RESEARCH ARTICLE

Evidence of spawning among Pacific bluefin tuna, *Thunnus orientalis*, in the Kuroshio and Kuroshio–Oyashio transition area

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Abstract – Reproductive characteristics are one of the key factors for understanding population dynamics in fishes. This study describes the spawning habitat of Pacific bluefin tuna (*Thunnus orientalis*) in the Kuroshio and the Kuroshio–Oyashio transition area. A total of 551 adult fish (fork length > 120 cm) were collected during 1994–2007 (except in 2001 and 2003) and 2016. Based on a histological analysis of the gonads, we concluded that actively spawning females were mainly present in late May to early July. Relative batch fecundity was significantly lower than that reported in the Sea of Japan but was similar to that observed in the Nansei area. Whereas most spawning adults in the Sea of Japan are 3–6 years old and those in the Nansei area are over 10 years old, the majority of the specimens in this study ranged from 160 to 180 cm in length, which corresponds to 6–8 years of age. Our results indicate that Pacific bluefin tuna spawn in the study area and provide important data for understanding the spatiotemporal differences in spawning strategy with growth in this species.

Keywords: Kuroshio–Oyashio transition area / relative batch fecundity / spawning strategy

1 Introduction

The Pacific bluefin tuna (PBF, *Thunnus orientalis*) is one of the most valuable fisheries species in the world and is exploited by many countries (Collette and Nauen, 1983). The species is distributed mainly in the North Pacific Ocean and is also occasionally caught in the southern hemisphere (Bayliff, 1994). Recent stock assessment indicates that PBF spawning-stock biomass is near historic lows, the stock is overfished, and overfishing is occurring (ISC, 2016). Despite the low spawning-stock biomass, PBF recruitment does not currently show a clear declining trend as has been observed several times in the past (ISC, 2016), which may be due to a weak stock recruit relationship (Nakatsuka et al., 2017) or due to environmental factors such as sea surface temperature (Harford et al., 2017; Muhling et al., 2018).

Ecosystem-based fisheries management (EBFM) has emerged as an important framework for fisheries management.

The objective of EBFM is to sustain healthy marine ecosystems and fisheries (Pikitch et al., 2004). The principles of EBFM, which were first elaborated in the Principles for the Conservation of Wild Living Resources (Mangel et al., 1996), state that ecological and sociological assessments are an essential tool for effectively utilizing wild resources. Typically, EBFM entails a shift from single species to multi species or ecosystem management. This is important in the case of PBF, which is a large apex predator, as its population dynamics could affect prey species dynamics. In addition, a better understanding of the spatial ecology of this species is necessary to implement effective conservation of this highly valuable resource.

Ascertaining biological characteristics such as spawning dynamics and maturation is key to determining species population dynamics. PBF spawn in two major areas: one extends from the waters north of the Philippines to the Ryukyu (Nansei) Islands in the northwestern Pacific Ocean, and is used from April to June (Ashida et al., 2015). The other area is located in the Sea of Japan, and is used from June to August (Fig. 1; Okochi et al., 2016). Larvae hatched in the Nansei area

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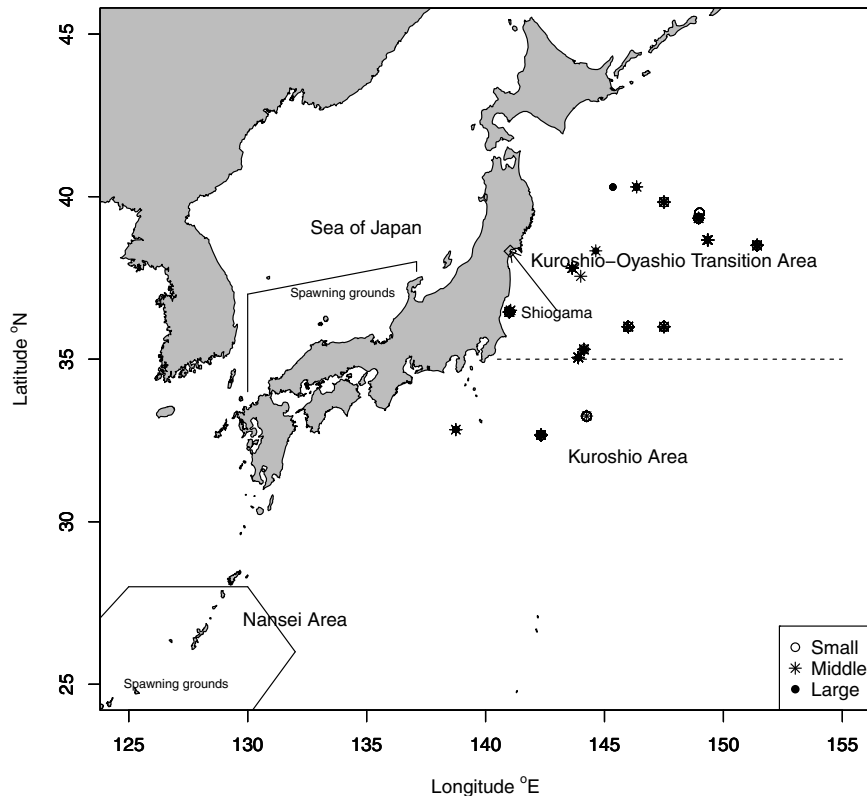
Fig. 1. Map of capture sites (black dots) of adult Pacific bluefin tuna used for this study. Open circles, asterisks, and closed circles represent capture locations of small (FL < 156 cm), medium ($156 \leq$ FL < 177 cm), and large (177 cm $\leq$ FL) fish, respectively.

and the Sea of Japan are carried to coastal areas of southwestern Japan by the Kuroshio and the Tsushima Warm Current, respectively (Ohshimo et al., 2017). Generally, recruitment in fishes depends on spawning stock size and early life-stage survival. Whereas, as mentioned above, the stock size of PBF is known to be near historic lows (ISC, 2016), we have only limited ability to assess any trends in early life-stage survival. Studies of growth-dependent mortality in PBF larvae have suggested that higher larval growth rates enhance survivorship to recruitment (Tanaka et al., 2006; Watai et al., 2017). Juvenile PBF found in the Pacific Ocean in summer originate from the northwestern Pacific Ocean spawning grounds (Masujima et al., 2014; Suzuki et al., 2014; Furukawa et al., 2016), whereas those in the Sea of Japan have mixed origins and come from both the Sea of Japan and the northwestern Pacific Ocean (Itoh, 2006; Tanaka et al., 2007). Spawning adults in both areas are also of mixed origins (Uematsu et al., 2018). Age-0 PBF migrate southward in the Sea of Japan in winter (Ichinokawa et al., 2014) and before moving eastward to the offshore region of the western Pacific (Fujioka et al., 2018a). Understanding the underlying spawning status of PBF is important for predicting recruitment strength and is therefore crucial to understanding the species' population dynamics.

