Progress in Oceanography 162 (2018) 52–65

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Spatial and temporal variability in the trans-Pacific migration of Pacific bluefin tuna (*Thunnus orientalis*) revealed by archival tags

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A R T I C L E I N F O

Keywords:
Habitat use
Highly migratory species
Horizontal movement
Kuroshio-Oyashio transition region
Pacific bluefin tuna
Subarctic frontal zone
Trans-Pacific migration

A B S T R A C T

Archival electronic tags were internally implanted in 713 age-0 Pacific bluefin tuna (PBF) caught in their nursery waters off the southern coast of Japan and in the East China Sea over an extended study period (1995–2015) to clarify the spatial and temporal variability of their trans-Pacific migration. Two hundred twenty-five of these tagged tuna were recaptured by fisheries (31.6%), and we successfully retrieved tag data from 14 of 21 individuals recovered in the Eastern pacific. Furthermore, one archival tag recovered in the Western Pacific revealed that the individual had performed a trans-Pacific migration, so in total 21 tagged PBF were shown to have migrated to the Eastern Pacific (2.9% of the total tags released). We successfully downloaded data from 15 of these 21 archival tags, which revealed that some age-1 PBF migrate rapidly (123.9 ± 82.8 km day^{-1}) and directly from waters offshore of Japan to the eastern Pacific (160.0°E to 130.0°W), a journey that takes an average of 2.5 months (ranging from 1.2 to 5.5 months) through relatively cool waters (14.7 ± 2.0 °C). All juvenile PBF began their trans-Pacific migration shortly after exposure to cooler water temperatures (< 14 °C), suggesting that sustained residence in lower water temperatures presents a physiological challenge for this age class. Three patterns were identified in the timing of the departure of juvenile PBF from the western Pacific: departing 12–14 months post-hatch ($N = 7$) in early summer (May-July), departing 17–19 months post-hatch ($N = 7$) in late autumn (October-December), and departing 21 months post-hatch ($N = 1$) in late winter (February). The PBF tagged along the southern coast of Japan (SCJ) arrived in the eastern Pacific earlier than those tagged in the East China Sea (ECS), most likely due to the shorter travel distance. Additionally, the PBF that began their trans-Pacific migration in the earlier period remained in an offshore foraging zone (the Kuroshio-Oyashio transition region) for shorter periods (2.8 months on average) and at lower latitudes (35.0°N) during the spring, while the PBF that delayed their migration spent more time (6.7 months on average) in the productive waters between 35.0 and 45.0°N during the spring-autumn months. The variability in the departure timing of the trans-Pacific migration of age-1 PBF may be related to geographic differences between nursery areas in addition to oceanographic conditions and foraging opportunities encountered by the tuna in the offshore waters of Japan during their first year.

1. Introduction

Pacific bluefin tuna (PBF; *Thunnus orientalis*) are highly migratory and travel long distances between tropical and subarctic waters throughout their life histories (Bayliff, 1994; Fujioka et al., 2015), and archival tag technologies that estimate the location of an animal and record behavioral and oceanographic data are helping to reveal their population dynamics (Block et al., 2005; Fujioka et al., 2015; Teo and Boustany 2015; Hobday et al., 2015). PBF are widespread throughout the northern and southern Pacific Ocean during their various life stages

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https://doi.org/10.1016/j.pocean.2018.02.010
Received 14 March 2017; Received in revised form 2 February 2018; Accepted 13 February 2018
Available online 14 February 2018
0079-6611/

(Bayliff, 1994; Smith et al., 2001; Fujioka et al., 2015). A major feature of the PBF life history is the migration across the northern Pacific (over 8000 km) conducted by juvenile PBF, which was initially revealed through extensive conventional mark-recapture tagging studies (Orange and Fink, 1963; Clemens and Flittner, 1969; Bayliff et al., 1991; Bayliff, 1994) and through fisheries catch analysis (Polovina, 1996). It is generally accepted that this migration from the western Pacific Ocean (WPO) to the eastern Pacific Ocean (EPO) occurs during the first or second year of life. However, research in the past two decades has employed miniaturized electronic archival tags that are implanted internally in the body cavities of juvenile PBF to examine their migration patterns (Inagake et al., 2001; Itoh et al., 2003; Kitagawa et al., 2009, 2013). These studies have described the movements of PBF tagged and released in their nursery area in the East China Sea (ECS), but the spatial and temporal patterns of the beginning of the trans-Pacific migration have not been closely examined.

Adult PBF are known to spawn in the waters between the Philippines and the Ryukyu Islands in the northwestern Pacific Ocean from April to June and in the Sea of Japan from July to August (Yabe et al., 1966; Okiyama, 1974; Ashida et al., 2015; Okochi et al., 2016; Ohshimo et al., 2017). Field surveys and numerical particle tracking experiments have shown that PBF larvae are transported northward by the Kuroshio Current to nursery waters off the coast of Japan after hatching in the spawning grounds (Bayliff, 1994; Tanaka et al., 2006; Kitagawa et al., 2010; Masujima et al., 2014; Ohshimo et al., 2017). The waters off Nagasaki Prefecture in the ECS and off Kochi Prefecture along the southern coast of Japan (SCJ) are well-known summer habitats (July-August) for age-0 PBF (2–3 months old, 15–32 cm fork length [FL]) (Bayliff, 1994; Tanaka et al., 2006; Fujioka et al., 2015). Tracking data indicate that juvenile PBF remain in nursery waters until winter (Itoh et al., 2003; Kitagawa et al., 2004, 2006; Fujioka et al., 2015, 2018), but although these two winter habitats are at similar latitudes, they are separated by more than 1000 km of Japanese coastline (Kitagawa et al., 2006; Fujioka et al., 2018) (Fig. 1).

A fraction of the late age-0 PBF that overwinter in the ECS are known to move south around the Japanese coast and up to the SCJ in the early spring (March). They proceed northeastward along the coast through the spring, heading to offshore waters east of Japan in May (Inagake et al., 2001; Itoh et al., 2003; Kitagawa et al., 2004). Other juvenile PBF from the ECS nursery area move north through the Sea of Japan, exiting through the Tsugaru Strait towards offshore waters east of Japan in November, though some exit through the Soya Strait (north of Hokkaido) and the Okhotsk Sea in August (Inagake et al., 2001; Kitagawa et al., 2004). Alternatively, the juvenile PBF from the SCJ nursery grounds begin moving northeastward along the SCJ during the winter, arriving in offshore waters during the spring (March) at late age-0 (Bayliff et al., 1991; Bayliff, 1994; Fujioka et al., 2018). No tagging study to date has provided evidence of juvenile PBF migration from the SCJ to the ECS nursery area (Bayliff et al., 1991; Bayliff, 1994; Fujioka et al., 2018). A previous large-scale conventional tagging study found that many PBF that are originally tagged in the ECS are recaptured at age-2 in the EPO, whereas PBF tagged along the SCJ are typically recaptured in the EPO during their first year of life (Bayliff et al., 1991). Our hypothesis is that this shift in age-at-capture observed by Bayliff et al. (1991) is a result of the geographic distance between the ECS and SCJ nursery regions, and we have sought to test this hypothesis by closely examining the departure timing of juvenile PBF as they embark on their trans-Pacific migration to the EPO.

In this study, archival tags were utilized to investigate the spatial and temporal variability in the departure times for the trans-Pacific migration of PBF from the WPO to the EPO (160.0°E–130.0°W). Information on the trans-Pacific migration of PBF (N = 15) is derived from horizontal movement data obtained from tags deployed between 1995 and 2015. Our main objective was to reveal the differences in the migration timing of PBF between different release locations in the ECS and along the SCJ to describe their general migratory route across the Pacific and to examine behavioral variability in young PBF in relation to oceanographic conditions.

2. Materials and methods

2.1. Fish tagging and definition of fish age

Several models of archival tags were implanted into age-0 PBF, including the NMT tag (16.0 mm in diameter, 100 mm long, 52.0 g in air; Northwest Marine Technology, Inc., USA), the LAT 2310 tag (16.0 mm in diameter, 76 mm long, 45.0 g in air; Lotek Wireless Inc., Canada), and the LAT 2910 tag (7.8 mm in diameter, 26 mm long, 2.3 g in air; Lotek Wireless Inc., Canada). Light level, external (ambient) temperature, internal (peritoneal cavity) temperature, and pressure data were archived in the tag memory every 30–128 s, and the predicted tag lifetime was 1–3 years (depending on the model).

