



Spatial and temporal differences in the reproductive traits of skipjack tuna *Katsuwonus pelamis* between the subtropical and temperate western Pacific Ocean

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ABSTRACT

The reproductive traits of skipjack tuna (*Katsuwonus pelamis*) in the subtropical (10–25°N) and temperate (25–42°N) western Pacific Ocean were investigated to examine the geographical differences in spawning potential. In total, 91% of spawning capable female specimens appeared in waters with sea surface temperatures (SSTs) of over 24 °C. The length of the spawning season for females varied among sampling areas according to the seasonal fluctuations in SSTs, with shorter spawning seasons in the high latitudinal areas (north of 25°N). Mature males were observed during almost all sampling months in all sampling areas. The total spawning fraction during the spawning season in each sampling area ranged from 0.23 to 0.46. Seasonal fluctuations in the spawning fraction were observed in the temperate western Pacific Ocean. The mean relative batch fecundity differed significantly between sampling areas ($p < 0.05$) and ranged from 67.2 to 106.1 oocytes per gram of body less the ovary weight. The estimated mean relative batch fecundity tended to be lower in the temperate western Pacific Ocean than in the subtropical western Pacific Ocean and the tropical western and central Pacific Ocean. The reproductive traits observed in the present study indicated that the spawning grounds of skipjack tuna in the western Pacific Ocean were expanded in the temperate western Pacific Ocean in the boreal summer, and that the spawning potential per individual in these areas was inferior to those in the subtropical western Pacific Ocean and tropical western and central Pacific Ocean.

1. Introduction

Skipjack tuna (SKJ, *Katsuwonus pelamis*) are widely distributed from 44°N to 37°S in the western and central Pacific Ocean (WCPO, Matsumoto et al., 1984; Wild and Hampton, 1994). In 2015, the annual catch of SKJ in the WCPO was reportedly 1.78 million tons, with the main fishing areas located in tropical waters (WCPFC, 2017). SKJ utilize the temperate western Pacific Ocean (WPO), including the waters around Japan, as a seasonal habitat, and in these areas SKJ serve as an important target species of coastal and offshore fisheries (Matsumoto et al., 1984). The main fishing season of SKJ fisheries varies among these waters due to the seasonal migration of the species (Yasui and Mori, 1985; Tashiro and Uchida, 1989). For example, large-scale fishing operations in the Kuroshio-Oyashio transition area, the northernmost fishing area in the temperate WPO, mainly occur between June and October and for a shorter period than other fishing areas in the temperate WPO, such as around the Nansei, Izu, and Ogasawara Islands (Masuda and Nihira, 1999; Yamashita et al., 2018).

Based on the results of larval surveys, SKJ generally spawn in waters

where sea surface temperatures (SST) exceed 24 °C (Ueyanagi, 1969; Matsumoto et al., 1984; Nishikawa et al., 1985; Wild and Hampton, 1994). Although SKJ larvae are observed year-round in the tropical and subtropical WCPO, their horizontal distribution varies among seasons (Ueyanagi, 1969; Nishikawa et al., 1985) and expands to waters around 35°N from the 2nd to the 3rd quarter (April–September) of the year (Nishikawa et al., 1985). The appearance of SKJ larvae tends to be especially concentrated in the Nansei Islands in the 2nd quarter (Nishikawa et al., 1985). These findings suggest that SKJ primarily spawn in the subtropical and temperate WPO.

SKJ are assumed to be multiple spawning fish with an indeterminate fecundity (Hunter et al., 1986; Ashida et al., 2008; Grande et al., 2012). The accurate knowledge of the reproductive biology of the species requires elucidation of key reproductive parameters such as the sex ratio, spawning season, spawning ground, and size-at-maturity. Furthermore, it is essential to determine the batch fecundity (BF) and spawning fraction (SF) of spawning fish with indeterminate fecundities to assess their reproductive potential. The reproductive traits of SKJ have been examined in the tropical WCPO, and spawning females and mature fish

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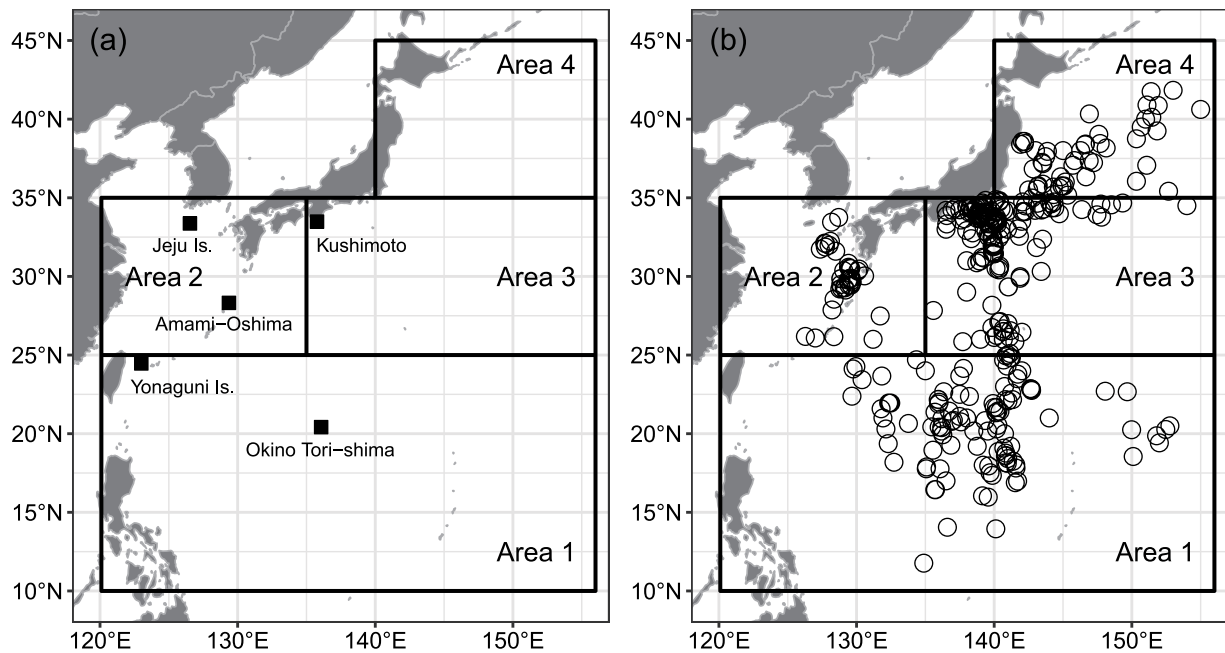


Fig. 1. Area definitions (a) and sampling locations (b) of the skipjack tuna (*Katsuwonus pelamis*) used in the analyses. Area 1, Kuroshio-Oyashio transition area; Area 2, Nansei Islands area; Area 3, Izu and Ogasawara Islands area; and Area 4, subtropical western Pacific Ocean. Solid squares show each location described in this paper.