The mean body length of PBF in the Nansei area exceeds that in the Sea of Japan (Ashida et al., 2015; Okochi et al., 2016; Shimose et al., 2018). Most individuals in the Nansei area are over 10 years old (fork length (FL) > 200 cm) (Ashida et al., 2015), whereas the predominant age range in the Sea of Japan is 3–6 years (110 < FL < 150 cm) (Okochi et al., 2016).

These data indicate that PBF segregate on each spawning ground by age and size and mid-sized (age 7–9) adults are not often found on either spawning ground. Archival tagging data could provide some insights into the lack of mid-sized adults on the two major spawning grounds. Although such data exist for migrating Atlantic Bluefin tuna (ABF), *Thunnus thynnus* (Lutcavage et al., 1999; Teo et al., 2007), there is a lack of archival tagging studies on spawning-age PBF. Instead, we collected mid-sized PBF landed at Shiogama Port in northern Japan and examined their sexual maturity. We use these results in the present study to describe the reproductive characteristics of PBF in the waters of the Kuroshio and the Kuroshio–Oyashio transition area (KOTA). The KOTA is located off the east coast of Japan and is a confluence of the two western boundary currents of the wind-driven subtropical and subarctic gyres, as well as the western boundary currents of intermediate and deep circulation in the North Pacific (Yasuda, 2003). Our objectives are to describe the maturation characteristics of PBF in the Kuroshio area and the KOTA, which is one of the most productive regions around Japan, and to investigate the spawning strategy and possible spawning grounds of this species.

2 Materials and methods

2.1 Sample collection and data

A total of 551 adult female Pacific bluefin tuna (FL > 120 cm) were collected in the Kuroshio and the KOTA by purse seine and landed at Shiogama Port in Miyagi Prefecture.

Ovaries were collected from May to September between 1994 and 2016 (Tab. 1). FL (cm), gilled and gutted body weight (BW, kg) and ovary weight (GW, g) were recorded. The collected ovaries were weighed to the nearest 0.1 g at the laboratory. Gonad-somatic index (GSI) was calculated as follows:

$$GSI = GW \times 100/BW \times 1000. \quad (1)$$

We obtained date-of-catch data from the fishermen's logbooks to analyze seasonal maturity. Specimens with an unknown catch date were assumed to have been caught 1 day before the landing date. Sea surface temperature (SST) was obtained from satellite-derived, advanced very high-resolution radiometer data (http://podaac.jpl.-nasa.gov/dataset/NCDC-L4LRblend-GLOB-AVHRR_OI) at the locations where the purse seines were operated. This dataset is available from the NOAA National Climatic Data Center at a spatial grid resolution of 0.25° and a temporal resolution of 1 day. It is highly correlated with observed SST records, such that $SST\_obs = 1.00SST\_sat$ ($R^2 = 0.998$; data not shown), where SST_obs is observed SST and SST_sat is satellite-derived data.

Table 1. The number of collected female Pacific bluefin tuna binned by month and year.

Year	May	June	July	August	September	Total
1994		26		2		28
1995		50				50
1996			47			47
1997			28	31		59
1998				24		24
1999		27				27
2000		25				25
2002		24	25			49
2004		17	20			37
2005			16		16	32
2006		64				64
2007	42			38		80
2016		10	19			29
Total	42	243	155	95	16	551

2.2 Histological treatment and maturity phase

The collected ovaries were preserved in 10% formalin ($n = 551$). Tissues from the fixed ovaries were dehydrated and then embedded in paraffin wax. Each embedded ovary was sectioned at a thickness of 4–6 µm and stained with hematoxylin–eosin.

The oocytes were classified into one of six developmental stages: the perinucleolus stage, lipid stage, early yolked stage, advanced yolked stage, migratory nucleus stage, or hydrated stage (Schaefer, 1996; Okochi et al., 2016). The most advanced group of oocytes (MAGO) was defined for each individual. The presence of postovulatory follicles (POFs) and atresia (α and β types) was also determined.

Based on observations of MAGO, in the presence of POF, and atresia, the ovarian maturity phases were classified into the following six phases: immature, developing, spawning-capable, spawning, regressing, or regressed (Tab. 2; Farley et al., 2013; Okochi et al., 2016). Because we did not record the presence or absence of maturity markers (Farley et al., 2013), we were unable to distinguish between the resting and immature phases. The spawning-capable and spawning phases were distinguished by whether or not we observed post-ovulatory follicles and/or oocytes at final maturation (i.e., at the migratory nucleus stage or hydrated stage).

2.3 Spawning frequency and interval

We followed the procedures of Okochi et al. (2016). Spawning frequency was estimated by the POF method in accordance with Hunter and Goldberg (1980) and Hunter and Macewicz (1985). Spawning frequency was calculated using the ratio of females with POFs to all mature females. The inverse of the spawning frequency was considered the spawning interval.

2.4 Batch fecundity and calculation of the relative batch fecundity

Batch fecundities were estimated from ovaries with MAGOs in the hydrated stage and without new POFs (Hunter et al., 1985). A 0.5-g subsample was removed from the interior side in the middle part of a formalin-fixed ovary, and hydrated oocytes were separated from the tissue under a dissecting microscope. The number of hydrated oocytes was counted in

Table 2. Histological classification criteria for Pacific bluefin tuna.

Class	Maturity status	Development class	MAGO and POFs	α and β atresia of yolked oocytes
1	Immature	Immature-regenerating (resting)	PNS or YVS, no POFs	Absent
2	Immature	Developing	EYS, no POFs	<50% α atresia, β atresia may be present
3	Mature	Spawning-capable	AYS, no POFs	<50% α atresia, β atresia may be present
4	Mature	Spawning	MNS or HS, and/or POFs	<50% α atresia, β atresia may be present
5	Mature	Regressing-potentially reproductive	AYS, no POFs	≥50% α atresia, β atresia present
6	Mature	Regressed	PNS or YVS, no POFs	100% α atresia, β atresia may be present

AYS, advanced yolked stage; EYS, early yolked stage; HS, hydrated stage; MAGO, most advanced group of oocytes; MNS, migratory nucleus stage; PNS, perinucleolus stage; POF, postovulatory follicles; YVS, yolk vesicle stage.

each subsample. Subsamples were taken from the ovary at least twice, and the mean number of hydrated oocytes between subsamples was converted into batch fecundity (BF) based on the total gonadal weight. When the coefficient of variation between two subsamples was higher than 10%, extractions from the subsample continued until the coefficient of variation was less than 10%. The BF was calculated as follows:

$$BF = GW \times N_{subsample}/W_{subsample}, \qquad (2)$$

where GW is the gonad weight, and $N_{subsample}$ and $W_{subsample}$ are the number and weight of hydrated oocytes, respectively.