The PBF in this study were caught in five regions off the coast of Japan (Fig. 1) by trolling with small, barbless hooks. Tags were implanted using a sterile scalpel to make a small (1.0–2.0 cm long) incision through the ventral wall, through which tags were inserted into the peritoneal cavity. The incisions were closed with one suture or no suture, depending on the size of the incision and the calmness of the fish. A conventional tag (Hallprint, Australia) was inserted in the dorsal musculature at the base of the second dorsal fin, crossing the pterygiophores to ensure retention. The entire implantation procedure generally took from 30 to 120 s. During the tagging period of 1995–2007, the fish were released immediately after surgery. However, smaller PBF (18.0–33.0 cm FL) tagged during 2012–2015 were placed in holding tanks with circulating seawater aboard the tagging vessel before the archival tags were implanted (Fujioka et al., 2018). After the implantation, these individuals were placed in near-shore floating net pens for observation during a recovery period lasting up to four days. Daily underwater observations were made to confirm that the tagged fish were swimming normally.

A total of 713 age-0 PBF were outfitted with archival and conventional tags between 1995 and 2015, and 225 were recovered during the survey period (31.5% recapture rate). Of these recovered fish, 46% were recaptured within one month, and 70% were recaptured within 6 months. We successfully obtained tag data from 208 of these recaptured fish as 17 internal tags suffered mechanical failures or fell out of the bodies of the fish (only the external conventional tags were recovered). A total of 21 tagged PBF were recovered after migrating to the EPO, and 15 of these tags were successfully downloaded to reveal complete records of the trans-Pacific migration (the other 6 tags only recorded partial records or could not be downloaded). All other recaptured tags showed movements throughout Japanese waters (Inagake et al., 2001; Kitagawa et al., 2000, 2001, 2004, 2006, 2009, 2013; Itoh et al., 2003; Fujioka et al., 2015, 2018; Furukawa et al., 2017). As the goal of this study was to examine patterns in the trans-Pacific migration of juvenile PBF, we focused our analysis on these 15 tag records. The release and recapture details of all PBF tagged throughout the survey period are shown in Table 1. The straight fork length (FL: straight line distance from the tip of the rostrum to the fork of the caudal fin) of the ECS PBF tagged and released off the Nagasaki (33.59–34.49°N, 129.01–129.13°E) and Kagoshima prefectures (31.62°N, 129.44°E) in November-January ranged from 52.0 to 55.0 cm (mean ± SD: 50.1 ± 3.8 cm). The SCJ PBF tagged and released off the Kochi (33.28–33.30°N, 133.25–134.22°E), Kanagawa (34.58–35.14°N, 139.30–139.35°E), and Ibaraki prefectures (36.06°N,

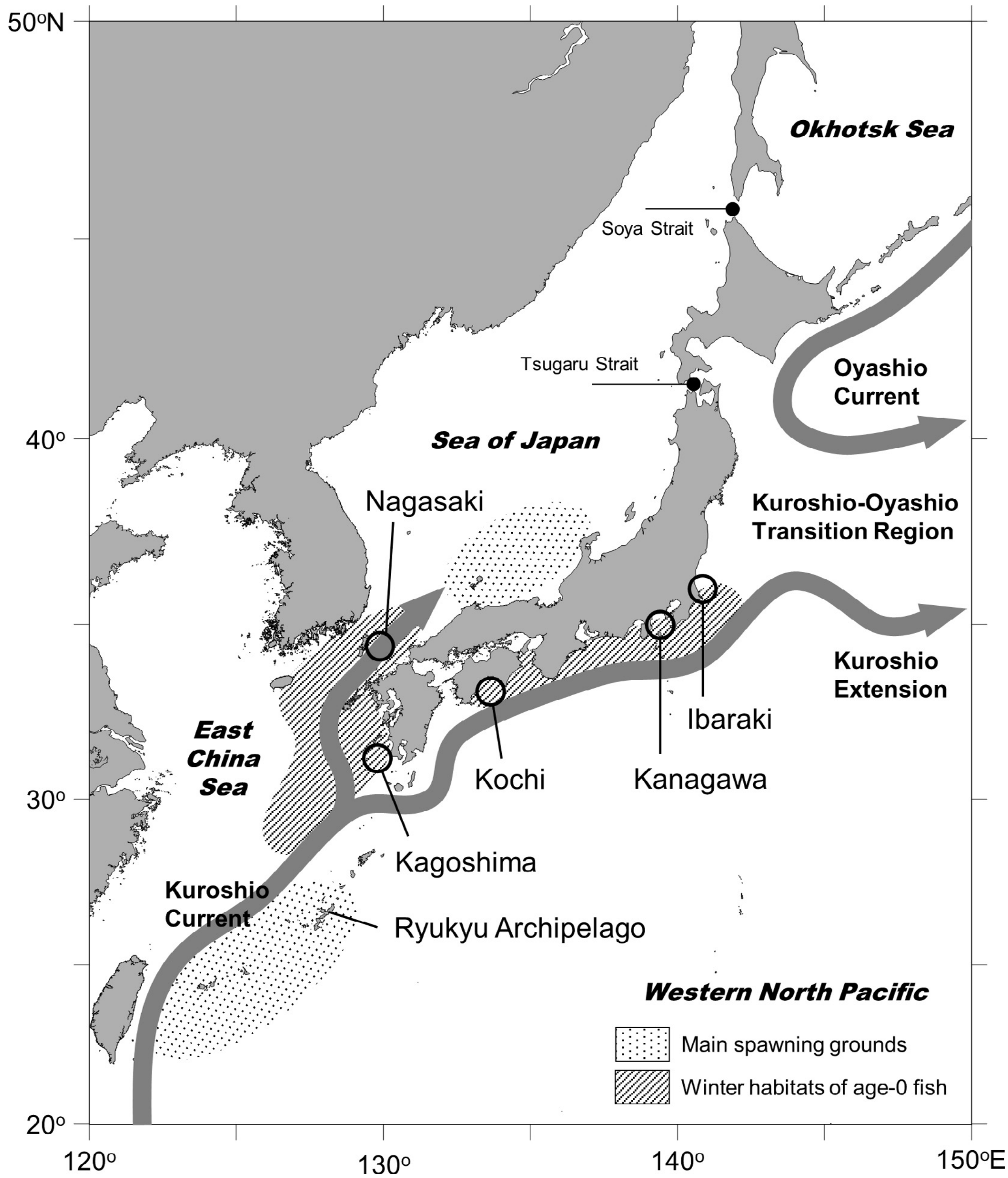

Fig. 1. Map of the western North Pacific Ocean showing tagging locations of juvenile Pacific bluefin tuna (PBF) (white circles). Schematic illustration of the near-surface currents around Japan: Kuroshio Current, Kuroshio Extension, and Oyashio Current (gray arrow). Dotted areas represent the known spawning grounds of PBF, and slashed areas represent the known nursery habitats of juveniles (age-0) in the East China Sea (ECS) and along the southern coast of Japan (SCJ) (Kitagawa et al., 2006; Fujioka et al., 2018).

140.48°E) in August–December ranged from 22.5 to 52.0 cm (mean ± SD: 35.5 ± 12.1 cm). Details of the tag record duration, tag date and location, and FL at release and FL and/or body weight (kg) at recapture are presented in Table 2. Additionally, we reanalyzed tag records from two PBF released in the ECS (ID227 and ID241) that were examined in previous studies (Inagake et al., 2001; Itoh et al., 2003; Kitagawa et al., 2009, 2013).

The methods described by Tanaka et al. (2006) were used to calculate the ages of the tagged PBF and their FL at the time of tagging. The peak in the spawning period for mature PBF in the waters around the Ryukyu Archipelago is May (ranging from April to June) (Yabe et al., 1966; Ueyanagi, 1969; Okiyama, 1974; Tanaka et al., 2006; Ashida et al., 2015). Consequently, the PBF tagged along the SCJ during August-December were defined as 3–7 months old. However, the PBF tagged in the ECS may represent a mixture of individuals hatched from the spawning grounds in both the Ryukyu Archipelago and the Sea of Japan. A previous study revealed that PBF catches in the ECS during the winter months exhibited a bi-modal pattern in the length frequency distribution (Itoh, 2009), likely due to the different hatching dates for the different spawning grounds (i.e., April–June in the waters around the Ryukyu Archipelago and July–August in the Sea of Japan) (Yabe et al., 1966; Ueyanagi, 1969; Okiyama, 1974; Ashida et al., 2015; Okochi et al., 2016). It is presumed that small PBF (35–45 cm FL) captured in the ECS winter fishery likely hatched in the Sea of Japan, whereas larger individuals (45–55 cm FL) likely hatched in the waters around the Ryukyu Archipelago. Therefore, PBF of 52.0–55.0 cm FL tagged

Table 1
Details of Pacific bluefin tuna (PBF) from 1995 through 2015. The tagging year, prefecture, the number of tagged fish, fork lengths (FL, cm), the number of recaptures (with the percentage), and the recapture area (ECS: East China Sea, SOJ: Sea of Japan, SCJ: southern coast of Japan: ECJ: east coast of Japan, EPO: eastern Pacific Ocean) are given for each tagged fish.