have been observed year-round in these regions (Ashida et al., 2007, 2008, 2010, 2017). However, knowledge regarding the reproductive traits of this species in the subtropical and temperate WPO is limited (Asano and Tanaka, 1971; Naganuma, 1979; Ashida et al., 2013; Ashida and Horie, 2015). Based on histological assessments of ovaries and seasonal changes in the gonad index (GI), Asano and Tanaka (1971) reported that the spawning of SKJ occurred in summer and winter in the subtropical WPO. However, this finding was inconsistent with the temporal distribution of SKJ larvae (Ueyanagi, 1969; Nishikawa et al., 1985). Although spawning females were found in waters off Kushimoto (33°29'N, 135°46'E), Yonaguni Island (24°28'N, 123°00'E), and Okino Tori-shima (20°25'N, 136°04') in Japan (Fig. 1), the duration of the spawning season in each sampling area remains unknown (Ashida et al., 2013). Ashida and Horie (2015) estimated the spawning season, SF, and BF of SKJ caught around Amami-Oshima (28°19'N, 129°22'E). Their results were consistent with the larval survey and gonad examination of SKJ in the subtropical and temperate western Pacific Ocean, which indicates that SKJ spawn in the subtropical and temperate WPO (Ueyanagi, 1969; Nishikawa et al., 1985; Ashida et al., 2013; Ashida and Horie, 2015). However, the reproductive traits of SKJ have not been fully clarified.

Grande et al. (2016) suggested that SKJ is an income breeder. This breeding strategy has the advantage of enabling the fine-tuning of the reproductive output relative to the existing environmental conditions; i.e., pertaining to both the maternal condition and potential survival of the offspring (MacBride et al., 2015). Geographical differences in the reproductive traits of SKJ probably occur in the WCPO because the spawning of SKJ depends on oceanographic conditions. Geographical differences in reproductive traits, such as the spawning season, BF, and fork length (FL) at 50% maturity (FL₅₀), have been observed in SKJ, black skipjack tuna (*Euthynnus lineatus*), yellowfin tuna (*Thunnus albacares*), and albacore (*Thunnus alalunga*), which spawn for a long time over a broad spawning area (Schaefer, 1987, 1998; Itano, 2000; Farley et al., 2013, 2014; Schaefer and Fuller, 2019). For example, the FL₅₀ of SKJ in the eastern Pacific Ocean (EPO) tends to be longer in higher latitudinal waters (Schaefer and Fuller, 2019), the spawning season of yellowfin tuna in Hawaiian waters is shorter than in the tropical WCPO (Itano, 2000), and the relationship between FL and BF in yellowfin tuna

and black skipjack tuna differ significantly among sampling areas in the EPO (Schaefer, 1987, 1998).

When examining the reproductive traits of SKJ in the subtropical and temperate WPO, it is essential to understand the geographical differences in the reproductive traits and clarify the reproductive strategy of SKJ in the WCPO. Therefore, the present study aimed to determine the geographical differences in the spawning potential of SKJ in the WPO by assessing their reproductive traits and comparing them among study areas. The objectives were to examine and compare the relative condition factor (Kn), sex ratio, length at maturity, spawning season, SF, and BF of SKJ caught in the subtropical and temperate WPO.

2. Materials and methods

2.1. Sampling and data collection

A total of 7194 SKJ were collected from the subtropical and temperate WPO between 2009 and 2016 (Fig. 1; Table 1). The sampled specimens were caught by pole and line ($n = 6394$), purse seine ($n = 433$), and trolling ($n = 367$) fisheries. The capture date (but not the time of capture) and sampling location were recorded for all specimens. Sampling areas were divided into four areas (i.e., Areas 1, 2, 3, and 4) based on the seasonal variation of the fishing locations in the Japanese SKJ fishery, bathymetric and oceanographic features, and the larval distribution of SKJ. Areas 1, 2, 3, and 4 corresponded to the Kuroshio-Oyashio transition area, Nansei Islands, Izu and Ogasawara Islands, and the subtropical WPO, respectively. The fork length (FL, cm) and body weight (BW, g) of the sampled specimens were measured. Gonads were removed and weighed to the nearest 1 g (GW, g). Tissue samples were obtained from the middle of the gonad and fixed in 10% neutral buffered formalin. The gonad index (GI) was calculated as:

$$GI = (GW/FL^3) \times 10^4.$$

Kn, an index of nutritional condition, was calculated as follows:

$$Kn = BW/a \times FL^b$$

where the parameters a and b were estimated using a non-linear regression analysis. Kn was estimated using FL and BW data from 7169

Table 1Annual variation in skipjack tuna (*Katsuwonus pelamis*) sampled by region in the subtropical and temperate western Pacific Ocean between 2009 and 2016.

Month	Area 1			Area 2			Area 3			Area 4		
	n	FL (cm)	Range	n	FL (cm)	Range	n	FL (cm)	Range	n	FL (cm)	Range
Jan	nd	nd	nd	59	43.9 ± 1.3	41.5–46.5	37	58.8 ± 9.2	40.2–68.6	220	49.3 ± 10.5	36.2–77.5
Feb	nd	nd	nd	102	45.8 ± 6.1	37.9–60.0	161	54.9 ± 8.8	41.1–71.4	403	54.9 ± 10.5	35.0–78.8
Mar	nd	nd	nd	80	43.7 ± 1.4	39.9–46.3	185	50.6 ± 7.6	40.9–74.5	189	53.2 ± 11.9	38.0–77.5
Apr	nd	nd	nd	60	44.7 ± 2.2	39.9–49.0	215	46.4 ± 5.2	39.5–69.6	181	48.5 ± 7.2	35.6–68.8
May	55	45.9 ± 2.7	41.5–51.3	119	44.1 ± 1.1	41.2–47.7	687	47.1 ± 4.3	39.9–71.7	11	62.5 ± 3.5	55.6–68.2
Jun	169	49.2 ± 3.7	40.8–63.2	140	45.9 ± 3.3	42.0–56.2	749	46.4 ± 4.0	31.5–68.0	nd	nd	nd
Jul	159	48.4 ± 4.7	32.5–62.0	190	50.5 ± 3.7	41.3–59.0	456	46.5 ± 4.3	37.0–64.5	nd	nd	nd
Aug	119	50.3 ± 2.5	45.2–55.2	165	50.2 ± 5.9	36.0–60.2	290	46.9 ± 5.0	33.1–69.2	nd	nd	nd
Sep	130	53.2 ± 2.3	44.7–61.5	204	50.7 ± 5.4	43.8–64.0	264	45.3 ± 6.1	30.6–61.3	117	53.3 ± 9.1	35.8–68.2
Oct	204	49.5 ± 6.2	35.0–56.7	119	55.0 ± 10.5	39.8–71.0	173	49.4 ± 5.8	32.1–65.5	54	65.1 ± 8.5	48.2–76.2
Nov	25	53.3 ± 0.8	51.8–54.8	121	45.3 ± 5.9	37.4–60.5	177	47.6 ± 5.5	39.3–62.8	346	54.9 ± 11.1	34.2–75.0
Dec	nd	nd	nd	59	58.2 ± 12.0	39.7–73.3	nd	nd	nd	nd	nd	nd
Total	861	49.7 ± 4.6	32.5–63.2	1418	48.5 ± 6.9	36.0–73.3	3394	47.5 ± 5.7	31.5–74.5	1521	53.4 ± 10.9	35.0–78.8

Area 1, Kuroshio-Oyashio transition area; Area 2, Nansei Islands area; Area 3, Izu and Ogasawara Islands area; Area 4, subtropical western Pacific Ocean; FL, fork length (mean ± standard deviation); n, number of specimens; nd, no data.

specimens.