Relative batch fecundity (RBF) and expected body weight (exBW) were calculated as follows:

$$exBW = aFL^b, \qquad (3)$$

$$RBF = BF/exBW, \qquad (4)$$

where FL is measured fork length, and a and b are coefficients that are calculated from the relationship between the actual body weight and fork length using the nonlinear least squared method. Our reasons for using the expected BW were (i) our samples had already been gutted on board, and therefore had artificially reduced body weight, and (ii) because of their high economic value, we were not permitted to handle the fish.

3 Results

3.1 Body length and age

The minimum and maximum FLs of the fish we collected for histological study were 124 and 225 cm, respectively. The second and fourth quartiles were 156 and 177 cm, respectively. Therefore, three size categories were defined as follows: small (FL < 156 cm), middle (156 ≤ FL < 177 cm), and large (177 cm ≤ FL). There were no discernable patterns in the spatial distribution of the three size categories (Fig. 1). The frequency distributions of the FLs for each month and year are shown in Figures 2 and 3, respectively. Unfortunately, we only achieved limited temporal and spatial coverage with our sampling locations in each year (Figs. 1 and 3), which is a weakness of this study. The mean fork length (FL; ±SD) of individuals collected from June through September was 169.6 ± 15.0 cm, and the predominant FLs ranged from 150 to 200 cm (Fig. 2). FLs were smaller in May than in the other months (Fig. 2). Based on the reported age–FL relationships of PBF (Shimose et al., 2009), the predominant FLs in this study correspond to an age of 6–8 years. The predominant FL of the sampled individuals varied by year, and we observed both unimodal and bimodal frequency distributions (Fig. 3).

3.2 Ovarian development

The GSI was slightly higher in June than in the other months (Fig. 4a) and included a large number of outliers. There were numerous outliers in July as well; however, the median was somewhat lower. The relationship between SST and GSI is shown in Figure 4b. Median GSI peaked at an SST of 22 °C.

We classified 192 ovaries in the immature/resting phase: 37 in the developing phase, 51 in the spawning-capable phase,

152 in the spawning phase, 9 in the regressing phase, and 110 in the regressed phase. The immature phase made up the highest proportion of the total sample (34.8%), followed by the spawning phase (27.6%).

The relative abundance of each ovarian maturity phase varied over the sampling period (Fig. 5). Immature and regressed phases appeared in all seasons and accounted for 12.0–87.0% and 4.3–68.4% of the total sample, respectively. The relative frequency of the developing phase varied but remained below 13% from late May to early August. The spawning phase showed a seasonal pattern wherein the relative frequency increased to 62.7% in early June and was almost completely absent in late August.

3.3 Body size–maturity relationships

The relative frequency of each ovarian maturity phase by FL is shown in Figure 6. All females larger than 210 cm ($n = 4$ individuals) had ovaries in the spawning phase. The minimum FLs for the spawning-capable and spawning phase were 132 and 143 cm, respectively. The regressed phase, however, appeared only at FL ≥ 125 cm, suggesting that females may start to reach reproductive maturity in our study area at age 3 (Shimose et al., 2009). The fraction of individuals between 145 and 205 cm FL in the spawning phase ranged from 4.3 to 41.5%, and the fractions of small fish (FL < 160 cm) were low (4.3–18.8%).

3.4 The effect of water temperature on ovarian maturation

The relative frequency of each ovarian maturity phase by SST at the fishing grounds is shown in Figure 7. Ovaries in the immature and regressed phases were collected throughout the range of water temperatures recorded in this study. Individuals with ovaries in the developing phase were captured at 19.0–26.0 °C. The highest number of spawning-capable females was caught at temperatures of 21.0–24.0 °C (Fig. 7). Spawning phase ovaries were collected at higher temperatures (21.0–25.5 °C) than spawning-capable ovaries (19.0–23.5 °C). Ovaries containing MAGOs in the migratory nucleus or hydrated stages, which appear just prior to spawning, were collected at 21.0–25.5 and 22.5–24 °C, respectively, suggesting that spawning may occur at these water temperatures. The mean monthly SST in the Kuroshio area (32° N < latitude ≤ 35° N) of our study area was approximately 18–22 °C in May, warmer than 21 °C in June, warmer than 24 °C in July, and 26–28 °C in August; however, the mean SST north of the Kuroshio Current (latitude > 35° N) was cooler than 20 °C in May, and cooler than 24 °C during August (http://www.data.jma.go.jp/gmd/kaiyou/data/db/kaikyo/monthly/sst_HQ.html?areano=1), and these horizontal SST distributions did not vary strongly interannually, compared to the seasonal cycle.