Year	Release			Recapture						
	Area	*N*	FL cm	*N*	*Rate (%)*	Area				
						ECS	*SOJ*	*SCJ*	*ECJ*	*EPO*
1995	Nagasaki	58	45–71	13	22.4	6	1	2	4	0
1996	Nagasaki	47	47–78	12	25.5	7	4	0	0	1
1997	Nagasaki	61	43–68	14	23.0	10	4	0	0	0
1998	Nagasaki	63	48–59	15	23.8	11	2	0	1	1
2000	Kochi	10	47–50	6	60.0	0	0	5	1	0
	Kanagawa	13	42–53	6	46.2	0	0	2	2	2
	Ibaraki	8	41–44	1	12.5	0	0	0	0	1
2001	Kochi	21	44–48	15	71.4	0	0	15	0	0
	Kanagawa	7	45–49	4	57.1	0	0	3	0	1
2002	Kochi	7	40–51	3	42.9	0	0	2	1	0
	Kanagawa	5	46–51	1	20.0	0	0	0	0	1
2003	Kochi	39	40–52	20	51.3	0	3	15	0	2
2004	Kanagawa	2	52–56	0	0.0	0	0	0	0	0
2005	Kanagawa	36	41–52	16	44.4	0	0	15	1	0
2006	Kagoshima	1	50	0	0.0	0	0	0	0	0
2007	Kagoshima	14	40–57	6	42.9	0	1	3	1	1
2012	Kochi	75	23–33	23	30.7	0	0	14	0	9
2013	Kochi	62	18–28	8	12.9	0	0	7	0	1
2014	Kochi	77	20–32	23	29.9	0	0	21	1	1
2015	Kochi	107	19–28	39	36.4	0	0	39	0	0
Total		713	18–78	225	31.5	34	15	143	12	21[a]

[a] Including fish whose tags were not successfully downloaded or recovered (only the conventional tags were recovered).

during November-January in the ECS were defined as 6–8 months old after hatching in the waters around the Ryukyu Archipelago. The estimated age (months) at release for each tagged PBF is shown in Table 2.

2.2. Estimation of fish geolocation

Daily estimates of the positions of archival-tagged PBF were derived using light-based geolocation techniques and further refined using the sea surface temperature (SST) measurements recorded by the tags, coupled with remote sensing data (e.g., Teo et al., 2004). An integrated state-space extended Kalman filter statistical model was used to estimate geolocation errors, movement parameters, and the most likely tracks (Lam et al., 2008; Galuardi et al., 2010). Based on data acquired from the NOAA National Center for Environmental Information website (https://www.ncdc.noaa.gov/oisst), we generated an 8-day composite of gridded (0.25°) optimum interpolated SSTs (OISSTs) constructed from various observation platforms (satellites, ships, and buoys). Geolocation estimates were further improved through bathymetric corrections that compared the daily maximum swimming depth relative to the regional sea-floor depth (Teo et al., 2007; Galuardi et al., 2010). Track estimations were constructed using the UKFSST package (Nielsen et al., 2012) in the R statistical environment (The R Project for Statistical

Table 2
Release and recapture information for 15 PBF tagged from 1995 through 2015.

Fish	Duration of the analyzed data (days)	Release					Recapture				
ID		Area	Latitude	Longitude	FL cm	Age (month)	Date	Latitude	Longitude	FL cm	BW (kg)
227	10 December 1995 to 31 May 2000 (1635)[a]	ECS	33.59	129.01	52.0	7	31 May 2000	33.00	141.51		76
241	29 November 1996 to 1 August 1998 (611)	ECS	34.25	129.08	55.0	6	1 August 1998	31.48	−117.18	88	
668	26 November 1998 to 24 September 2000 (669)	ECS	34.49	129.13	53.5	6	24 September 2000	35.26	−121.32	93	17
1920	16 January 2007 to 6 July 2008 (538)	ECS	31.62	129.44	54.0	8	6 July 2008	30.40	−116.35	90	15
1503	20 November 2000 to 27 August 2002 (646)	SCJ	34.58	139.35	50.0	6	27 August 2002	33.17	−117.53	84	14
1585	20 November 2000 to 19 July 2002 (607)	SCJ	34.58	139.35	52.0	6	19 July 2002	28.18	−115.28		15
1643	30 November 2000 to 20 July 2002 (598)	SCJ	36.06	140.48	43.0	6	20 July 2002	28.30	−116.30		15
1562	17 November 2001 to 15 August 2003 (637)	SCJ	35.14	139.30	46.0	6	15 August 2003	30.42	−117.20	91	18
2251	19 November 2002 to 3 August 2004 (624)	SCJ	35.09	139.35	51.0	6	3 August 2004	31.44	−117.17		20
1722	11 December 2003 to 26 Jun 2005 (564)	SCJ	33.29	134.19	49.0	7	26 Jun 2005	26.30	−114.51	90	
2104	11 December 2003 to 28 April 2006 (870)	SCJ	33.30	134.22	46.0	7	28 April 2006	26.50	−114.31		
1100	9 August 2012 to 10 August 2013 (367)	SCJ	33.28	133.25	22.5	3	16 Jun 2015	32.35	−117.50	140[b]	25[b]
1116	12 August 2012 to 9 August 2013 (363)	SCJ	33.28	133.25	29.5	3	9 Jun 2015	32.33	−117.80	160[b]	50[b]
1127	23 August 2012 to 28 July 2013 (340)	SCJ	33.28	133.25	26.5	3	28 July 2013	31.51	−117.14		
1128	23 August 2012 to 3 September 2013 (377)	SCJ	33.28	133.25	27.0	3	3 August 2014	32.16	−119.09		14

[a] Inaccurate recording of ambient water temperature 991 days after release (26 August 1998).
[b] Fork length measured after rearing in an aquaculture pen for an unspecified period.

Computing, http://www.r-project.org). Additionally, KFTRACK (Sibert et al., 2003) was used to refine the estimated track of one tagged PBF (ID227; see Table 2) as that tag did not record ambient water temperature. This package was obtained from the Pelagic Fisheries Research Program website (https://github.com/positioning/kalmanfilter/wiki).

The model parameters quantifying the northward and eastward movement components ranged from 3 to 7 nautical miles per day, in accordance with previous observations of daily travel rates by tagged juvenile PBF (Fujioka et al., 2018). The random error in the estimation of longitude and latitude was set at 0.5–1.0° and 1-5°, respectively, based on a similar study of yellowfin tuna (Schaefer et al., 2011). We chose to define the smoothing radius of the SST data as a range between 30 and 90 nautical miles, in accordance with the recommendations in the published literature (Nielsen et al., 2006). These selected values were input into a comprehensive 128-scenario model to account for any variability in the selected parameters. We chose the lowest negative log likelihood scenario from the convergent models to represent the best-fit track for each tag record. This analysis followed the techniques utilized in Fujioka et al. (2018).

2.3. Analysis

We utilized a Mann-Whitney *U* test to compare the daily distance traveled (km day^{-1}) and the SSTs experienced when tagged PBF were in Japanese waters (< 160.0°E), crossing the Pacific (160.0°E–130.0°W), and in the EPO (< 130.0°W). We also performed a *V*-test (Zar, 2009) to examine patterns in the migration direction during the trans-Pacific migration period (Kitagawa et al., 2009, 2013).

To clarify patterns in the timing of the trans-Pacific migration of juvenile PBF for different tagging locations in the ECS and along the SCJ, we calculated the average monthly longitude for each individual tag record. The month of departure from the WPO was defined as when a tagged PBF moved east of 160.0°E longitude, and the month of arrival in the EPO was defined as when a tagged PBF reached 130.0°W longitude. Migratory patterns were categorized based on the month of departure eastward from the 160.0°E longitude mark, not the month of arrival in the EPO. Finally, we examined the residence duration of juvenile PBF in the WPO in addition to the seasonal (summer, June–August; autumn, September–November; winter, December–February; spring, March–May) and latitudinal variations in the ambient water temperatures experienced by the juvenile PBF in the Kuroshio-Oyashio transition region prior to their trans-Pacific migration.

The spatial and temporal distributions of two tagged PBF (ID1503 and ID1585) released along the SCJ on the same date were uniquely different in the Kuroshio-Oyashio transition region (see Section 3). We compared their tracks using composite SST images (OISSTs) to explore the variability of movement patterns in the region and to elucidate departure behaviors and the environmental preferences of PBF as they cross the Pacific. To identify the factors that trigger the trans-Pacific migration, we calculated 8-day averages of the daily horizontal distance traveled by the juvenile PBF (Kitagawa et al., 2009, 2013). Finally, given that PBF exhibit regional endothermy, we thought it was prudent to compare peritoneal body temperatures to ambient water temperatures in order to fully explore the role of thermal triggers on the onset of the eastward migration.