2.2. Histological procedures and observations

Histological sections were made for all collected gonad samples ($n = 7194$). Testes were cut according to previously defined methods (Grier and Taylor, 1998; Ashida et al., 2010) to assess the morphological features of the germinal epithelium. Following fixation in formalin, ovary and testis samples were dehydrated in a series of ethanol concentrations, embedded in Paraplast (Sigma-Aldrich Inc. USA), sectioned at a thickness of 6–8 μm , and stained with Mayer's hematoxylin and 1% eosin (HE stains). Sexes were determined based on the observations of histological sections.

The oocyte developmental process was divided into seven stages (i.e., perinucleolus, cortical alveolar, primary yolked, secondary yolked, tertiary yolked, germinal vesicle migration, and hydrated oocytes) following Hunter et al. (1986), Grande et al. (2012), and Ashida et al. (2017) (Fig. S1). The degeneration stage in postovulatory follicles (POF) was also classified into three stages (i.e., early, mid, and late stage), following Hunter et al. (1986) and Ashida et al. (2008). Atretic oocytes were classified as α and β atretic oocytes, following Hunter et al. (1986) (Fig. S1). The relative intensity of atresia (IA; Kjesbu, 2016) was calculated under the light microscope (50 \times magnification) as the percentage of α -atretic oocytes in relation to all vitellogenic oocytes.

Male germ cells were classified into four developmental stages (i.e., spermatogonia, spermatocytes, spermatids, and spermatozoa) following Schaefer (2001), Abascal et al. (2004), and Ashida et al. (2010). Morphological features of the germinal epithelium in the lobules were classified as continuous (CGE) or discontinuous (DGE) following Grier and Taylor (1998) and Brown-Peterson et al. (2002, 2011) (Fig. S2).

Based on the histological observations, the ovarian maturity phase was classified into the immature-regenerating, developing, spawning capable, and regressing phases, following Ashida et al. (2017) (Fig. S1; Table 2). The testicular maturity phase was also classified into four phases: immature, developing, spawning capable, and regressing-regenerating, following modified protocols from Grier and Taylor (1998), Brown-Peterson et al. (2002, 2011), and Ashida et al. (2010) (Fig. S2; Table 3).

Female specimens containing vitellogenic oocytes in the ovary (i.e., developing, spawning capable, and regressing phases) were defined as sexually mature. Male specimens exhibiting mid maturation, late maturation, and regressing-regenerating phases were defined as sexually mature, based on the classification of Grier and Taylor (1998); Brown-Peterson et al. (2002, 2011), and Ashida et al. (2010).

2.3. Sex ratio

The sex ratio (proportion of females) in each FL class (i.e., classes of 5 cm intervals) was calculated for each sampling area. A binomial test (Zar, 1984) was used to examine whether the sex ratio in each FL class and sampling area deviated from an expected 1:1 per FL class or not ($p = 0.05$).

2.4. Length at maturity

A generalized linear mixed-effects model (GLMM) analysis with binomial distribution (logit function) was conducted to examine the relationship between FL and the proportion of mature fish (p). Area was included as a random effect in the model to account for inter-Area differences. In this analysis, the Areas were classified as either subtropical (i.e., Area 4) or temperate WPO (i.e., Areas 1, 2, and 3). The model was:

$$\ln\left(\frac{p}{1-p}\right) = \alpha + \beta \text{FL} + \text{Area}.$$

The relationship between FL and the proportion of mature females was analyzed using specimens caught in the main spawning season (i.e., Area 1: July–August, Area 2: June–October, Area 3: June–September, Area 4: all sampling months). The relationship between FL and the proportion of mature males was analyzed using specimens caught in the months when the spawning capable phase was observed in each sampling area (i.e., Area 1: June–October, Areas 2 and 4: all sampling months, and Area 3: February–November). This analysis was conducted in R (ver. 3.3.3, R core Team, 2015) using the lme4 package.

2.5. Batch fecundity and spawning fraction

BF was estimated using the gravimetric method (Hunter et al., 1985; Murua et al., 2003) using specimens ($n = 203$) with germinal vesicle migration or hydrated oocytes. BF was estimated according to the procedure reported by Hunter et al. (1985). In tunas, the oocyte diameter distribution in specimens with germinal vesicle migration or hydrated oocytes generally forms two cohorts as the most advanced oocytes grow and ovulate (Nikaido et al., 1991; Schaefer, 1998; Ashida et al., 2008; Grande et al., 2012).

Three subsamples (~ 0.05 g) were removed from the ovaries. The number of oocytes in the germinal vesicle migration and hydrated phase were counted in each subsample using a stereomicroscope camera system (Moticam 2300, Shimadzu Rika Co., Tokyo, Japan). Then the resulting counts were raised to the total weight of the ovaries

Table 2

Histological characteristics of the ovarian maturity phase, and gonad index of female skipjack tuna (*Katsuwonus pelamis*) caught in the subtropical and temperate western Pacific Ocean.

Maturity phase	n	MAGO	POF	IA (%)	Mean GI \pm SD (Range)
Immature-Regenerating	2783	Pn or Ca	Absent	Absent	0.94 \pm 0.53 ^c (0.03–5.84)
Developing	413	Py or Sy or Ty	Absent	IA < 50	3.31 \pm 1.47 ^b (1.08–10.90)
Spawning capable	203	Gvm or Hy	May be present	IA < 50	5.13 \pm 2.38 ^a (1.07–15.50)
Spawning capable	283	Py or Sy or Ty	Present	IA < 50	
Regressing	37	Py or Sy	Absent	IA \geq 50	2.69 \pm 0.99 ^b (1.41–6.17)
Regressing	19	Pn or Ca	Absent	IA = 100	

A photograph of a histological section of a mature ovary is shown in Fig. S1. Different superscript letters indicate significant differences in each maturity phase (Steel-Dwass test, $p < 0.01$). Ca, cortical alveolar; GI, gonad index (mean \pm SD); Gvm, germinal vesicle migration; Hy, hydrated oocytes; IA, relative intensity of atresia; MAGO, most advanced group of oocytes; n, number of specimens; POF, postovulatory follicles; Pn, perinucleolus oocytes; Py, primary yolked oocytes; Sy, secondary yolked oocytes; Ty, tertiary yolked oocytes.

to obtain the BF. The mean value of the three subsamples was taken as the BF for the specimens. A generalized linear model analysis (log-link function and gamma distribution) was conducted to examine the relationship between FL and BF based on Yoneda and Wright (2004). The relative BF (RBF) was calculated as follows:

$$\text{RBF} = \text{BF}/(\text{BW} - \text{GW}).$$

The POF of SKJ can be observed in the ovary for 1 day or less after ovulation (Hunter et al., 1986; Ashida et al., 2017; Schaefer and Fuller, 2019). The SF was estimated using the number of specimens with POF in the mature females (POF method; Hunter and Macewicz, 1985). In SKJ, the SF tends to be underestimated depending on when the specimens were caught (Ashida et al., 2008, 2017). Capture times of the specimens were unknown in this study, therefore, revised SFs (Rev-SFs) were estimated following Ashida et al. (2017). Rev-SF was described as the ratio of spawning capable phase to mature fish (Ashida et al., 2017). Spawning intervals were estimated as the inverse of SFs and Rev-SFs (Hunter and Macewicz, 1985).