3.5 Spawning frequency and interval

The mean spawning frequency reached a maximum of 0.41 during May, before declining to 0.00 by August (Tab. 3). The corresponding spawning intervals in May, June, and July were 2.41, 4.30, and 3.48 days, respectively. The overall spawning
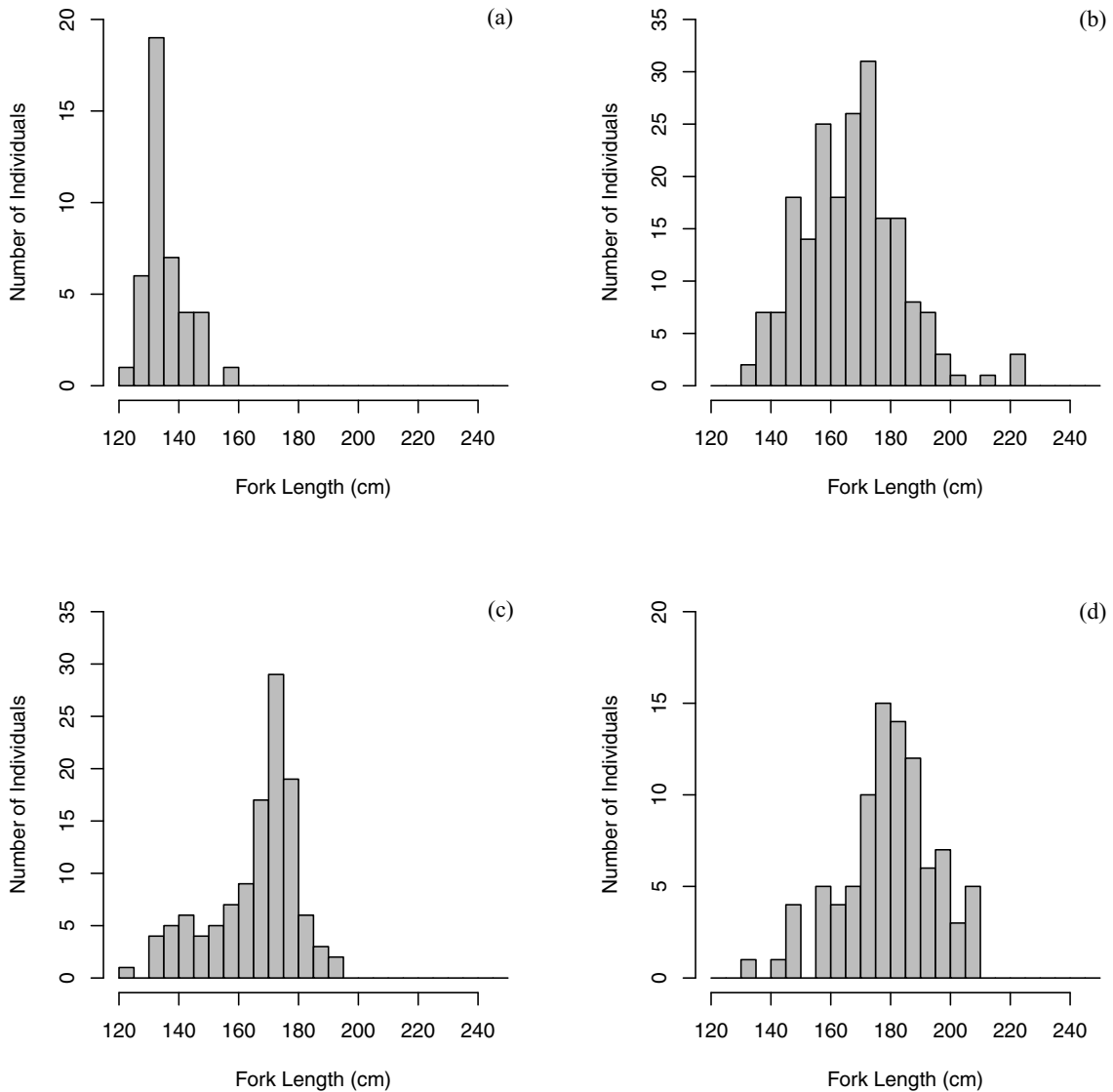
Fig. 2. Size distribution of Pacific bluefin tuna in (a) May, (b) June, (c) July, and (d) August from 1994 to 2016. Although specimens were also collected in September, FL data were not recorded at the fish market during this month.

frequency from May to August was 0.25 days, while the spawning interval was 3.96 days.

3.6 Batch fecundity and relative batch fecundity

There was a significant positive relationship ($p = 0.020$) between BF and FL (cm) (Fig. 8a), with the following regression equation:

$$BF = 0.26\,FL - 39.88\,(R^2 = 0.20, n = 27). \quad (5)$$

However, there was no significant relationship between relative batch fecundity and BW (Fig. 8b). The mean fecundity (eggs/g-exBW) in the present study was 52.6 ± 20.2 (mean $\pm$ SD) eggs/g. In comparison, previous reports have found mean fecundity values of 56.4 ± 37.9 in the Nansei area (Ashida et al., 2015) and 109.8 ± 34.0 in the Sea of Japan

(Okochi et al., 2016) (Fig. 8c). Our results were significantly different from reported fecundities in the Sea of Japan (Tukey–Kramer test, $p < 0.001$) but did not differ significantly from those reported in the Nansei area ($p = 0.956$).

4 Discussion

Our results show the maturity status of Pacific bluefin tuna caught in the Kuroshio and the KOTA and reveal the presence of females in spawning condition, although temporal and spatial coverage with our sampling locations in each year were limited. To evaluate the spatial spawning habitat in the present study area, more sophisticated sampling designs would be needed. Previous studies used histological methods to show that the major PBF spawning grounds are located in the Nansei area, which extends from the waters southeast of Taiwan to the
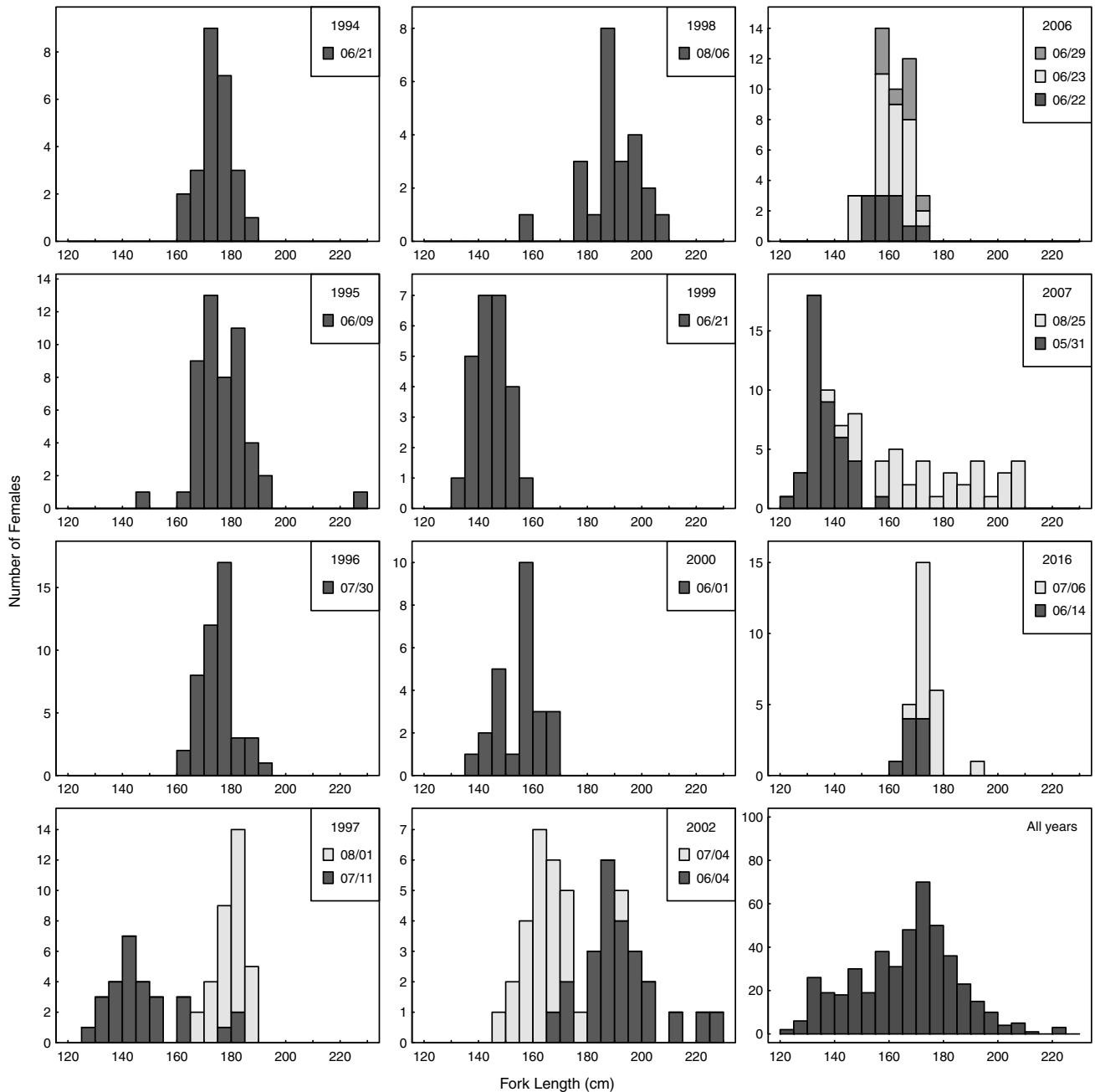
Fig. 3. Size distribution of female Pacific bluefin tuna in each sampling year and across all years (bottom right). Colors indicate different sampling dates.