3. Results

3.1. Trans-Pacific migration

Tag data was successfully downloaded from 14 tagged PBF caught by purse-seine and sport fisheries in the EPO, and one PBF was caught in the WPO after returning from the EPO. A total of 15 PBF with tag record durations ranging from 340 to 1635 days were used in the present study (Table 2). The travel distance per day and the SSTs recorded by the archival tags during the trans-Pacific migration phase are shown in Table 3. The travel distances were longer (123.9 ± 82.8 km day^{-1}) during the migratory phase (160.0°E–130.0°W) than during other periods before and after crossing the Pacific (< 160.0°E and < 130.0°W) (60.8 ± 70.1 km day^{-1}) for all individuals (*U* test, $p < 0.01$). On average, it took the PBF 2.5 months to cross the Pacific, with transit times ranging from 1.2 to 5.5 months. A *V*-test for uniformity revealed that all the tagged fish were highly consistent in their migration direction during this crossing (*V*-test, $p < 0.01$), and the travel direction ranged from 65.9° northeast to 104.8° southeast (due north is 0°) (Table 3).

3.2. Migration timing and path

Fig. 2 shows the longitudinal distribution of the tagged PBF after release on different dates in the ECS and along the SCJ. The tagged PBF migrated rapidly across the Pacific Ocean to the EPO during their age-1 period after spending time around Japan (Fig. 2a). The trans-Pacific migrations of the tagged PBF were characterized by three patterns in the onset of migration (early, middle, and late), defined as the date on which an individual swam east of 160.0°E. The PBF migrations began either 12–14 months post-hatch ($N = 7$) in early summer (May–July), 17–19 months post-hatch ($N = 7$) in late autumn (October–December), or 21 months post-hatch ($N = 1$) in late winter (February). Individual classifications of departure timing are given in Table 3, and we observed temporal differences in departure behavior between the different release locations along the SCJ and in the ECS. The PBF tagged in the SCJ nursery area began their trans-Pacific migration primarily in the early ($N = 7$) and middle ($N = 4$) periods, however, fish tagged in the ECS left in the middle ($N = 3$) or late periods ($N = 1$). Arrival times at the 130.0°W longitude mark in the EPO followed similar temporal patterns. The PBF arrived in the EPO in the summer (July–August) at 14–15 months post-hatch, in the winter (December–February) at 19–21 months post-hatch, and in the spring (May) at 2 years old. Two individuals (ID1643 and ID2104) took longer to cross the basin (5.2–5.5 months), deviating from their migration paths between 150.0 and 170.0°W. They started their migrations in the early and middle periods but arrived in the middle and the late period, respectively.

One individual PBF tag record (ID227) illustrated a return transit to the WPO (Fig. 2b). This tagged PBF spent over two years (812 days) in the EPO after arriving in January (20 months post-hatch). The fish left the EPO in April at the end of age-3 and remained for nearly a year (358 days) in the waters between 160.0°E and 180.0°, an area characterized by features such as the Shatsky Rise (30–40°N, 155–165°E) and the Emperor Seamounts (30–55°N, 165–175°E). The fish then migrated rapidly back to Japanese waters where it was recaptured by a purse-seiner off Hachijo-jima (33.0°N, 141.5°E) at age-5.

Fig. 3 illustrates the trans-Pacific pathway for each of the 3 migration periods (early, middle, and late) identified from the tag records. The PBF that began the migration early transited quickly (2.8 months on average; see Table 3) from Japanese waters to the Shatsky Rise along a relatively low latitude pathway (35.0°N) during the spring. In the summer, these fish moved northward (40.0°N) and eastward (170.0°W), eventually arriving at higher latitudes (44.4°N on average, ranging from 40.5 to 47.8°N) (Fig. 3A). In contrast, the PBF from the middle period tended to inhabit a wider range of latitudes (30.0–45.0°N) in the waters east of Japan for an average of 6.7 months (Table 3) during the spring and autumn (Fig. 3B). Like the early-period migrants, middle-period

Table 3
Travel duration of PBF crossing from coastal nursery habitats (ECS and SCJ) to waters east of Japan and the eastern Pacific. Daily travel distances and sea surface temperatures experienced during the trans-Pacific migration, the results of the *V*-test, the mean travel direction (due north is 0°), and the classification of the migration timing for all individuals are also shown.

Fish ID	Migration duration (months)		Daily travel distance	Sea surface temperature	*V*-test		Migration pattern
	140–160°E	160°E–130°W	(km/day) Mean ± SD	(°C) Mean ± SD	*p*-value	Mean direction	
227	2.5	2.8	171.9 ± 109.6	14.9 ± 1.9	< 0.01	87.9°	Middle
241	5.2	2.5	158.7 ± 91.6	15.0 ± 2.8	< 0.01	104.8°	Middle
668	2.0	3.2	174.6 ± 100.6	13.4 ± 1.3	< 0.01	95.4°	Late
1920	5.9	1.6	129.9 ± 89.3	14.0 ± 1.4	< 0.01	96.6°	Middle
1503	7.0	3.5	69.1 ± 38.5	14.3 ± 1.8	< 0.01	99.4°	Middle
1585	2.6	1.5	136.5 ± 53.5	15.5 ± 1.6	< 0.01	80.9°	Early
1643	11.4	5.5	78.2 ± 51.6	14.1 ± 1.7	< 0.01	90°	Middle
1562	5.9	1.4	162.5 ± 43.8	14.6 ± 0.9	< 0.01	90.6°	Middle
2251	9.2	2.2	127.1 ± 74.4	14.3 ± 1.4	< 0.01	100.7°	Middle
1722	2.1	2.2	163.5 ± 91.8	16.6 ± 2.2	< 0.01	65.9°	Early
2104	3.5	5.2	87.1 ± 51.3	15.2 ± 2.0	< 0.01	101.7°	Early
1100	2.3	1.4	155.9 ± 53.2	14.0 ± 1.2	< 0.01	85.4°	Early
1116	2.2	1.4	176.0 ± 77.8	14.9 ± 1.4	< 0.01	81.9°	Early
1127	3.0	2.0	134.7 ± 89.9	15.5 ± 2.2	< 0.01	85°	Early
1128	3.8	1.2	192.4 ± 59.0	14.1 ± 1.2	< 0.01	86.5°	Early

migrants left the waters of eastern Japan along the 40.0°N latitude until they reached 170.0°W. They traveled at gradually lower latitudes and arrived at an average of 38.7°N (ranging from 34.2 to 42.9°N) through the winter months. The single individual that began the trans-Pacific migration during the late period remained in the Sea of Japan for several months before crossing through the Tsugaru Strait in winter and passing quickly (2.0 months, Table 3) through the waters east of Japan along 40.0°N latitude (Fig. 3C), arriving in the EPO in the spring.

3.3. Habitat use and ambient water temperature east of Japan

The temporal variation in the onset of the trans-Pacific migration of juvenile PBF is likely due in part to differences in the thermal habitat of the waters east of Japan (140-160°E). Fig. 4 shows the relationship between the latitude of the PBF and the SST recorded by the tag for each of the three migration periods (early, middle, and late). The average SST recorded by all the tagged PBF between 140 and 160°E was 17.7 °C (ranging from 13.9 to 20.7 °C in 95th percentile values) (Fig. 4a). In the early migration period, the SST was 18.0 °C on average (ranging from 12.3 to 22.3 °C) for the PBF remaining at approximately 35.0°N latitude for a short period during the spring (Fig. 4b). The PBF in the middle migration period experienced 17.7 °C temperatures on average (ranging from 11.2 to 25.3 °C) and were distributed more widely between 30.0 and 45.0°N over a longer period during the spring and autumn (Fig. 4c). The single PBF in the late migration period experienced an average SST of 13.2 °C (ranging from 8.1 to 15.6 °C) in the region east of Japan (Fig. 4d). Regardless of the study year and season, the lowest water temperatures recorded by each tagged PBF (ranging from 8.1 to 13.9 °C) prior to the onset of the trans-Pacific migration were in the vicinity of 160.0°E (arrow 2 in Fig. 6).

The thermal data and migratory pathways of the two PBF (ID1503 and ID1585) released from the same location along the SCJ on the same day exhibited different spatial and temporal patterns (Fig. 5). Both fish migrated along the Kuroshio front to the waters east of Japan in April, but in May, ID1585 moved rapidly to the east along the Kuroshio Extension through 18.0 °C waters, while ID1503 remained in the warm (16.0–20.0 °C) frontal region at approximately 145.0°E. ID1585 shifted into a colder (16.0 °C) frontal region in June, occasionally crossing the frontal boundary into even colder temperatures (as low as 12.8 °C). After 2.6 months in the region east of Japan (140.0–160.0°E), this individual began its trans-Pacific migration in the early departure period (Table 3). In contrast, ID1503 remained through June in the warm frontal region (15.8 °C daily minimum value) between 145.0 and 150.0°E and later migrated to higher latitudes as the waters warmed throughout the summer. Eventually, ID1503 departed for the EPO in October (middle period) after ranging widely in the region east of Japan for 7.0 months (Table 3) and experiencing cold waters (11.0 °C) at approximately 160.0°E (Fig. 6).