3. Results

3.1. Sex ratio

The total sex ratio in each sampling area was 0.50–0.53 and was female-biased in Areas 2 and 3 (binomial test, $p < 0.05$, Table 4). The sex ratio in the FL classes of Areas 1, 2, and 3 ranged from 0.38 to 1.00 and no significant differences were detected (binomial test, $p > 0.05$, Table 4), except in two FL classes (Areas 2 and 3, Table 4). No significant differences were observed in all FL classes in Area 1 (binomial test, $p > 0.05$, Table 4).

3.2. Relative condition factors

The values of a and b (\pm standard errors) were estimated from the equation for Kn using the biometric data for 7169 sampled fish and were $5.927 \times 10^{-6} \pm 1.346 \times 10^{-7}$ (t -value = 43.87, $p < 0.01$) and

$3.321 \pm 5.580 \times 10^{-3}$ (t -value = 593.4, $p < 0.01$), respectively. The mean Kn values \pm standard deviations (SDs) were 1.02 ± 0.06 , 1.01 ± 0.06 , 0.99 ± 0.07 , and 1.00 ± 0.11 in Areas 1, 2, 3, and 4, respectively. The order of Kn for each sampling area was statistically described as follows:

Area 1 > Area 2 > Area 4 > Area 3 (Steel-Dwass test, $p < 0.01$).

3.3. Gonadal maturity phases

Of the total analyzed gonads ($n = 7194$), the gonadal maturity phase could not be correctly assessed in 548 specimens because of histological abnormalities in the germ cells, e.g., the breakdown of the cytoplasm of oocytes and germinal epithelium. The maturity phase assessment of the total ovarian specimens ($n = 3738$) identified 2783 ovaries as immature-regenerating, 413 as developing, 486 as spawning capable, and 56 as regressing (Table 2). The GI in the spawning capable phase was significantly higher than in the other ovarian maturity phases (Steel-Dwass test, $p < 0.01$, Table 2). The percentage of spawning-capable females was highest in the IA = 0 class (Table 5), but rapidly decreased as the IA increased, and was very low when IA > 10% (Table 5).

The maturity phase assessment of 2908 testicular samples revealed that 341 males were immature, 933 were in the developing, 1415 in the spawning capable, and 219 in the regressing-regenerating phases (Table 3). The GI in the spawning capable phase was significantly higher than in the other maturity phases (Steel-Dwass test, $p < 0.01$, Table 3).

3.4. Relationships between SSTs and the mature and spawning capable phase

Mature females (i.e., those in the developing, spawning capable, and regressing phases) and females in the spawning capable phase appeared in the SST ranges of 19.5–31.0 °C and 20.1–31.0 °C, with 90.1% and

Table 3

Histological characteristics of the testicular maturity phase, and gonad index of male skipjack tuna (*Katsuwonus pelamis*) caught in the subtropical and temperate western Pacific Ocean.

Maturity phase	n	Germ cell	GE state	Mean GI \pm SD (Range)
Immature	341	SG	CGE	0.15 \pm 0.19 ^d (0.02–2.23)
Developing	933	SG, SC, ST. SP may be present.	CGE	0.90 \pm 1.95 ^b (0.02–15.70)
Spawning capable	885	SG, SC, ST, SP	CGE and DGE	2.22 \pm 1.95 ^a (0.04–11.80)
Spawning capable	530	SG, SC, ST, SP	DGE	
Regressing-regenerating	219	SG, RSP	CGE or DGE	0.29 \pm 0.37 ^c (0.02–3.16)

A photograph of a histological section of a mature testis is shown in Fig. S2. Different superscript letters indicate significant differences in each maturity phase (Steel-Dwass test, $p < 0.01$). CGE, continuous germinal epithelium; DGE, discontinuous germinal epithelium; GE, germinal epithelium; GI, gonad index (mean \pm SD); n, number of specimens; RSP, residual sperm; SC, spermatocyte; SG, spermatogonia; ST, spermatid; SP, sperm.

Table 4Sex ratio of skipjack tuna (*Katsuwonus pelamis*) in each fork length (FL) interval (5 cm) from four areas in subtropical and temperate western Pacific Ocean.

FL class (cm)	Area 1			Area 2			Area 3			Area 4			Total		
	M	F	F ratio	M	F	F ratio	M	F	F ratio	M	F	F ratio	M	F	F ratio
30.0–34.9	0	2	1.00	0	0	nd	16	20	0.56	0	1	1.00	16	23	0.59
35.0–39.9	6	12	0.67	20	17	0.46	45	49	0.52	38	45	0.54	109	123	0.53
40.0–44.9	51	64	0.56	245	277	0.53	476	493	0.51	186	197	0.51	958	1031	0.52
45.0–49.9	122	138	0.53	198	223	0.53	724	838	0.54*	111	114	0.51	1155	1313	0.53*
50.0–54.9	186	188	0.50	87	93	0.52	181	203	0.53	85	92	0.52	539	576	0.52
55.0–59.9	39	47	0.55	59	90	0.60*	90	114	0.56	76	86	0.53	264	337	0.56*
60.0–64.9	1	5	0.83	29	22	0.43	39	42	0.52	78	91	0.54*	147	160	0.52
65.0–69.9	0	0	nd	23	23	0.50	24	32	0.57	126	83	0.40	173	138	0.44
70.0–74.9	0	0	nd	6	6	0.50	5	3	0.38	42	46	0.52	53	55	0.51
75.0–79.9	0	0	nd	0	0	nd	0	0	nd	15	9	0.38	15	9	0.38
Total	405	456	0.53	667	751	0.53*	1600	1794	0.53*	757	764	0.50	3429	3765	0.52*

Area 1, Kuroshio-Oyashio transition area; Area 2, Nansei Islands area; Area 3, Izu and Ogasawara Islands area; Area 4, subtropical western Pacific Ocean; Asterisks indicate significant differences ($p < 0.05$). F, number of females; F ratio, proportion female; M, number of males; nd, no data.

Table 5

Relationship between the relative intensity of atresia (IA) and appearance rate of spawning capable skipjack tuna (*Katsuwonus pelamis*) caught in the subtropical and temperate western Pacific Ocean.

