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Distinct natal origins based on vertebral ring analysis corroborate the migration pattern of Pacific bluefin tuna in the North Pacific Ocean

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ABSTRACT: Pacific bluefin tuna (PBF) *Thunnus orientalis* have 2 major spawning grounds and migrate widely in the North Pacific Ocean. To understand the population structure and migratory ecology, we analyzed vertebral samples collected from a wide range of ages and areas and then estimated their natal ground from the first annulus in the vertebra, which does not change significantly after formation. Both spawning groups of PBF, including fish that originated from the Sea of Japan (assigned as group SJ) and from the waters around the Ryukyu Archipelago and Taiwan (group RT), were observed in all sampling areas and age classes. In younger age classes, the percentages of group SJ were higher around Japan, whereas those of group RT were higher in the eastern Pacific Ocean (EPO). The percentage of group RT decreases around Japan as they migrate to the EPO and then increases when they return. These results suggest a tendency toward different migration patterns depending on the natal area. Interestingly, the results suggest that fish from the EPO rarely migrate to the Sea of Japan. The percentages of group RT for age 10+ were similar and higher in all sampling areas, and these are considered to be the final percentages of the relative contribution of the 2 natal grounds. This is a useful approach that enables us to easily examine the relative contribution of the 2 spawning grounds across time and space, providing insights into the dynamics of movement around the Pacific based on variations in the population composition.

KEY WORDS: Trans-Pacific migration · Spawning period · *Thunnus orientalis* · Age · Vertebrae

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1. INTRODUCTION

Migration patterns of fish vary among as well as within species (Chapman et al. 2012). Larvae that hatch in the ocean surface layer or in areas with strong currents passively move as they grow, typically into habitats with suitable temperatures and forage. As they become reproductively mature, they return to waters suitable for spawning during their spawning season. The migration route can vary depending on the marine environment, the hatching area, and the time of year. Accurate and quantitative determination of population level-migration data can contribute to understanding stock dynamics and

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devising fisheries management strategies (Fromentin & Powers 2005, Chapman et al. 2012). For example, spatially explicit population models require inputs associated with movements between regions. Additionally, understanding migration patterns is an important step toward examining patterns in growth and recruitment. Finally, determining connectivity between regions is necessary for characterizing overlap with fisheries.

Pacific bluefin tuna (PBF) *Thunnus orientalis* are widely distributed mainly in the North Pacific Ocean and are among the most important fishery resources for several countries managed by the Western and Central Pacific Fisheries Commission (WCPFC) and the Inter-American Tropical Tuna Commission (IATTC) based on stock assessments performed by the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (ISC). PBF stock started to decline in the mid-1990s, but in recent years, the spawning stock biomass has been recovering as a result of strict stock management (ISC 2022). Presently, the PBF assessment model uses biological factors such as growth in addition to catch information but is not spatially explicit due to 'the lack of direct information on movement rates' (ISC 2022, p. 29). Improving our understanding of migration rates and routes is expected to advance efforts aimed at realizing sustainable management.

Despite the extensive migrations of PBF in the North Pacific Ocean, their known spawning grounds are found in a limited area of the western North Pacific Ocean (WPO), specifically, 2 main areas west and south of Japan. Spawning periods differ in each area, occurring in May–June in waters around the Ryukyu Archipelago (hereafter termed 'the Ryukyu area') and off Taiwan, and in July–August in the Sea of Japan (Itoh 2009, Ashida et al. 2015, Okochi et al. 2016, Ohshimo et al. 2017, Shiao et al. 2017). Juveniles that hatch in the Ryukyu area are transported to waters off the southern coast of Japan or the East China Sea by the Kuroshio Current (Kitagawa et al. 2010). In contrast, most of the juveniles that hatch in the Sea of Japan remain there during their first year (Ichinokawa et al. 2014), and PBF that originate from the 2 spawning grounds become intermixed in the waters around Japan (Itoh 2009, Watai et al. 2018). In recent years, PBF larvae were collected off the Pacific coast of northeastern Japan (Tanaka et al. 2020), although there are no reports of age-0 fish collected after the juvenile stage in this area, and other information is presently unavailable.