Qualitatively, the peritoneal cavity temperatures of the juvenile PBF were consistently warmer than the ambient water temperatures across the trans-Pacific migration, and the peritoneal cavity temperatures decreased as the ambient water temperatures decreased. Unfortunately, complete time-series temperature records were not retrieved from 4 PBF due to problems with the memory of the tag. An in-depth examination of the endothermic capacity of juvenile PBF and its relevance to habit selection and migration timing will be the focus of a future study.

4. Discussion

Our efforts to implant archival tags in age-0 PBF (22.5–55.0 cm FL; estimated 3–8 months post-hatch) returned detailed records that reveal temporal patterns and migration pathways across the Pacific. The spatial and temporal variations in the trans-Pacific migration of age-1 PBF can be classified into three distinctive migration periods (early, middle, and late). The different migratory timings and pathways exhibited by the PBF are likely related to the release locations in the SCJ and ECS nursery areas. Previous archival tagging studies conducted on juvenile PBF in the ECS reported trans-Pacific migration departure dates consistent with the timing of the middle migratory group identified in the present study (Inagake et al., 2001; Itoh et al., 2003; Kitagawa et al., 2009, 2013). The PBF released along the SCJ departed for and arrived in the EPO earlier than PBF released from the ECS, although fish tagged in both locations were found to migrate during the middle period (Fig. 2a). Finally, only through continued tagging efforts will we be able to determine if the single late-migrating PBF represents an outlier in this data set or if it is indicative of another migratory pathway.

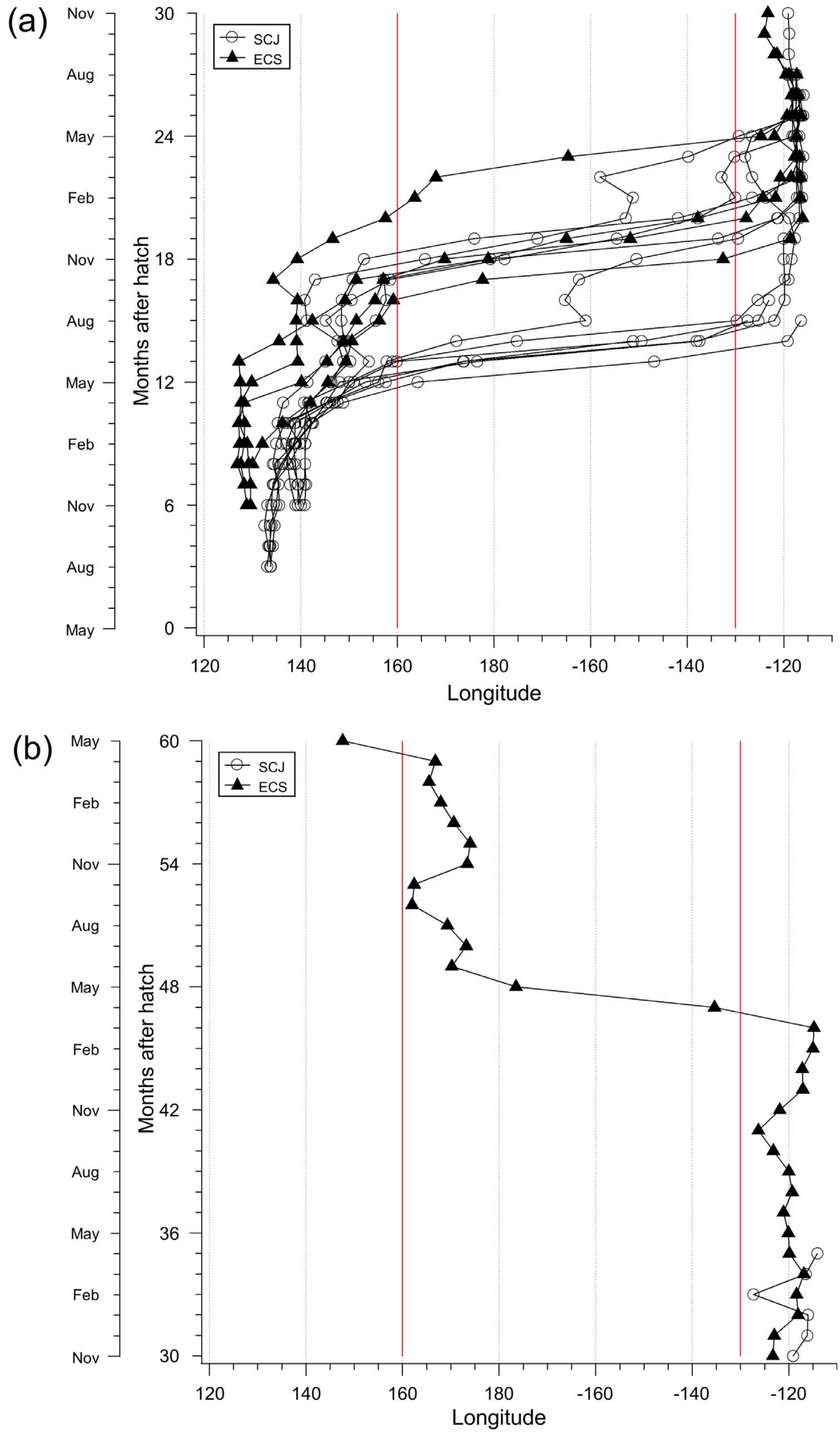

Fig. 2. Monthly average longitudinal locations of tagged PBF with estimated months post-hatch and absolute months showing the trans-Pacific migration from a) the western Pacific Ocean (WPO) to the eastern Pacific Ocean (EPO) and b) the return migration from the EPO to the WPO. The white circles and black triangles indicate the release locations along the southern coast of Japan (SCJ) and in the East China Sea (ECS), respectively. The vertical red lines delineate the WPO (< 160.0°E) and the EPO (< 130.0°W), as defined in the Methods section.

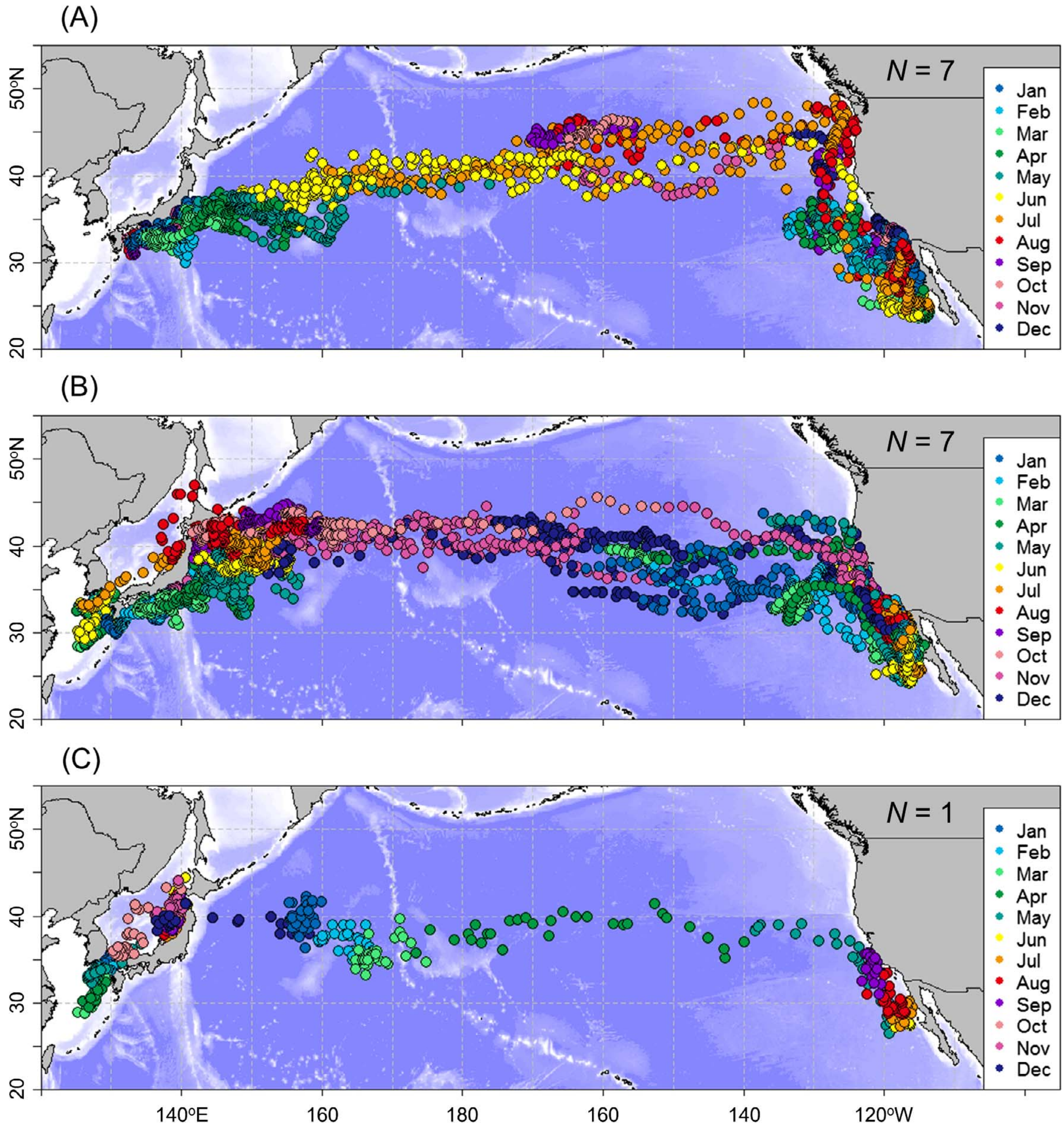

Fig. 3. Estimated daily distributions of tagged PBF with bathymetry for each migration timing (A: early, B: middle, C: late) of the trans-Pacific migration (see Section 3 for definitions).