IA class (%)	n	Number of spawning capable fish	Frequency (%)
IA = 0	695	445	64.0
0 < IA < 10	108	36	33.3
10 ≤ IA < 20	34	2	5.9
20 ≤ IA < 30	26	2	7.7
30 ≤ IA < 40	16	0	0.0
40 ≤ IA < 50	19	0	0.0
50 ≤ IA	57	1	1.8

n, Number of mature fish.

91.5% of them appearing in areas with SSTs $> 24^{\circ}\text{C}$, respectively (Fig. 2). Mature males (i.e., those in the spawning capable and regressing-regenerating phases) and males in the spawning capable phase appeared in SST ranges of $18.6\text{--}31.0^{\circ}\text{C}$ and $18.6\text{--}31.0^{\circ}\text{C}$, with 74.1% and 77.3% of them appearing in areas with SSTs $> 24^{\circ}\text{C}$, respectively (Fig. 2).

3.5. Spawning season in each sampling area

The monthly changes in the GI and ovarian maturity phases were

determined using the aggregated data for all sampling years. In Area 1 (Kuroshio-Oyashio transition area), the monthly mean SSTs tended to rise in May, peak in August (23.4°C), and rapidly decrease between September and November (Fig. 3a). Overall, the monthly mean GI slightly increased in August and tended to decrease from September to November (Figs. 4a and 5a). A low number of females in the spawning capable phase were found between June and August, with most occurring in August (Fig. 4b). Female specimens with ovaries in the developing phase appeared between June and September, and very few in the regressing phase appeared in July and August (Fig. 4b). Males in the spawning capable phase were dominant between June and August, and those in the immature and developing phase were dominant between September and November (Fig. 5b).

In Area 2 (Nansei Islands area), the monthly mean SSTs tended to increase in April and peak in August (29.0°C) (Fig. 3b). Although the monthly mean SSTs in Area 2 remained above 24°C between September and December, they tended to decrease during this period. The monthly mean GI in both females and males increased in June, peaked in August, and decreased between September and December (Figs. 4c and 5c). Female in the spawning capable phase appeared between June and December, except for November, and those in the developing phase appeared between June and December (Fig. 4d). A few females in the regressing phase appeared between June and December, except in July (Fig. 4d). Males in the spawning capable phase appeared year-round

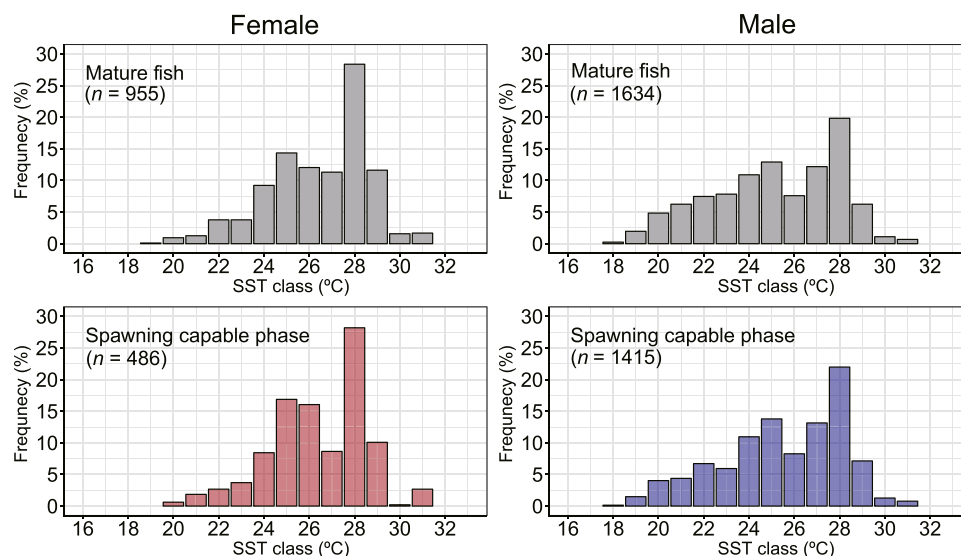


Fig. 2. Distribution of sea surface temperature (SST) in which mature and spawning capable female and male skipjack tuna (*Katsuwonus pelamis*) appeared.

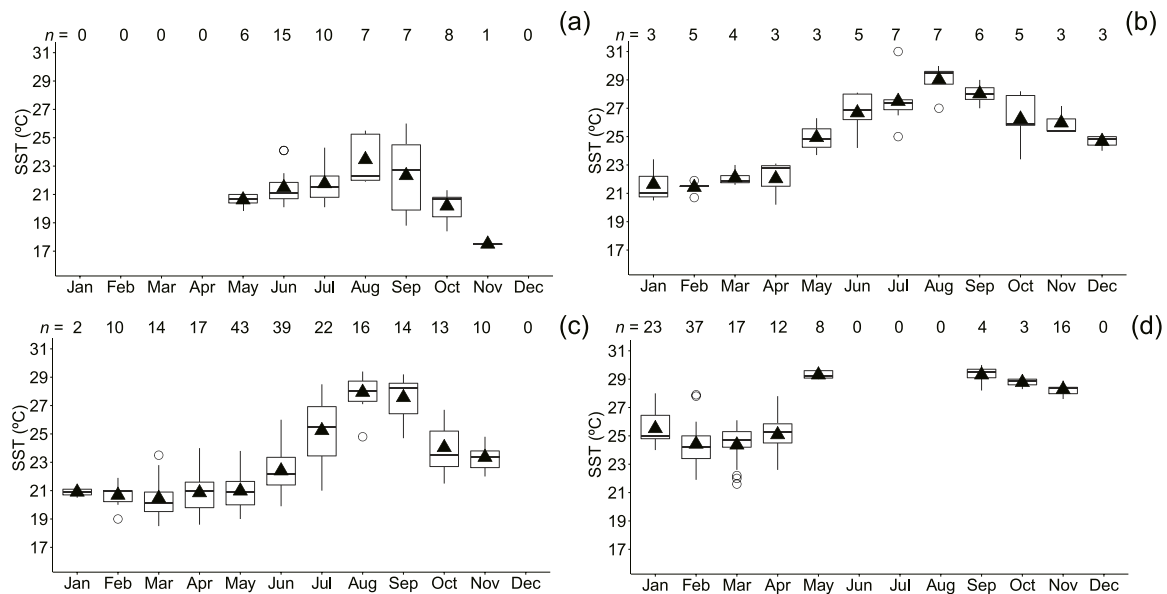


Fig. 3. Seasonal changes in sea surface temperature (SST) data collected during the gonad sampling of skipjack tuna (*Katsuwonus pelamis*) in the subtropical and temperate western and central Pacific Ocean. (a) Area 1 (Kuroshio-Oyashio transition area), (b) Area 2 (Nansei Islands area), (c) Area 3 (Izu and Ogasawara Islands area), (d) Area 4 (subtropical western Pacific Ocean). *n*, number of SST measurements. Triangles indicate mean values.

