habitat of juvenile PBF is the dynamic interaction of PBF with their prey resources. Surgically implanted archival tags enable us to isolate feeding events through sensitive measurements of changes in body temperature associated with digestion (Carey, Kanwisher, & Stevens, 1984; Kitagawa et al., 2004). Furthermore, it is also possible to estimate the energy content of a meal based on the heat increment produced during the digestive process (Aoki, Kitagawa, Kiyofuji, Okamoto, & Kawamura, 2017; Whitlock et al., 2013). Previous studies have constructed heat budget models for young PBF (>56 cm FL) that suggest that body insulation increases and internal heat production decreases with increasing body size (Kitagawa, Nakata, Kimura, & Tsuji, 2001; Kitagawa, Kimura, et al., 2006). As discussed above, juvenile PBF are unable to maintain high body temperatures as the countercurrent heat exchange system, or rete mirabilia, appears to develop later in life (Kubo et al., 2008). Therefore, the peritoneal cavity temperature of juvenile PBF is primarily influenced by ambient water temperature during this early life stage. If they become cold while foraging at depth, PBF can quickly recover their internal body temperature in warm surface waters, and they may have a limited ability to warm their core through the digestion process. Further research is needed to understand how the feeding ecology of age-0 PBF is related to the complex physiological developments during this life stage.

In conclusion, the habitat use of juvenile PBF was restricted to the coastal waters inshore of the Kuroshio along the southern coast of Japan and related to oceanographic conditions influenced by the path of the current. When the current shifted offshore, the habitat coverage of juvenile PBF changed accordingly (Figure 7). The path of the Kuroshio varies seasonally (Sakamoto, 1971) and interannually (Kawai, 1998), and consequently causes fluctuations in the primary and secondary production of coastal waters, influencing the distributions of the prey of juvenile PBF (Kasai, Kimura, Nakata, & Okazaki, 2002; Kimura et al., 1997; Nakata et al., 1995, 2000). The movements of age-0 PBF observed in this study appear to be driven by thermal, energetic (swimming speed), and foraging responses to a dynamic frontal system. A parallel example may be found in southern bluefin tuna (*Thunnus maccoyii*) which utilize coastal waters in their early life stage and later shift their distribution in relation to the Leeuwin Current as they grow (Fujioka et al., 2010, 2012). We suggest that future monitoring of the behavior of the Kuroshio might provide useful predictors of the habitat coverage and departure time of juvenile PBF from their coastal habitat. Such predictors could contribute to the analysis of seasonal catch availability and the selectivity of juvenile PBF to improve estimates of recruitment abundance and assist in the management of this important stock.

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