The migratory patterns observed in this study are supported by the results of previous research using stable isotope analysis, which also revealed three waves of juvenile PBF migration to the EPO with corresponding differences in FL at arrival (Madigan et al., 2014). Bayliff (1993) also noted that PBF catch data from the EPO had a bi-modal distribution, with smaller (55–70 cm) and larger (70–90 cm) length modes. This pattern may be a result of the differences in migration timing from the various nursery areas in the WPO. The winter nursery habitats along the SCJ and in the ECS are approximately 1000 km apart along the coastline of southern Japan (Kitagawa et al., 2006; Fujioka et al., 2015, 2018), and this large distance may generate temporal offsets in the trans-Pacific migration of juvenile PBF. Despite the relationship between the nursery location and the arrival time in the EPO observed in this study, we identified examples of age-0 PBF that were tagged and released from the same location yet displayed divergent migratory patterns (Fig. 2a).

Oceanographic features and SSTs also influenced the distribution of juvenile PBF across the Pacific. Travel pathways varied among the three observed migratory patterns, and the tagged PBF usually arrived in the EPO at higher latitudes (44.4°N on average) in the summer and lower latitudes (38.7°N on average) in the winter (Fig. 3A, B). The differences in the migration pathways appear to be related to seasonal shifts in the latitude of the Subarctic Frontal Zone (Bograd et al., 2004; Kitagawa et al., 2009, 2013; Polovina et al., 2017). Additionally, the Kuroshio-Oyashio transition region (140.0–160.0°E) plays an important role as a nutrient-rich foraging habitat for species including anchovies and PBF (Sugimoto and Tameishi, 1992; Tameishi, 1996; Takahashi and Watanabe, 2005; Shiozaki et al., 2014). Juvenile PBF in the Kuroshio-Oyashio transition region experienced water temperatures ranging from 13.9 to 20.7 °C (Fig. 4a), and exposure to cold waters (< 14 °C) may trigger the onset of the trans-Pacific migration. Furthermore, the tagged PBF exhibited distinct latitudinal movements in relation to seasonal

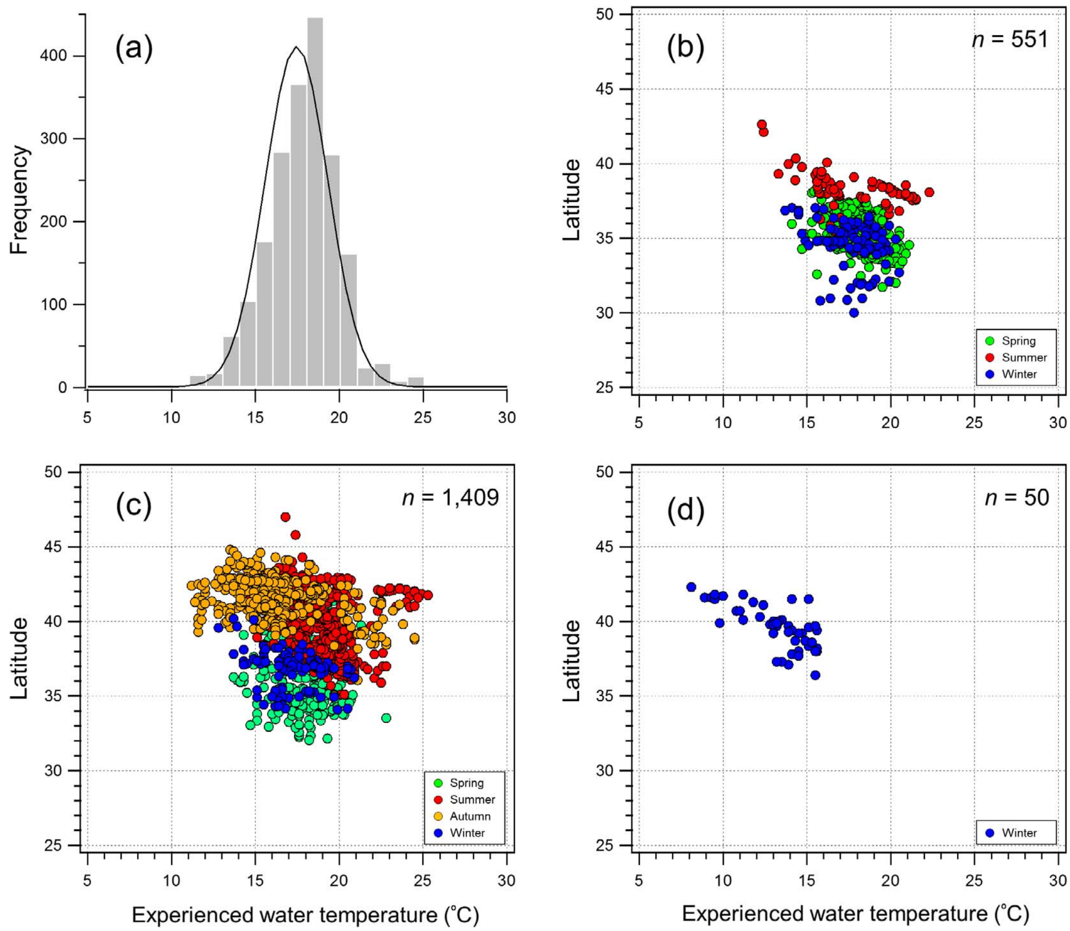

Fig. 4. (a) Frequency of the ambient surface water temperatures (SSTs) experienced by all tagged PBF in the Kuroshio-Oyashio transition region (140.0°–160.0°E) with a Gaussian distribution. Seasonal differences in the relationship between SSTs and the latitudinal distributions for each timing of the trans-Pacific migration (b: early, c: middle, d: late).

shifts in the cold Oyashio Current system, moving northward from 38.8°N in the spring to 41.2°N in the autumn (Yasuda, 2003). Inter-annual variability in the oceanographic conditions in the WPO, in addition to variation in the recruitment levels of PBF from the different spawning grounds, are likely key factors influencing the variability in the overall number, timing, and pathways of PBF migrants to the EPO each year. Combined research approaches, including tagging, stable isotope analysis, and oceanographic modeling, are needed to elucidate the inter-annual variability in the trans-Pacific migration of juvenile PBF.

A pair of tagged PBF (ID1503 and ID1585) released at the same location along the SCJ on the same date exhibited different movement patterns prior to making the trans-Pacific migration (Table 3, Fig. 5). Both fish arrived at the Kuroshio front by early May, but by June, the early-migrating individual (ID1585) had moved farther eastward (160.0°E) along the 18 °C isotherm, making occasional excursions to the colder side (< 14 °C) of the front before beginning its trans-Pacific migration. In contrast, ID1503 crossed the Pacific later in the middle period, having spent most of its time in a consistently warm region (18 °C) of the Kuroshio Extension that is known to produce warm-core eddy structures (Kawai, 1998; Yasuda, 2003). This individual proceeded to move northward during the warm summer-autumn season before eventually beginning its migration to the EPO in October. Thus, eddies and warm-core rings derived from the crest of the northern Kuroshio Extension may be important habitats for PBF that are delayed during their trans-Pacific migration (Sugimoto and Tameishi, 1992; Tameishi, 1996; Takahashi and Watanabe, 2005). PBF released along the SCJ that delay their migration and remain in the eddy structures therefore likely migrate to the EPO in the middle migratory period with PBF released from the ECS. When favorable foraging habitats within eddy structures occur in response to seasonal fluctuations in the region (Kawai, 1998; Yasuda, 2003), PBF could spend even longer (up to 7.0 months) in the waters to the east of Japan.