Several studies in recent years have identified the natal origin of PBF in specific areas using various approaches. Otolith trace element analysis was used for age-1 fish caught in the eastern Pacific Ocean (EPO) (Wells et al. 2020), as well as for adult fish (227.9 ± 21.2 cm fork length [FL]) caught in waters around Taiwan (Rooker et al. 2021). Shiao et al. (2021) used stable isotope analysis for fish mostly larger than 200 cm FL caught in waters around Taiwan. Although these studies used chemical analysis of otoliths to estimate the natal origin of each individual, Itoh (2009) used the difference in length of age-0 fish resulting from the difference in hatching periods to calculate the ratio of the natal origin of age-0 fish in the waters around Japan. Uematsu et al. (2018) devised a similar method for estimating the natal area by simply estimating the body length in their first winter from the radius of the first ring of the vertebrae, applying it to fish caught in the Sea of Japan and the Ryukyu area. The distance from the focus to the first ring was larger for fish that hatched earlier in the Ryukyu area because of the longer time it took for the first ring to form.

PBF have a complex migratory history and change their habitat depending on their age (Bayliff 1994, Fujioka et al. 2015). Some proportion of the juveniles migrate to the EPO, returning to the WPO usually after age 3, where they mix with the fish that never left the WPO (Madigan et al. 2017, Tawa et al. 2017). The timing of PBF migrations to the EPO differs depending on the natal area; those that hatched in the Ryukyu area and the Sea of Japan migrate after age 1 and 2, respectively (Fujioka et al. 2018, Kawazu et al. 2020). Although the migration route is not clear around Japan, fish up to around age 6 are distributed mainly in the Sea of Japan, and most of these fish over age 3 are mature (Okochi et al. 2016), while most spawning adult PBF over age 10 are distributed mainly in the Ryukyu area and Taiwan (Ashida et al. 2015, Shiao et al. 2017, Ishihara et al. 2022). At present, neither the influence of natal origin on migrations and distribution nor the relative contribution of fish from the 2 natal grounds to different age classes and spawning stock biomass is well understood. Although previous studies on the above have documented fish from both spawning grounds, both the regions examined and the ages of fish sampled in these studies were limited relative to the distribution areas of PBF.

Utilizing vertebral analysis, which is inexpensive and does not take much time to perform, to estimate the natal origin of PBF enables the analysis of large sample numbers. In addition, although the vertebrae are resorbed and replaced as they grow (Sakashita et al. 2019), this process does not affect the position of the first ring formation (Uematsu et al. 2018), making this approach applicable across size classes. Accordingly, this method can be used to compare PBF populations from multiple areas and different ages, and to discuss the relationship between variation in the population composition and migration pattern.

Therefore, to understand the population structure of PBF in the North Pacific Ocean, the objective of this study was to examine the radius of the first annulus in the vertebrae as a proxy of the natal origin of PBF using a wide spatiotemporally sample collection of PBF vertebrae to enable assessment of the population structure and migratory ecology across size and age classes as well as regions.

2. MATERIALS AND METHODS

2.1. Sample collection

PBF specimens were caught between 1998 and 2020 by commercial fisheries around Japan and Taiwan as well as recreational fisheries off the coast of Southern California, USA (Fig. 1, Table 1). Sampling areas were defined according to the ISC stock assessment: the East China Sea, the Sea of Japan, off the Pacific coast of Japan, Tsugaru Strait, the Ryukyu area, Taiwan, and the EPO (ISC 2022). The main fishing methods vary by area (Table 1). Except for a few individuals for which only vertebrae were collected, all specimens were measured for straight FL (SFL, cm), and both the 34th caudal vertebra and sagittal otoliths were collected individually.

2.2. Sample preparation

The otoliths were embedded in resin and sectioned, following the protocol adopted by Shimose & Ishihara (2015). Accordingly, otolith sections were examined under a light microscope and estimates of PBF age were determined based on counting the number of annual opaque zones (Shimose & Ishihara 2015).

After remnant tissue was removed, the vertebrae were cut into 2 longitudinal parts with a high-speed diamond cutter (Maruto Instrument) and soaked in 1.65% (w/v) Alizarin Red S stain solution for 2–5 h, with reference to Rodríguez-Marín et al. (2007). Each vertebra was then rinsed in running water for a few minutes and then dried, and the distance from the focus to the first annulus on the anterior cone of the vertebra (r_1, Fig. 2) was measured with a caliper in increments of 0.01 mm, following Uematsu et al. (2018).