Ryukyu archipelago, and the Sea of Japan (Chen et al., 2006; Ashida et al., 2015; Okochi et al., 2016). Ohshimo et al. (2017) reported on the distribution of PBF larvae and found that larvae were distributed from the Nansei area to the southern main islands of Japan (west of 140° E), although the number of PBF larvae collected in the Nansei area far exceeded that collected around the southern main island of Japan (Ohshimo et al., 2017). PBF larval surveys have never previously been conducted in the KOTA (Ohshimo et al., 2017). Therefore, despite the limited temporal and spatial extent of our sampling effort, our data constitute the first evidence of spawning in the KOTA.

4.1 Body length–maturation relationships

The FL of collected PBF ranged from 124 to 225 cm, and the mean FL was approximately 170 cm. Based on age determination analysis (Shimose et al., 2009), their ages ranged from 1 to 9 years. Itoh (2006) reported on the size of PBF in different regions of the western Pacific during 1993–1997. Although he did not make observations on the maturation phase, these data still provide useful context for our results. The lengths of PBF in the present study area were mostly larger than 160 cm, compared to lengths of less than 160 cm in the Sea of Japan and more than 220 cm in the region
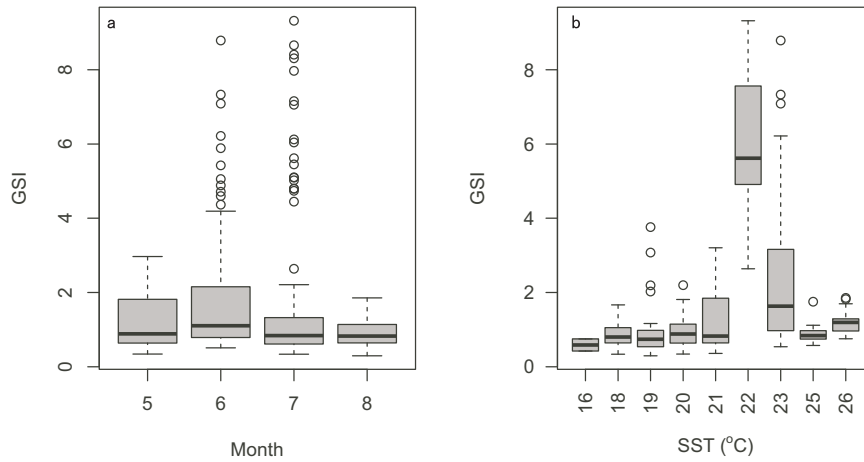
Fig. 4. Boxplots of GSI (gonad somatic index) across (a) months and (b) sea surface temperature. Median values (solid horizontal lines), 50th percentile values (box outline), 90th percentile values (whiskers), and outlier values (open circles) are indicated in the figure.
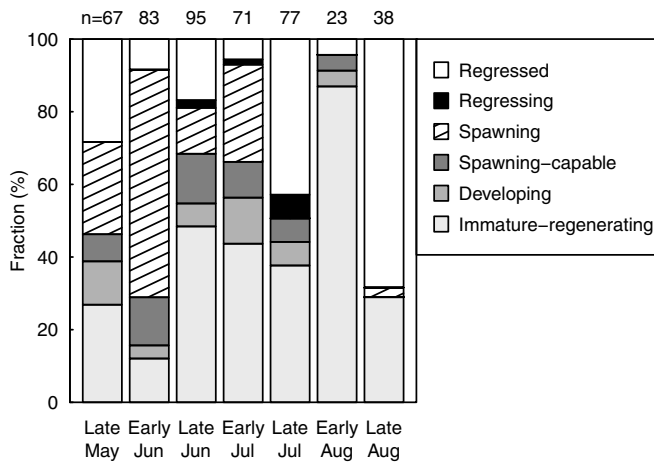
Fig. 5. Relative frequency of ovary maturity phases by season. Numbers above the figure indicate the number of samples in each bin.
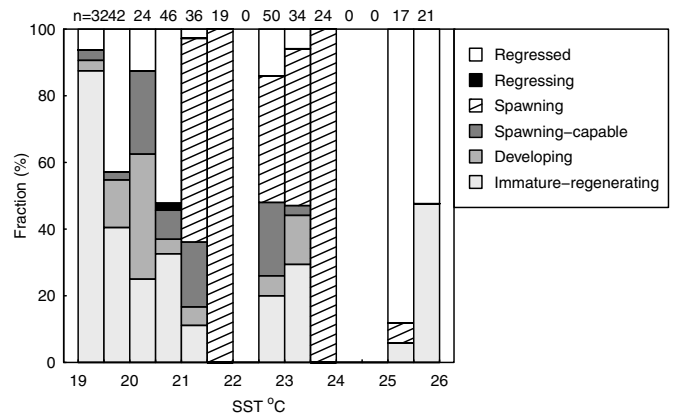
Fig. 7. Relative frequency of ovary maturity phases by sea surface temperature. Numbers above the figure indicate the number of samples in each bin.
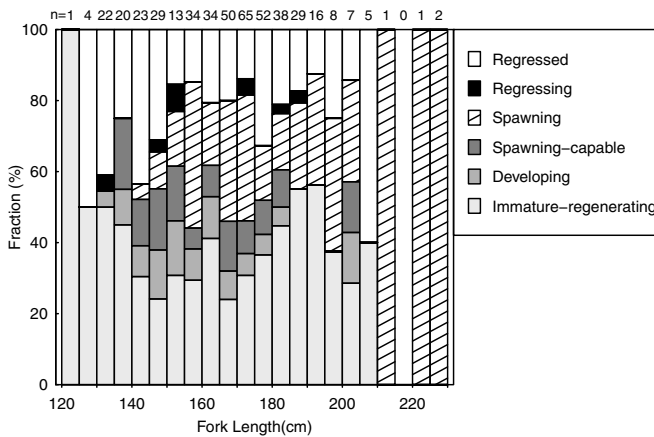