A previous study analyzing catch data found that juvenile PBF are typically captured in SSTs ranging from 14 to 19 °C (Uda, 1957), but more recently, archival tagging results suggest that they prefer a range from 16.3 to 21.5 °C (Kitagawa et al., 2000, 2001). However, Fujioka et al. (2018) found that juvenile PBF utilize a wider SST range from 14.8 to 28.8 °C (90th percentile values, across the water column). Temperatures lower than 14 °C have been found to adversely affect the metabolism (Blank et al., 2007) and cardiac output (Jayasundara et al., 2013) of juvenile PBF and have resulted in mortality in aquaculture (Tsuda et al., 2012). These previous studies indicate that sub-14 °C temperatures represent a physiological challenge for juvenile PBF, a finding that is supported by the tagging data presented here (Fig. 4a). Finally, an additional source of complexity in understanding the thermal tolerance of juvenile PBF as they migrate across the Pacific is that their endothermic capacity develops as they grow (Furukawa et al.,

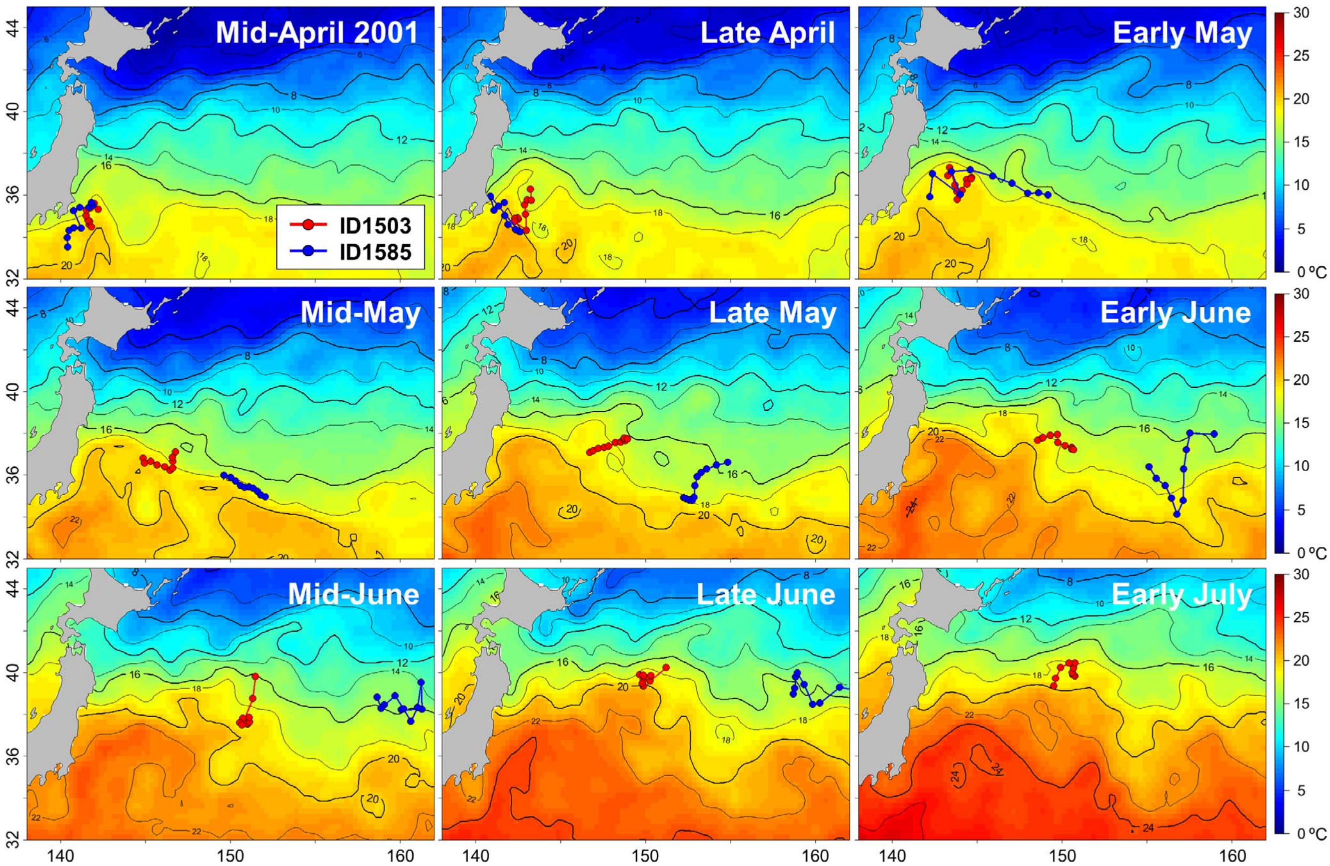

Fig. 5. Differences in the daily distribution of two tagged PBF (ID1503 and ID1585) released in the same area (SCJ) on the same date in the Kuroshio-Oyashio transition region (140.0°–160.0°E). Blue and red dotted lines indicate the distribution of the locations of PBF in the early migration group (ID1585) and the middle migration group (ID1503), respectively. The 10-day SST images (0.25° × 0.25°) were calculated by the daily optimum interpolated SST (OISST) product provided by the NOAA National Center for Environmental Information (https://www.ncdc.noaa.gov/oisst).

2017; Kitagawa and Fujioka, 2017). Indeed, the internal archival tags deployed in this study recorded significantly elevated peritoneal cavity temperatures relative to the ambient surface water temperatures. Future analysis of this tagging data will focus on the ecological role played by the ontogenetic development of endothermic capacity in PBF during this dynamic early life stage.

This study provides initial evidence that exposure to waters colder than 14 °C may trigger the onset of the trans-Pacific migration in PBF. For example, one PBF from the late migration period proceeded rapidly (within 2 months) from the Tsugaru Strait to the offshore waters east of Japan after experiencing temperatures below 14 °C in December (Figs. 3C and 4d). Such tag records tend to support the hypothesis that juvenile PBF undertake rapid, directed movements eastward when cold waters extend to lower latitudes during the winter and spring. In fact, all the PBF tagged in this study experienced < 14 °C temperatures in the waters east of Japan near the subarctic boundary (40.0°N, 160.0°E) (Yasuda, 2003) (Fig. 6). After experiencing this stimulus, juvenile PBF proceed through cold waters (14.7 ± 2.0 °C) from 160.0°E to 130.0°W along the Subarctic Front (Suga et al., 2003) (40.0°N) in transit to the warmer waters of the EPO (Figs. 3 and 6); indeed, PBF primarily occupy warmer waters before and after they cross the Pacific (See Supplemental Materials, Fig. S1). Finally, juvenile PBF that utilize the warm-core eddies of the Kuroshio Extension are less likely to experience cold conditions (< 14 °C), and they may delay their trans-Pacific migration in order to remain in these warmer waters. Due to the relatively small sample size of recovered tags, we cannot say with certainty that exposure to cold waters is a major trigger for PBF to begin their trans-Pacific migration, but future research will examine this new hypothesis in more detail.

In addition to recording several west-to-east migratory records, one archival-tagged PBF performed a return migration from the EPO. After spending two years in the EPO, this PBF remained in the vicinity of the Shatsky Rise and the Emperor Seamounts (160.0°E-180.0°) for approximately one year (age-4) before being recaptured off the SCJ at age-5 (Fig. 2b). Older, westward-migrating PBF may be more prone to exploit forage resources found around offshore topographical features (Block et al., 2003; Boustany et al., 2010) than the younger, eastward-migrating PBF that take a more direct route.

To date, we have recovered a relatively small yet precious amount of tag data covering the trans-Pacific migration phase of juvenile PBF, and in this study, we sought to describe some of the interesting patterns observed within this impressive phenomenon. With the limited amount of currently available data, we are unable to identify a clear ecological advantage of the migratory strategies exhibited by juvenile PBF, nor could we provide a robust examination of the actual behavioral modes, inter-annual variability, or response to environmental changes in PBF trans-Pacific migration. However, these data represent an important step in understanding the early life history of PBF, and it is increasingly clear that the selection of rich foraging habitats in thermally optimal waters is important for promoting increased growth rates during this early life stage. Therefore, thermal limitations and the availability of suitable prey may play important roles in influencing the population dynamics and migratory patterns of juvenile PBF (Polovina, 1996). Future analysis of the archival tag data presented here, along with the large-scale conventional tagging dataset that was collected simultaneously, will contribute to estimates of natural mortality, growth, and west-to-east migration rates to improve the stock assessments of this valuable fisheries resource. These findings rely on the direct monitoring