2.3. Age determination

The age of PBF whose otoliths could be collected was determined based on the annuli of otoliths because age determination methods using vertebrae have not been established for PBF. For a few individuals whose otoliths could not be collected, age was determined from body length, using the growth curve published by the ISC (2022). Only individuals whose otoliths were collected or whose age could be estimated from body length were used as samples. Individual PBF were categorized into 6 age classes (1, 2, 3, 4–6, 7–9, and 10+) to ensure an adequate sample size. Ages 4–6 and 10+ are the estimated ages of spawning fish in the Sea of Japan and the Ryukyu area, respectively.

2.4. Statistical data analysis

Itoh (2009) divided age-0 PBF into 2 sub-cohorts according to body length data and reported that fish in one sub-cohort spawned earlier in the Ryukyu Archipelago and Taiwan (group RT) and those in the

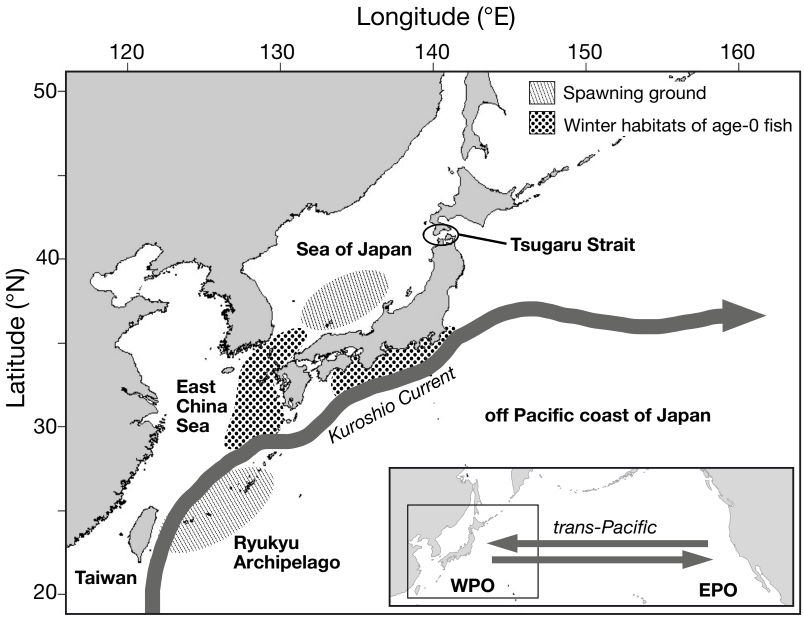

Fig. 1. Sampling locations of Pacific bluefin tuna. Striped areas represent the main spawning grounds, and dotted areas represent the known nursery habitat of age-0 fish in winter. WPO (EPO): western (eastern) Pacific Ocean

Table 1. Number, straight fork length (SFL) range, and main fishing equipment for the Pacific bluefin tuna samples by sampling area

Sampling area	Sampling year					SFL (cm)		Main fishing equipment
	1998–2000	2001–2005	2006–2010	2011–2015	2016–2020	Min	Max	
Sea of Japan	30	219	100	165	540	43.1	216.0	Purse seine
Tsugaru Strait	0	4	174	14	478	74.4	260.0	Longline and troll
Off the Pacific coast of Japan	48	59	48	38	375	45.8	274.0	Set net, purse seine, and longline
East China Sea	29	1	95	0	270	41.5	78.0	Purse seine and troll
Eastern Pacific Ocean	1	0	0	0	72	56.8	97.7	Pole and line
Ryukyu area	0	0	16	60	302	162.0	264.0	Longline
Taiwan	0	0	37	0	0	203.0	255.0	Longline

second sub-cohort spawned later in the Sea of Japan (group SJ). Therefore, for an age-0 PBF population, the percentage of groups can be calculated as the percentage of groups RT and SJ from the length distribution data. Consistent with the results of Itoh (2009), Uematsu et al. (2018) found that r_1 represents body length at age 0, confirming that the composition of r_1 can be used to estimate the hatching area.