Fig. 6. Relative frequency of ovary maturity phases by fork length. Numbers above the figure indicate the number of samples in each bin.

around Taiwan (Itoh, 2006). The marked differences in FL between spawning grounds of this species indicates that the smaller adults may be spawning somewhere other than the two known spawning grounds.

The minimum FLs of individuals with ovaries in spawning-capable and spawning phase were 132 and 143 cm, respectively, which would correspond to 3–4 years of age. However, most of the fish examined in the present study were 160–180 cm, which corresponds to 6–8 years of age (Shimose et al., 2009). Okochi et al. (2016) reported that the size at first maturation of PBF in the Sea of Japan was 107 cm, the size at 50% maturation was 114.4 cm (corresponding to approximately 3 years of age), and the size at 95% maturation was 133.6 cm (corresponding to approximately 4 years of age). The predominant age range in the Sea of Japan is 3–6 years of age, and in the Nansei area it is over 10 years of age (Ashida et al., 2015). No individual less than 120 cm FL was examined in this study. Consequently, we are unable to determine the

Table 3. Number of mature females and females with postovulatory follicles (POFs) <24 h old, spawning frequency, and spawning interval for Pacific bluefin tuna in the Kuroshio and Kuroshio-Oyashio transition areas.

Year	Mature female with POF (n)					Mature female (n)					Spawning frequency					Spawning Interval				
	May	June	July	August	September	May	June	July	August	September	May	June	July	August	September	May	June	July	August	September
1994		0	0				2		0			0.00					NA			
1995		6					37					0.16					6.17			
1996			0					29					0.00					NA		
1997			0					17					0.00					NA		
1998				0					3					0.00					NA	
1999		0					24					0.00					NA			
2000	17					22					0.77					1.29				
2002		20	0				24	9				0.83	0.00				1.20	NA		
2004		0	16				17	18				0.00	0.89				NA	1.13		
2005			15		0			16		0			0.94		NA			1.07		NA
2006		7					29					0.24					4.14			
2007	0			0		19			27		0.00			0.00		NA			NA	
2016		0	0				9	19				0.00	0.00				NA	NA		
Total	17	33	31	0	0	41	142	108	30		0.41	0.23	0.29	0.00	NA	2.41	4.30	3.48	NA	NA
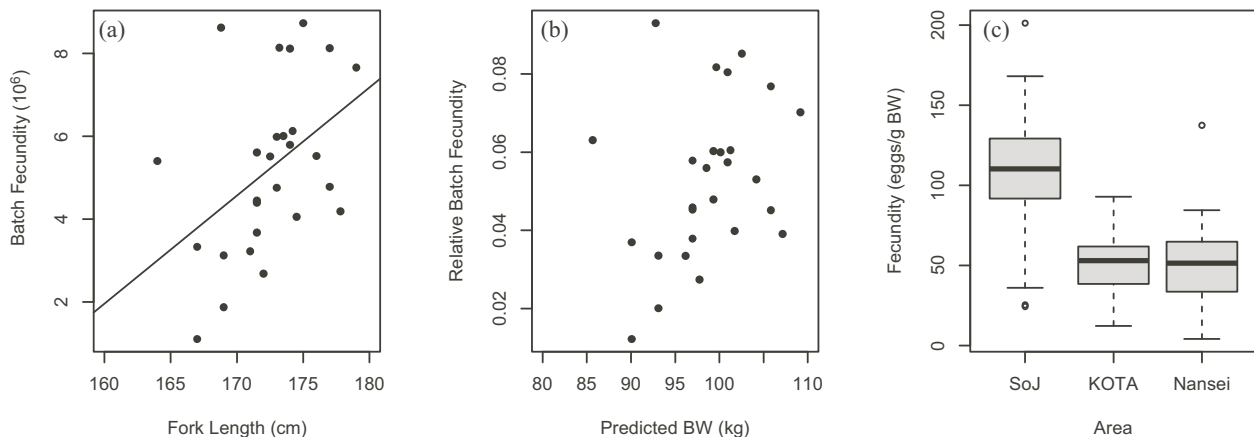
Fig. 8. Relationship between (a) fork length and batch fecundity, (b) expected body weight and relative batch fecundity, and (c) a comparison of relative batch fecundity among spawning grounds, SoJ, KOTA, and Nansei represent Sea of Japan, Kuroshio–Oyashio transition area, and Nansei area, respectively (Fig. 1).

minimum size of maturity in this area. Future studies should focus on this smaller size class to address this lack of data.