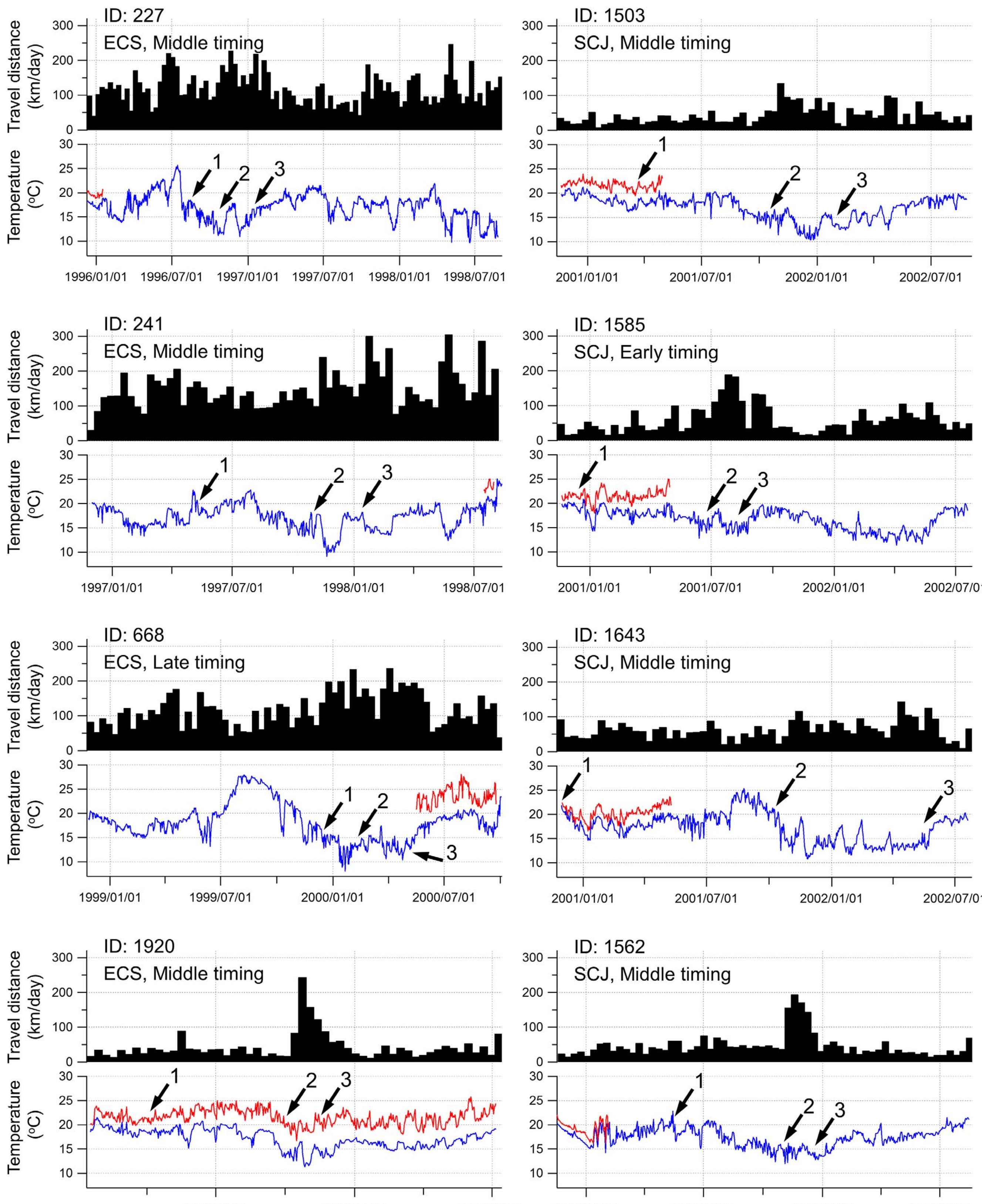

Fig. 6. Time-series data of horizontal travel distance per day (8-day average) with ambient SST and peritoneal cavity temperature measurements obtained from 15 tagged PBF. Arrows indicate the days when the bluefin moved east of 140°E (arrow 1), 160°E (arrow 2), and 130°W (arrow 3).

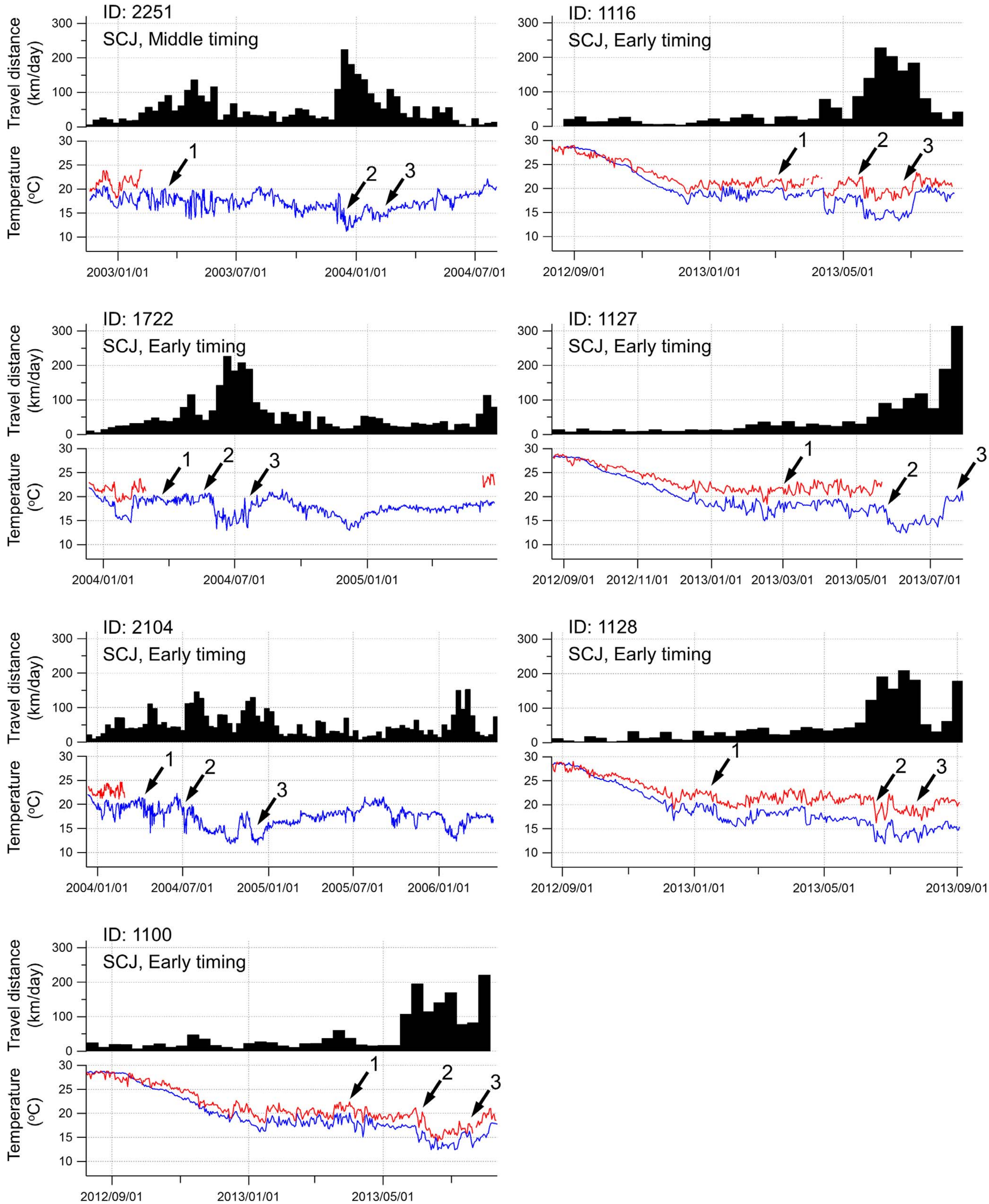

Fig. 6. (*continued*)

of individuals through archival tag technologies, but future experiments combined with isotopic analysis (Madigan et al., 2012, 2014; Tawa et al., 2017) and high-resolution oceanographic modeling will shed further light on PBF population dynamics. In this way, we will be able to improve our understanding of the foraging behaviors of PBF and more deeply explore the variability in and mechanisms underlying long-distance trans-Pacific migration.

Acknowledgements

We are grateful to Harumi Yamada, Tomoyuki Itoh, Denzo Inagake, Mio Takahashi, Yukio Takeuchi, Osamu Abe, Kohei Sasagawa, Junji Kinoshita, and Toshinori Takashi (National Research Institute of Far Seas Fisheries and the Seikai National Fisheries Research Institute of the Fisheries Research Agency of Japan) as well as Akira Nitta, Minoru Kato, Naohisa Kanda, and Tomoyuki Kuwahara (JANUS) for their assistance with the tagging study and their valuable advice. We also thank Steven L.H. Teo and Suzanne Kohin (NOAA) and Kurt Schaefer (IATTC) for their useful information on the recovery of tagged fish. The authors also extend their gratitude to three anonymous reviewers for their helpful comments. The research was funded by a grant from the Japan Fisheries Agency.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2018.02.010.

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