The frequency of r_1 in the population is a mixture of groups RT and SJ, which are normally distributed. Therefore, we applied the Gaussian mixture model (GMM) using the package 'mclust' (ver. 5.4.9; Scrucca et al. 2016) in R ver. 4.2.0 (R Core Team 2022), and the parameters (mean, standard deviation, and mixing percentage) of the normal distributions were estimated. In the GMM, initial values were not set for the number of groups or for the mean, and we selected the model with the lowest Bayesian information criterion

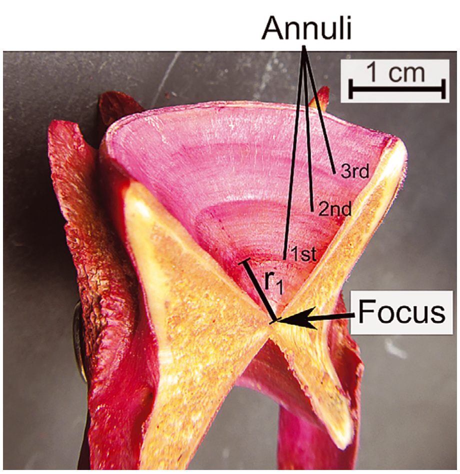

Fig. 2. Cross-section of the anterior cone of the 34th vertebra of a Pacific bluefin tuna (144.0 cm straight fork length) showing the annuli. r_1: distance from focus to first annulus

(BIC). GMM was performed on the r_1 values by sampling area and age class category. For each category, bootstrap analysis was performed with 500 replicates to calculate the percentage of groups SJ and RT, and the mean of the percentage of the number of individuals sorted into 2 groups was calculated.

3. RESULTS

3.1. Length and age compositions of collected samples

A total of 3175 PBF were sampled from 1998 to 2020, with the majority of samples collected after 2016, although there were periods when samples were not obtained in some areas (Table 1). The ages of 186 samples were estimated by body length. The specimens from the East China Sea and the EPO overall were small fish, with maximum SFLs of 78.0 and 97.7 cm, respectively (Fig. 3). In contrast, the fish in the Ryukyu area and off Taiwan were mostly larger than 200 cm SFL, with minimum sizes of 162 and 203 cm SFL, respectively. The SFLs of fish collected in the Sea of Japan, Tsugaru Strait, and off the Pacific coast of Japan ranged from around 50 to 250 cm (Fig. 3), and the SFL compositions formed a bimodal distribution. The modes of SFL in the Sea of Japan were around 80 and 150 cm. In the Tsugaru Strait, one mode was from around 120 to 150 cm SFL, which was comparable to the larger mode in the Sea of Japan, while the other was around 200 cm SFL. Most of the fish caught off the Pacific coast of Japan were smaller than 100 cm SFL, but larger fish (150–220 cm SFL) were also observed.

Among the 6 age classes, age 1 was the most abundant (963 individuals, 30.3% of the total), followed by age 3 (563 individuals, 17.7%) and age 4–6 (522 indi-