(Fig. 5d). Males in the regressing-regenerating phase appeared in all sampling months, except August (Fig. 5d).

In Area 3 (Izu and Ogasawara Islands area), the monthly mean SSTs tended to increase in June, peak in August (27.9 °C), and decrease between September and November (Fig. 3c). The monthly mean SSTs in Area 3 were lower than 24 °C in October and November. The monthly mean GI of females and males increased in June, peaked in July, and tended to decrease between August and November (Figs. 4e and 5e). Although females in the developing phase appeared between March and September, spawning capable specimens only appeared in March and between June and September (Fig. 4f). A few specimens in the regressing phase appeared from March to September. Males in the spawning capable phase appeared between February and November and dominated between June and September (Fig. 5f). A few males in the regressing-regenerating phase appeared in Area 3 throughout the year (Fig. 5f).

In Area 4 (subtropical WPO), the monthly mean SSTs varied from 24.3 to 28.7 °C (Fig. 3d), although data were missing in June, July, August, and December. The monthly mean GI of females and males caught in Area 4 did not fluctuate seasonally (Figs. 4g and 5g). Spawning capable females appeared in all sampling months (Fig. 4h). Females in the developing phase appeared in all sampling months, except May (Fig. 4h). Males in the developing and spawning capable phases dominated throughout all sampling months in Area 4 (Fig. 5h). A few males in the regressing-regenerating phase appeared between February and November (Fig. 5h).

3.6. Quarterly and latitudinal distribution of spawning capable phase

In the 1st quarter of the year, spawning capable females appeared from 17°N to 25°N and spawning capable males appeared from 11°N to 29°N (Fig. 6). The distribution of spawning capable fish expanded northwards in the 2nd quarter, with spawning capable male and female fish appearing from ~16°N to ~37°N (Fig. 6). The distribution of spawning capable fish in the 3rd quarter was the widest throughout the year, and spawning capable females and males appeared in 38°N and 40°N, respectively. In the 4th quarter, the distribution area of spawning capable fish tended to decrease, and female and male spawning capable fish appeared from 16°N to 29°N and from 16°N to 38°N, respectively (Fig. 6).

3.7. Length-at-maturity

The minimum size-at-maturity of females was 38.2 and 40.9 cm FL in the subtropical (Area 4) and temperate WPO (combined data of Areas 1, 2, and 3), respectively. The relationships between FL and the proportion of mature females (*p*) in the subtropical and temperate WPO based on the GLMM analysis were described by the following logistic equations (Table 6):

$$\text{Subtropical WPO: } \ln\left(\frac{p}{1-p}\right) = -6.7098 + 0.1207 \times \text{FL}$$

$$\text{Temperate WPO: } \ln\left(\frac{p}{1-p}\right) = -6.0384 + 0.1207 \times \text{FL}$$

The estimated FL_{50s} from the GLMM model were 50.0 and 55.6 cm in the subtropical and temperate WPO, respectively (Fig. 7).

The minimum size-at-maturity of males was 36.2 and 32.4 cm FL in the subtropical and temperate WPO, respectively. The relationships between FL and the proportion of mature males in the subtropical and temperate WPO based on the GLMM analysis were described by the following logistic equations (Table 6):

$$\text{Subtropical WPO: } \ln\left(\frac{p}{1-p}\right) = -3.4903 + 0.0876 \times \text{FL}$$

$$\text{Temperate WPO: } \ln\left(\frac{p}{1-p}\right) = -4.1250 + 0.0876 \times \text{FL}$$

The estimated FL_{50s} from GLMM model were 39.8 and 47.1 cm in the subtropical and temperate WPO, respectively (Fig. 7).

3.8. Batch fecundity and spawning fraction

Of the 203 specimens examined, the most advanced group of oocytes could not be clearly distinguished from the oocyte diameter distribution in 18 specimens. Hence, these specimens were excluded from the BF estimation. The mean BF \pm SD ($\times 1000$ oocytes, *n* = 185) estimated from the grouped data from all areas was 446.7 ± 421.4 (range: 31.7–1872.8), and the relationship between FL and BF was described by the following equation (Fig. 8, Table S1):