The ABF population in the Atlantic Ocean has two main spawning grounds: one in the Gulf of Mexico and the other in the Mediterranean Sea (Karakulak et al., 2004; Knapp et al., 2010; Knapp et al., 2014). Recently, another spawning ground has been identified in the Slope Sea (Richardson et al., 2016). In the eastern ABF stock, the size of the spawning fish differs by spawning location (Heinisch et al., 2008). The evidence from PBF indicates that, as in ABF, individuals segregate among spawning grounds by age. Itoh (2006) reported on the presence of different size frequencies of PBF in each fishing ground, including in the KOTA, the Nansei area, and the Sea of Japan. This segregation by age and size has not only been found for PBF (Itoh, 2006) and ABF (Karakulak et al., 2004; Knapp et al., 2010; Knapp et al., 2014) but also for other highly migratory species (e.g., *Isurus oxyrinchus*: Kai et al., 2015;

Thunnus alalunga: Nikolic et al., 2017; *Prionace glauca*: Ohshimo et al., 2016). It is likely that this type of segregation is a survival strategy employed by highly migratory species.

4.2 Spawning frequency and interval

Spawning frequencies in the genus *Thunnus* can be estimated using the proportion of ovaries in mature females containing postovulatory follicles. In the present study, the methodology for estimating spawning frequency and interval followed a previous study (Okochi et al., 2016). However, because we did not classify ovaries into the regenerating phase (Farley et al., 2014), our spawning frequency and interval estimates may have been affected by slight biases. Spawning frequencies of PBF have been reported to be much higher in the Sea of Japan (Okochi et al., 2016; Ohshimo et al., 2018b) than in the Nansei area (Chen et al., 2006; Ashida et al., 2015;

Shimose et al., 2018). The spawning frequency and interval we report in the present study are similar to previous reports for the Nansei area.

Spawning frequencies and intervals are known to vary in other tuna species. The spawning interval of ABF, for example, has been estimated at 1.2 days (Medina et al., 2002) and 1.2–3.1 days (Medina et al., 2007). Medina et al. (2007) also showed highly significant differences between purse seine and longline caught ABF, with spawning interval estimates of 1.2 and 3.1 days, respectively. Similarly, Schaefer (2001) found different spawning intervals for tuna species depending on sampling gear and area. In addition, spawning frequency and interval may also be affected by physiology or nutritional status. These effects require further study.

4.3 Skipped spawning

The highest relative frequency of individuals with ovaries in a spawning or spawning-capable phase was low even at FLs greater than 120 cm. Moreover, compared to reports from Nansei (Ashida et al., 2015) and the Sea of Japan (Okochi et al., 2016; Ohshimo et al., 2018b), the frequency of the spawning-capable phase was lower, and the frequency of the regressed phase higher, among the individuals we sampled. One reason for this may be the occurrence of skipped spawning. Skipped spawning has been reported in ABF on the basis of tagging data, histological examinations of the ovary, and energy allocation models (Lutcavage et al., 1999; Corriero et al., 2003; Goldstein et al., 2007; Heinisch et al., 2008; Zupa et al., 2009; Chapman et al., 2011). Secor (2007) suggested that the phenomenon of skipped spawning in ABF is related to spawning migrations, as migration entails a significant energy cost for an individual, which could lead to skipped spawning or other changes to the reproductive schedule. Nonreproductive fish have been reported in ABF in the Mediterranean Sea (Zupa et al., 2009). Experimental and field studies suggest that mature ABF females sometimes skip a spawning season when nutritional and environmental conditions are not suitable for reproduction (Zupa et al., 2009). Jørgensen et al. (2006) reported that skipped spawning was most common when the energetic and mortality costs in fish associated with migration and spawning were high. In the present study, the fraction of individuals in the regressed phase was much higher than in the other known spawning grounds (Ashida et al., 2015; Okochi et al., 2016; Ohshimo et al., 2018b), even though the fish in our study had large body lengths. Therefore, further study into the relationship between spawning fraction and nutritional/environmental conditions should be conducted in the near future. One possibility is that the SSTs we observed in our study area were too low for spawning in this species. In other words, the conditions may not have been adequate for spawning because the eggs and hatched larvae would experience high mortality. The relationship between temperature and PBF maturation will be discussed in a later section. Another possibility is that spawners from two spawning grounds migrate to this area after spawning. This would account for the difference in body length between individuals in the KOTA and Kuroshio Current and the two other spawning grounds (Itoh, 2006). Further studies on adult PBF migration and behavior based on archival tagging are needed in the future.

4.4 Batch fecundity

Our results show a positive relationship between batch fecundity and body length (Fig. 8a). Previous studies have also observed a similar relationship in the Sea of Japan (Okochi et al., 2016). Relative batch fecundity, which accounts for this body length relationship, is considered to be an important factor for estimating the maternal effect in individuals of different body sizes. Generally, energy allocation for reproduction in young adults is lower than in older adults, because more energy is allocated to growth in young adults (Roff, 1983). In our results, however, the relative batch fecundity we observed was significantly lower than what has been reported from much younger fish in the Sea of Japan (Okochi et al., 2016) but not significantly different from reported batch fecundity in the western Pacific (Ashida et al., 2015). This is a surprising result, because the younger PBF in the Sea of Japan would be expected to allocate more energy to growth than to reproduction. The fecundity of ABF in the Gulf of Mexico (28.14 eggs/g) is lower but not significantly different to fish sampled in the Mediterranean Sea (45.56 eggs/g) (Knapp et al., 2014). Although it is difficult to draw any conclusions from comparisons between ABF and PBF, we found that relative batch fecundity of ABF in the Mediterranean Sea was much lower than that of PBF in the Sea of Japan and was similar to that of PBF in the KOTA and in the western Pacific Ocean. In fish, egg quality, which includes factors such as batch fecundity and egg size, is generally affected by the nutritional condition of the female (Ma et al., 1998; Lambert and Dutil, 2000) and water temperature (Ouellet et al., 2001; Yoneda and Wright, 2005). Furthermore, egg quality affects larval survival (Brooks et al., 1997). Further investigations are required to examine the relationship between egg quality and female condition in tunas, possibly via study of lipid and fatty acid contents (Fuiman and Perez, 2015).

4.5 Environmental factors

Based on seasonal changes in the relative frequency of the spawning phase, the spawning season in our study area appears to occur between late May and June, possibly continuing into August. However, because no sampling occurred before May, the start of spawning is unclear. This spawning season overlaps with that of other PBF spawning grounds. In the Nansei area, the spawning season is estimated to occur between late April and early July (Chen et al., 2006; Ashida et al., 2015). In the Sea of Japan, it occurs from mid-June to August (Okochi et al., 2016). From these reports, it appears that the spawning season in the present study area is similarly timed to those on other spawning grounds, but occurs over a longer duration.