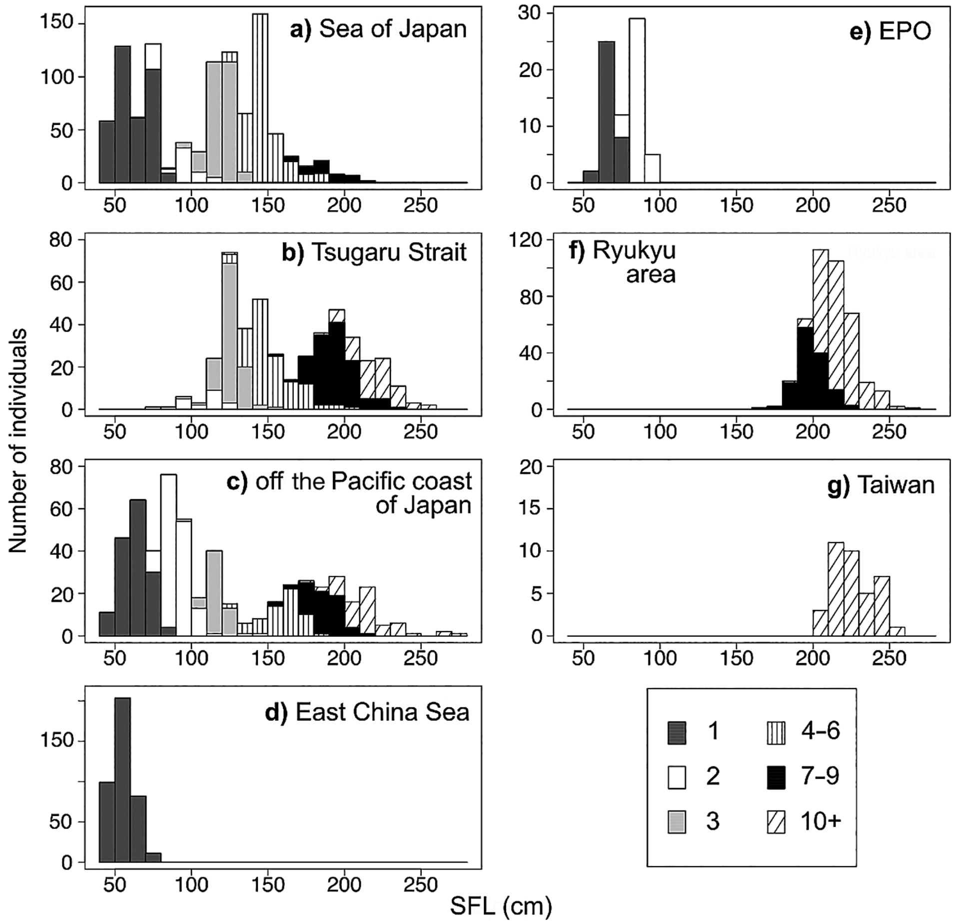

Fig. 3. Fish sizes in terms of straight fork length (SFL) and age composition of Pacific bluefin tuna samples in each study area: (a) Sea of Japan, (b) Tsugaru Strait, (c) Pacific coast of Japan, (d) East China Sea, (e) eastern Pacific Ocean (EPO), (f) Ryukyu area, and (g) Taiwan

viduals, 16.4%, Table 2). The age-class composition differed significantly according to sampling area. In the Sea of Japan (1054 individuals), where the sample size was the largest, age 1 was the most dominant (34.5%), followed by age 4–6 (29.5%) and age 3 (24.6%). In the Tsugaru Strait (670 individuals), age 3 (36.0%) dominated, while off the Pacific coast of Japan (568 individuals), age 1 (29.8%) and age 2 (26.4%) dominated. The East China Sea (395 individuals) consisted only of age 1. The Ryukyu area (378 individuals) consisted only of age 10+ (63.8%) and age 7–9 (36.2%), while Taiwan (37 individuals) consisted only of age 10+. Only samples of age 2 (52.1%) and age 1 (47.9%) were collected from the EPO.

Table 2. Number of Pacific bluefin tuna samples by age class and sampling area. Ages 4 and older were divided into 3 age classes: 4–6, 7–9 and 10+. Blank cells show that no fish in these size classes were caught

Age class	Sea of Japan	Tsugaru Strait	Off the Pacific coast of Japan	East China Sea	Eastern Pacific Ocean	Ryukyu area	Taiwan	Total (%)
1	364		169	395	35			30.3
2	78	77	150		38			10.8
3	262	241	60					17.7
4–6	311	150	61					16.4
7–9	39	125	64			137		11.5
10+		77	64			241	37	13.2

3.2. Estimates of the proportion of natal origin

GMM was performed on r_1 of all samples, and individual fish were separated into 2 groups with mean values of r_1 of 5.7 and 7.1 mm, based on the lowest BIC (Table 3, Fig. 4). These mean values were attributed to groups SJ (mean 5.5–5.7 mm) and RT (mean 7.0–7.3 mm), following Uematsu et al. (2018), and they were consistent with their respective groups. The percentages of the groups differed both by sample location and age class (Fig. 5).

In the Sea of Japan, the percentage (±SE) of group SJ was higher than that of group RT in all age classes but decreased from 82.3 ± 1.6 to 71.8 ± 5.5% with age. In the Tsugaru Strait and off the Pacific coast of Japan, the percentages of group SJ in age 4–6 and below were higher (53.8 ± 5.3 to 80.9 ± 4.8%) than those of group RT, but the percentages were reversed in age 7–9 and older, with a higher percentage in group RT (53.2 ± 3.8 to 63.0 ± 4.8%). In the East China Sea and the EPO, where only the younger age classes were sampled, the percentage of group SJ was high (81.3 ± 1.5%), as in the other areas in the WPO. In contrast, in the EPO, group SJ was low, at 22.8 ± 5.6 and 30.2 ± 6.6% for age 1 and 2, respectively. In the Ryukyu area and Taiwan, where only the older classes were sampled, the percentages of group RT were higher (54.9 ± 7.3 to 65.4 ± 3.5%) and similar to the proportions at age 7–9 and older in the Tsugaru Strait and off the Pacific coast of Japan.