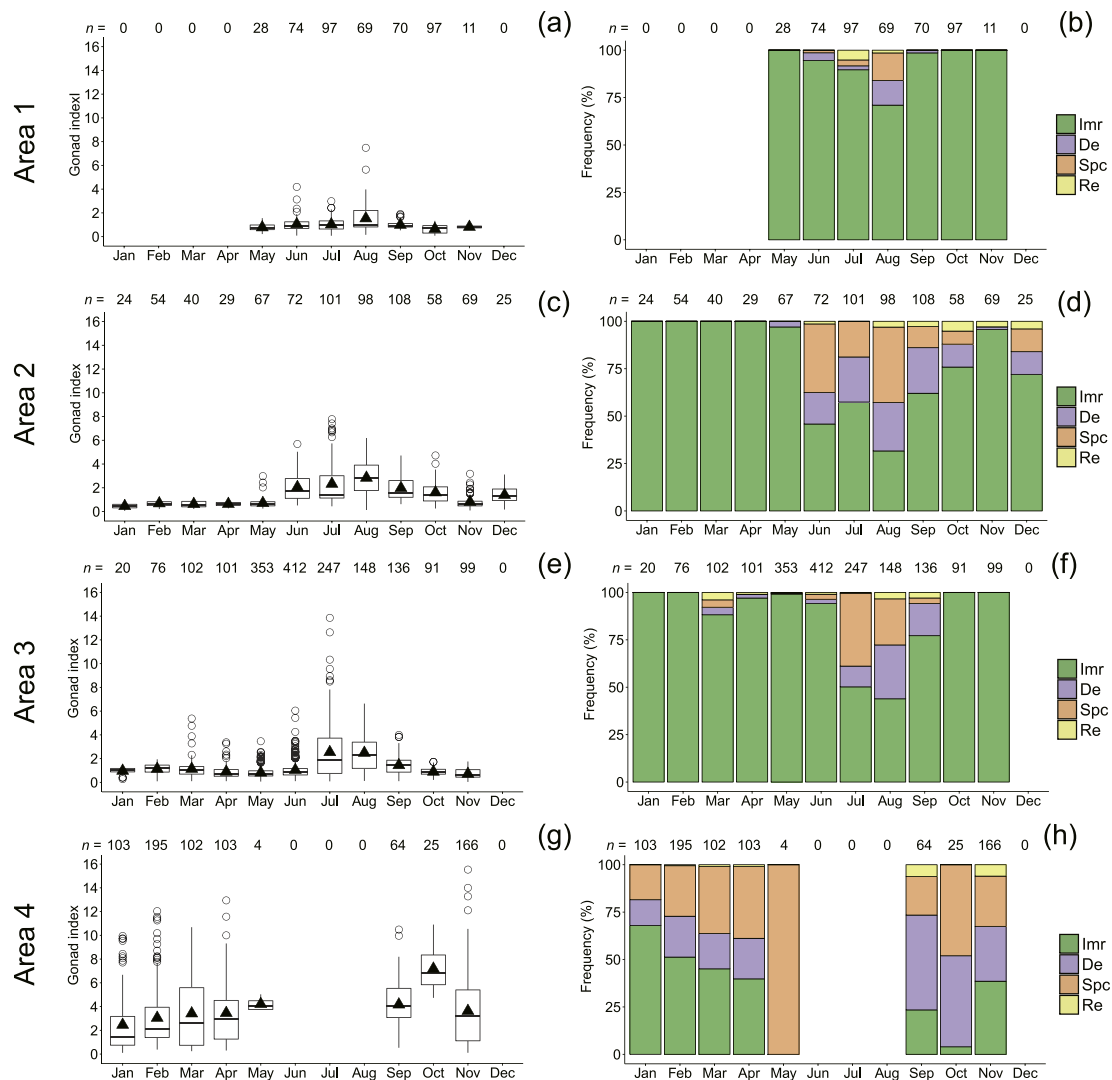


Fig. 4. Seasonal changes in the gonad index and maturity phase of female skipjack tuna (*Katsuwonus pelamis*) collected from four areas in the subtropical and temperate western Pacific Ocean. (a, b) Area 1 (Kuroshio-Oyashio transition area), (c, d) Area 2 (Nansei Islands area), (e, f) Area 3 (Izu and Ogasawara Islands area), and (g, h) Area 4 (subtropical western Pacific Ocean). De, developing phase; Imr, immature-regenerating phase; n, number of specimens; Re, regressing phase; Spc, spawning capable phase. Triangles indicate mean values.

$$BF = 3.8762 \times 10^{-2} \times FL^{3.9945} \quad (FL: p < 0.01).$$

The estimated overall mean RBF \pm SD (oocytes/g) was 97.1 ± 48.5 (range: 5.3–261.4), and no correlation between RBF and FL was detected ($r = 0.20$, Pearson's correlation test, $p < 0.01$). A weak positive correlation was detected between RBF and SST ($r = 0.27$, Pearson's correlation test, $p < 0.01$). The mean RBFs \pm SDs (oocytes/g) were 67.2 ± 36.7 ($n = 8$), 71.2 ± 39.8 ($n = 12$), 88.4 ± 43.1 ($n = 56$), and 106.1 ± 50.6 ($n = 109$) in Areas 1, 2, 3, and 4, respectively, and the RBFs were found to be significantly different among areas (One-way ANOVA, $p < 0.05$, Fig. 8).

The SFs were estimated using the data aggregated for all sampling years. Of the total of 381 individuals with POFs in the ovary, 10 individuals possessed only mid-stage POFs and 371 individuals possessed only late-stage POFs. Of all spawning capable fish with germinal vesicles or hydrated oocytes ($n = 203$, Table 2), 98 specimens possessed late-stage POFs in their ovaries. The estimated total SF (spawning interval) in each area ranged from 0.23 (4.38 days) to 0.46 (2.16 days, Table 7). The estimated total Rev-SF was slightly higher than SF in all areas and significant differences were detected between SF and Rev-SF in Areas 3 and 4 (Chi-square test, $p < 0.05$).

In Area 1, the SF and Rev-SF slightly increased between July and

August (Table 7). Although the SF and Rev-SF in Area 2 varied from 0.44 to 0.67 between June and August, they tended to decrease during the sampling months after September (Table 7). In Area 3, SF and Rev-SF increased in June, peaked in July, and decreased rapidly until September (Table 7). In Area 4, no seasonal fluctuations in SF and Rev-SF were observed (Table 7).

4. Discussion

4.1. Effect of SST variation on the spawning activity of SKJ

The spawning period of SKJ, as revealed by histological analyses, was found to differ among sampling areas, and varied depending on the SSTs of each sampling area (Figs. 3 and 4). Generally, changes in environmental conditions, such as water temperature and day length, and their interactions, affect gametogenesis and the spawning activity of fishes through the brain-pituitary-gonad axis (Wright and Trippel, 2009; Lowerre-Barbieri et al., 2011; Gen, 2016). Spawning female SKJ have been observed in waters with SSTs higher than 23–24 °C in WPO and EPO (Ashida et al., 2013; Ashida and Horie, 2015; Schaefer and Fuller, 2019). In the present study, almost all spawning capable females appeared in SSTs > 24 °C (Fig. 2). This finding is consistent with those