Spawning-capable and spawning phase ovaries were collected at 21.0–25.5 °C in the present study. Ashida et al. (2015) reported that adult PBF often spawn at about 26 °C in the western North Pacific. Similarly, PBF larvae distribute from 24 to 29 °C (Ohshimo et al., 2017). As already mentioned, the SST observed in the present study were lower than those in other spawning areas. PBF larvae experience high growth rates at temperatures around 27 °C (T. Ishihara, pers. comm.) and rapid initial growth is critical for survival in this species (Watai et al., 2017). Unfortunately, due to an insufficient sample size,

we were unable to identify any fine-scale features of the spawning grounds in the KOTA.

There are several similarities between PBF-spawning behavior we describe in this study and the spawning behavior of ABF. For example, sea surface temperatures in ABF spawning grounds in the Mediterranean and slope area are lower than in the Gulf of Mexico (Karakulak et al., 2004; Stokesbury et al., 2004; Richardson et al., 2016; Reglero et al., 2018). Also, the preferred sea surface temperatures for ABF larvae in the Mediterranean (Alemany et al., 2010) are lower than those in the Gulf of Mexico (Muhling et al., 2011), and spawning adults in the Mediterranean are also smaller than those in the Gulf of Mexico. This raises the possibility that both PBF and ABF may implement different spawning strategies on each spawning ground, and that eggs and larvae may possess different chemical components for tolerating exposure to low temperatures.

Spawning migrations in fishes are optimized for the survival of the eggs and larvae (e.g., Slotte and Fisken, 2000; Allain et al., 2007). Unfortunately, although archival tagging is the best tool for evaluating spawning migrations, tagging efforts for PBF around Japan have only examined juveniles (Kitagawa et al., 2002; Fujioka et al., 2018a, 2018b). Archival tagging of adult PBF is necessary to provide data on spawning migrations. In the present study, spawning females predominantly ranged between 160 and 180 cm FL, which corresponds to age 6–8. This was a marked contrast to previous reports of spawning females identified in the Sea of Japan (age 3–6) and Nansei area (age >10). These data indicate that adult PBF segregate by size or age and may reflect the spawning or survival strategy of this species. Although PBF larvae have been collected in the Kuroshio region (Ohshimo et al., 2017), the water temperature in the KOTA may be too low for PBF spawning and larval survival. Because larval sampling surveys were not conducted in the KOTA, we are unable to evaluate the survival of PBF larvae in this region. The sea surface temperatures observed in the present study were too low for optimal larval growth. In addition, fewer PBF larvae have been found in the Kuroshio area than in the Nansei area and the Sea of Japan (Ohshimo et al., 2017). Kitagawa et al. (2010) conducted particle tracking experiments of this species, and eggs or larvae spawned in the Nansei area were transported to the northeastern area by the Kuroshio. Our histological analysis of the spawning activity of adult PBF could benefit from similar particle tracking experiments in the future to determine the spawning area of this species.

4.6 Ecosystem impacts

The catch of large apex predators in the subtropical North Pacific is declining, indicating a shift in the ecosystem toward more mid-trophic level, fast-growing, and short-lived species (Polovina et al., 2009). Pacific bluefin tuna and other tuna species prey on small fish, squid, and crustaceans (Kitagawa et al., 2002; Ohshimo et al., 2018a). Cox et al. (2002) developed a multispecies model using the Ecopath with Ecosim software to evaluate the relative contributions of fishing and trophic impacts on tuna dynamics in the central Pacific, and they concluded that a decline in predation mortality owing to the depletion of large predators was greatest

for small yellowfin tuna and could possibly account for apparent increases in their biomass (Cox et al., 2002).

In addition, habitats of tuna and tuna-like species could be shifted by climate change (Reglero et al., 2014). However, there is a dearth of efforts to model the effects of climate change on interspecies relationship, recruitment fluctuations, and habitat shifts. EBFM is essential for maintaining ecosystem, species, and genetic diversity (Zhou et al., 2010). Our study describes a new spawning ground for PBF and indicates that spawning habits of this species are more complicated than previously thought (Ashida et al., 2015; Okochi et al., 2016; Shimose et al., 2018). The impact of climate change on these spawning grounds is an important unknown that should be addressed when implementing ecosystem-based management. Because the population dynamics of this species depends on recruitment strength, it is necessary to evaluate the spawning–recruitment relationship in order to construct a rational management scheme. Our findings may indicate the presence of another spawning ground for smaller adults. A better understanding of the relationship between recruitment and spawning stock biomass could inform predictions of climate change impacts in the future.

5 Conclusions

Our results indicate the existence of a new spawning ground for PBF in the KOTA. However, water temperature might be too low for larval survival in this area. Due to differences in the sampling period and the timing of sampling efforts among years, we were unable to examine the scale and consistency of spawning in this area. Continued monitoring of maturity and spawning condition, along with a larval survey, would help clarify many of the unanswered questions from this study. The predominant age group in the study area ranged from 6 to 8 years old, and these ages differ from those reported in the Sea of Japan (mainly ages 3–6) and the Nansei area (mainly over 10 years old). Therefore, adult PBF would appear to segregate by age or size. The spawning season in our study area was from May to August, and the highest proportion of spawning-capable individuals was observed in early June. In addition, the fraction of regressed phase individuals in the present study was higher than that in the two other spawning grounds (Ashida et al., 2015; Okochi et al., 2016). Compared to the western North Pacific, we observed lower sea surface temperatures in the study area during the spawning season. Relative batch fecundity in the KOTA was substantially lower than in the Sea of Japan, indicating that PBF in each area employ a spawning strategy distinct from those in other spawning grounds. Whereas the Nansei area features the optimum temperature for larval growth, the Sea of Japan and the KOTA have slightly lower temperatures. Concentrations of nutrients such as nitrate are also much higher in the Sea of Japan than in the western North Pacific (Kodama et al., 2011, 2015), although the KOTA is also a highly productive region. Reglero et al. (2018) showed that the reproductive schedule of ABF varies between spawning sites, suggesting plasticity to local environmental conditions. As such, matching the release of offspring to ocean productivity and prey availability peaks might be an important driver for ABF spawning phenology. In the Nansei area, although the sea water temperature is

optimum for PBF spawning and hatching, the productivity in this area is low. Meanwhile in the Sea of Japan and KOTA, the sea temperatures are slightly low but productivity is high. These findings indicate that PBF could gain resilience against climate change by changing spawning behavior in each area. The segregation of spawning adults by age or size and the use of different spawning strategies in various disparate spawning grounds may function to disperse the risks posed by environmental perturbations and reduce the probability of stock collapse.

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