Table 3. Parameters for groups SJ and RT estimated by the Gaussian mixture model. Group SJ indicates the late-hatched fish in the Sea of Japan and group RT includes the early-hatched fish in waters around the Ryukyu Archipelago and off Taiwan

Group	Mean	Variance	Mixing probability
SJ	5.7	0.26	0.65
RT	7.1	0.26	0.35

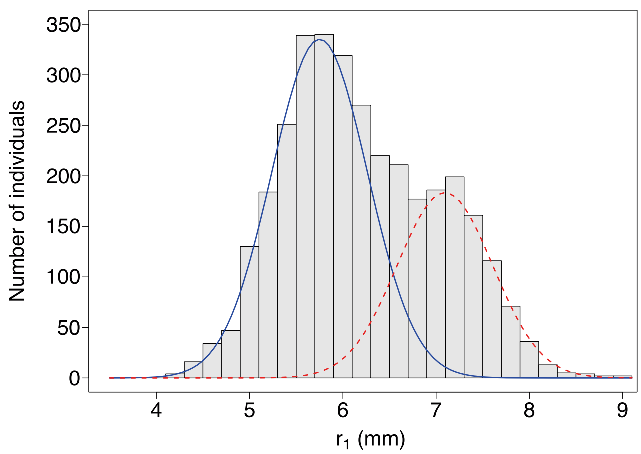

Fig. 4. Distance from the focus to the vertebral first annulus (r_1) in 0.2 mm bins of the Pacific bluefin tuna samples. The solid and dashed lines indicate the predicted normal distribution for group SJ and group RT (defined in Table 3), respectively

4. DISCUSSION

4.1. PBF distribution and sample collection

Although PBF are distributed throughout the Pacific Ocean, most research has focused on the Northern Hemisphere because the majority of PBF are found there. In the Southern Hemisphere, there are small catches of PBF in the waters around New Zealand (Smith et al. 2001, Murray 2005), but they are mainly larger than 160 cm FL (Itoh 2006), and their population density is lower than in our study area (Smith et al. 2001, Murray 2005). Although PBF are also landed in the Indo-Pacific (Bayliff 1994, Murray 2005), their migration route has not been clarified.

A comparison of the length composition of fish landed in the fishery and fish collected for this study indicates that, in general, the collected samples are representative of fisheries landings (ISC 2022) except for 2 areas in the Sea of Japan and the EPO. Specimens in the Sea of Japan included not only fish caught by purse seine but also fish as small as 50–80 cm SFL caught by set net. Their SFL composition was similar to the combined SFL composition based on commercial catches by purse sein and set net in the Sea of Japan (ISC 2022). Although larger, older fish have been landed in the EPO in recent years (James et al. 2021), our samples included only fish at age 1 and 2. However, given that significant eastward trans-Pacific immigrants are not expected at older age classes (Madigan et al. 2017), the ratio in the EPO would not be expected to change much in older age classes. Overall, this study covered the geographic area and age range of the majority of PBF caught in the North Pacific Ocean.

4.2. Natal origin proxy

This is the first study to use the vertebral first ring as a proxy for the natal origin of PBF across the North Pacific Ocean. The percentage of PBF that originated from the 2 spawning grounds varied by both region and age. Both groups SJ and RT were observed in all areas and across all age classes, consistent with previous studies involving several areas and a range of ages. Previous studies of adult fish from waters near Taiwan (Rooker et al. 2021) and on the Pacific coast of Japan (Hane et al. 2022) had higher percentages of group RT, similar to the percentages in this study. The percentages varied from year to year for fish at age 1 caught in the EPO (Wells et al. 2020), but the range of variation included the percentages observed in this study. In addition to these areas, this study expanded on previous research and found a similar pattern in the Tsugaru Strait, the East China Sea, the Sea of Japan, and the Ryukyu area over a wide age range. Importantly, both groups were observed when and where spawning was expected. In the Sea of Japan, both groups were found to occur at age 4–6 when nearly 100% of fish are expected to be mature (Okochi et al. 2016) although mature fish from group SJ dominated. In contrast, while both groups also occur in the Ryukyu area and Taiwan, where only mature fish migrate, group RT dominated. Our findings strongly support Nakatsuka (2020) and the current stock assessment that views PBF as a single stock.

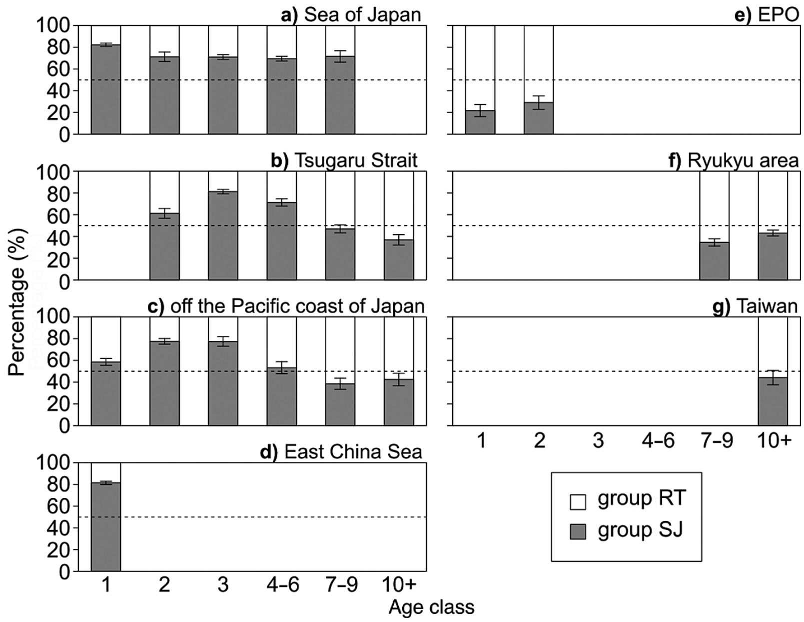

Fig. 5. Percentages of groups of Pacific bluefin tuna samples by sampling area and age class. Gray and white bars are groups SJ and RT (defined in Table 3), respectively. Error bars represent standard errors. (a) Sea of Japan, (b) Tsugaru Strait, (c) Pacific coast of Japan, (d) East China Sea, (e) eastern Pacific Ocean (EPO), (f) Ryukyu area, and (g) Taiwan

4.3. PBF movement pattern suggested by age class among areas

The estimated percentages of natal origin were different among areas and age classes. The percentages of group RT were higher than group SJ in the EPO, where they were the highest across all regions and age classes. In contrast, the percentages of group SJ were higher for the age class younger than 4–6 in the East China Sea, the Sea of Japan, the Tsugaru Strait, and off the Pacific coast of Japan (Fig. 5). In the latter 2 regions, these percentages decreased in the older age classes. In addition, in the Ryukyu area and off Taiwan, the percentage of group SJ was below 50% at age 7–9 and 10+ (Fig. 5). These variations in the percentages might be related to a number of factors, including recruitment, spawning stock biomass on each of the spawning grounds, and/or the dynamics of migration including trans-oceanic migration of PBF between the WPO and the EPO, as described below.

4.3.1. Low ratios of group RT in young populations in the WPO

Several studies have reported that the Ryukyu area spawning ground is more productive compared with the Sea of Japan. Itoh (2009) and Ishihara et al. (2022) both reported that the spawning stock biomass and larval abundance are higher in the Ryukyu area than in the Sea of Japan. Itoh (2009) estimated the percentage of each group for age-0 fish based on catch-at-length data, and the percentage of group RT was considerably higher in both the Pacific Ocean around Japan (87 ± 16%) and for the sum of the Sea of Japan and the East China Sea (72 ± 19%). In the present study, the percentages of group RT in ages 1 and 2 around Japan were much lower than those calculated by Itoh (2009) for age-0 fish. Although there may be temporal variability in patterns, this discrepancy might be explained by the trans-oceanic migration of juvenile PBF. According to studies of migration using archival tags, juveniles migrate to the EPO from off the southern coast of Japan, typically at age 1 or 2 (Madigan et al. 2017, Fujioka et al. 2018). Thus, the apparent reduction in the percentage of group RT in the WPO leads to the hypothesis that the majority of group RT is carried by the Kuroshio Current to off the Pacific coast of Japan after hatching and then migrates to the EPO after the first winter, while most of group

SJ remains in the waters around Japan, mainly in the Sea of Japan, with a low percentage migrating to the EPO. The higher percentages of group RT in the EPO support this hypothesis.

Temporal variability in factors impacting recruitment, abundance, and distribution can also influence the migration patterns. Thus, an additional potential explanation for the reduced percentages of group RT, based on a comparison of this study with Itoh (2009), is the increase in suitable habitat for spawning in the Sea of Japan and the associated northward shift in the distribution of PBF larvae presumably caused by ocean warming from the 1990s to the 2010s (Ohshimo et al. 2017). Thus, the relative contribution of group RT may have decreased due to the increased larval biomass in the Sea of Japan.

Both regional shifts in recruitment and/or migration to the EPO in most of group RT might potentially impact the proportions of the RT and SJ groups in the WPO. Although Polovina (1996) suggested that the abundance of prey in waters around Japan affects the trans-oceanic migration rate, the migrating fish consisted mainly of group RT in this study. Because migration to the EPO is considered to start from the Pacific side of Japan and follow the Kuroshio Current (Fujioka et al. 2018), the amount of migrating fish may be affected by the amount of spawning individuals in the Ryukyu area, with those fish being carried by the Kuroshio Current to the Pacific side of Japan.

4.3.2. Effect of westward trans-Pacific migration on group ratios in the WPO

The return of fish from the EPO to the WPO may help to explain the increase in the relative importance of RT fish in the older age classes in the WPO. Although trans-Pacific migratory patterns are complex, historically, the majority of PBF landed in the EPO have been between the ages of 1 and 3 (ISC 2022), after which time fish return to the WPO. Tawa et al. (2017) reported that PBF begin to return from the EPO to the waters around Japan at age 3, while most return at age 4 or older, with the rate of return increasing as the fish age. This increase in westward migration with age is consistent with the overall increased importance of group RT at higher age classes in the WPO.

The shift in ratios at larger size classes was not consistent across all regions and may reveal migration patterns. Off the Pacific coast of Japan, the percentage of group RT increased from age 3 to 4–6 before similar shifts were observed in the Tsugaru Strait. These increases indicate that the fish returning from the EPO to the WPO migrate to the waters off the Pacific coast of Japan and then continue on to the Tsugaru Strait and the Ryukyu area. There was no significant increase in group RT in the Sea of Japan even at older age classes, suggesting that few PBF from the EPO enter the Sea of Japan. If true, this may have implications for the stock management of the spawning stock biomass in the Sea of Japan.

4.3.3. Contribution of the entire PBF population

The percentages did not change much from age 7–9 to 10+ in 3 areas — the Tsugaru Strait, off the Pacific coast of Japan, and the Ryukyu area — and were higher in group RT, at around 60%. These results suggest that, by these ages, the majority of fish from the EPO and potentially other foraging regions are expected to have returned to the WPO (Madigan et al. 2017, Heberer & Snodgrass 2021, ISC 2022). Although the relative proportion of fish that migrate to other foraging regions is not known, most adult PBF are distributed in the WPO. Thus, that percentage, which is higher for group RT, is considered to be the final percentage of the relative contribution of the 2 natal grounds to the PBF for this study.

The hatch date of PBF larvae collected off the Pacific coast of northeastern Japan in recent years overlapped with that in the Sea of Japan (Tanaka et al. 2020). Thus, fish hatched off the Pacific coast of northeastern Japan might also have been included in group SJ in this study if they survived. The dynamics of this group hatching late off the Pacific coast and the older fish migrating to the Southern Hemisphere warrants further study. It may be possible to use chemical markers, given the differences in oceanography among the regions (Wells et al. 2020, Rooker et al. 2021).

5. CONCLUSIONS

Although PBF form a single stock, the results of this study suggest that they have different migration patterns depending on their natal area, with group SJ more likely to remain around Japan and group RT more likely to migrate to the EPO and later return to the Pacific coast of Japan. Studies on migration have generally utilized temporal patterns in fisheries data, conventional and electronic tagging (Furukawa et al. 2017, Fujioka et al. 2018), and chemical methods such as stable isotope analysis (Madigan et al. 2017, Tawa et al. 2017, Kawazu et al. 2020), which provide insight into the timing and season of migration. In contrast, the present study produced the first quantitative findings (e.g. mixing rates of different hatchery groups) and inferred the migratory ecology of highly migratory fish based on the variation in population composition. Future research should combine vertebral ring analysis with chemical tracers in otoliths and soft tissues of the same PBF in order to corroborate the inference from each method. In the present study, we analyzed samples collected over 20 yr as a combined data set. However, the spawning biomass and recruitment of PBF fluctuated during this period. Additional work is needed to ascertain the variability over time across regions and age classes. Utilizing the distance to the first annulus is a relatively simple and cost-effective approach for examining temporal and spatial patterns in the dynamics of movement. This approach could be applied to examine a range of questions related to the relative contribution of fish from each spawning ground to fisheries and spawning stock biomass and how shifts are related to environmental conditions that impact recruitment and movements. This would be of particular value when considering the potential for climate change to differentially influence the 2 spawning grounds.

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