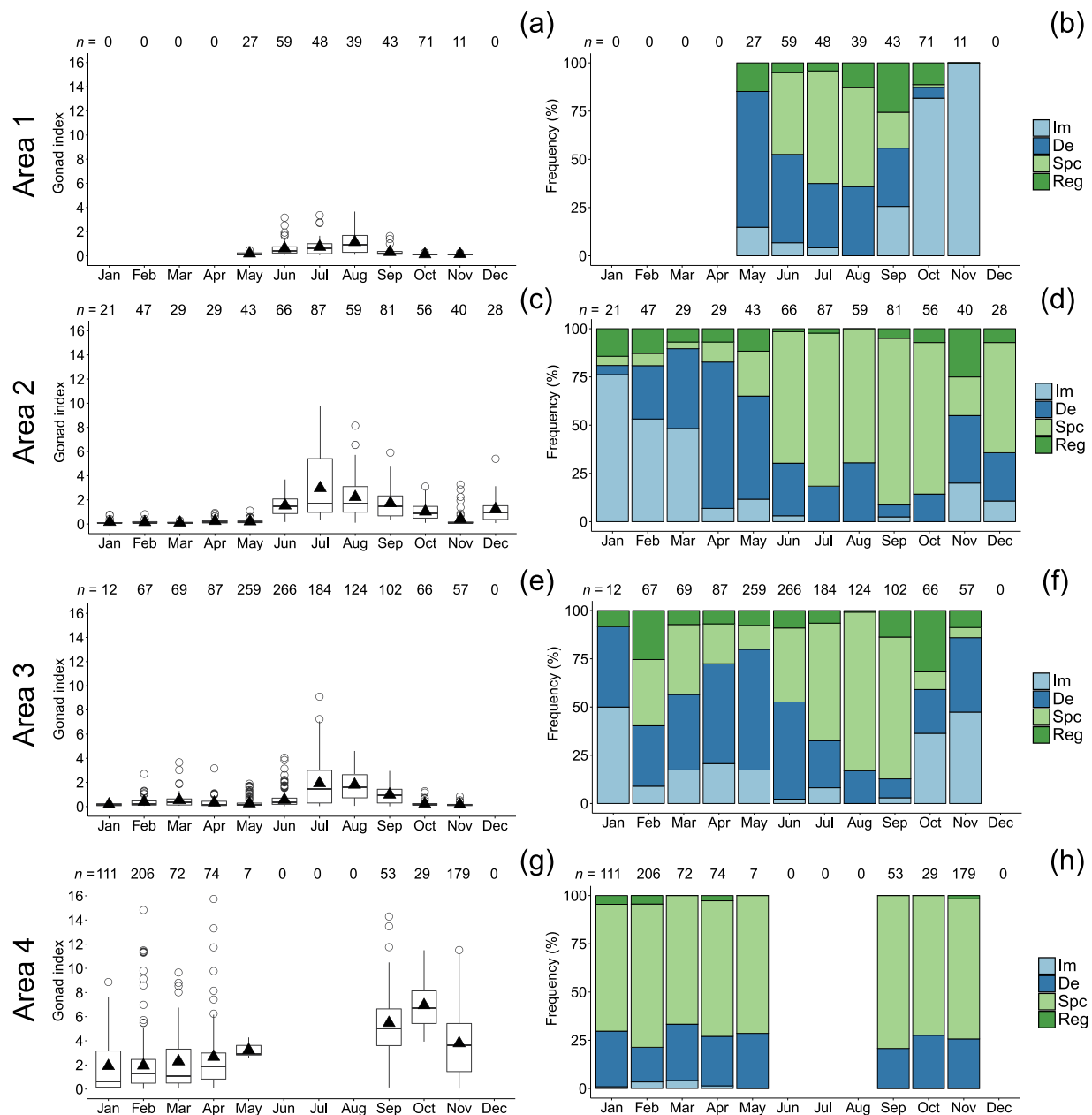


Fig. 5. Seasonal changes in the gonad index and maturity phase of male skipjack tuna (*Katsuwonus pelamis*) collected from four areas in the subtropical and temperate western Pacific Ocean. (a, b) Area 1 (Kuroshio-Oyashio transition area), (c, d) Area 2 (Nansei Islands area), (e, f) Area 3 (Izu and Ogasawara Islands area), and (g, h) Area 4 (subtropical western Pacific Ocean). De, developing phase; Im, immature phase; n, number of specimens; Reg, regressing-regenerating phase; Sp, Spawning capable phase. Triangles indicate mean values.

of previous larval surveys (Ueyanagi, 1969) and gonad examinations (Ashida et al., 2013; Ashida and Horie, 2015; Schaefer and Fuller, 2019).

Spawning activity in temperate WPO (Areas 1, 2, and 3) tended to be interrupted between September and December, even though the SSTs were favorable for spawning (Figs. 3 and 4). In SKJ and yellowfin tuna, this halt in spawning activity was reportedly related to a decrease in SST (Stéqueret and Ramcharun, 1996; Itano, 2000; Stéqueret et al., 2001; Zudaire et al., 2013; Ashida and Horie, 2015). A halt in spawning activity in captive yellowfin tuna was observed when the SSTs decreased below 24 °C or decreased by at least 0.5 °C for a minimum of 1 week (Margulies et al., 2007). These results indicated that the spawning activity of female SKJ in temperate WPO is greatly affected by seasonal decreases in SSTs, even if the SSTs are still favorable for spawning. In summary, the duration of the female SKJ spawning season in temperate

WPO differed according to the seasonal fluctuations in SST in each sampling area.

In tuna species, mature males are observed in the non-spawning season or non-spawning grounds (Abascal et al., 2004; Goldstein et al., 2007; Sawada et al., 2007; Ashida and Horie, 2015). In reared Pacific bluefin tuna *Thunnus orientalis*, sperm production was observed in the testes between January and February, which corresponded to the non-spawning season of females (Sawada et al., 2007). Mature and spawning capable males were observed during the non-spawning season or in the non-spawning area in Areas 1, 2, and 3 (Figs. 4–6). Mature and spawning capable males appeared at lower SSTs than mature females (Fig. 2). These results indicate that the SST condition required for gamete production differs between male and female SKJ.

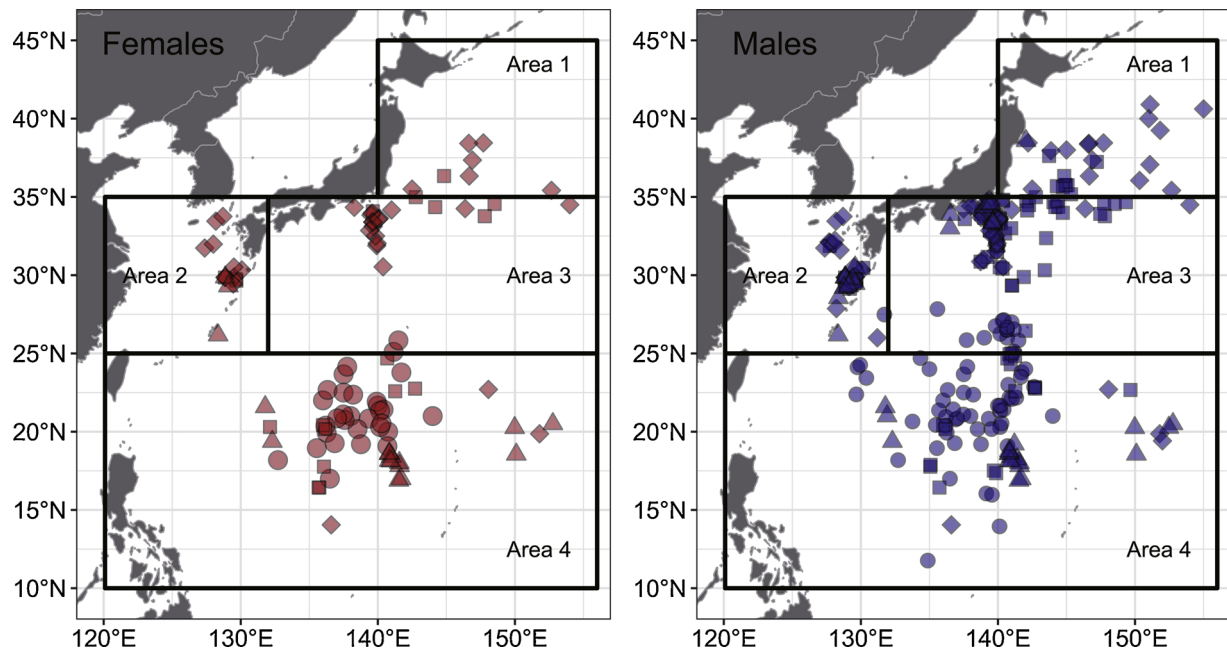


Fig. 6. Spatial and temporal variation in the distribution of the spawning capable phase in female (left panel) and male (right panel) skipjack tuna (*Katsuwonus pelamis*) caught in subtropical and temperate western Pacific Ocean. Circle, square, diamond, and triangle symbols indicate the 1st (January–March), 2nd (April–June), 3rd (July–September), and 4th quarter (October–December) of the year, respectively.

4.2. Main spawning season in the subtropical and temperate WPO

Masuda and Nihira (1999) reported that some female SKJ with $GIs > 6$ appeared in July in Area 1 (Kuroshio-Oyashio transition area). However, these authors did not assess the maturity phase based on histological observations. In the present study, we reported the spawning activity of SKJ in Area 1 for the first time using the histological analyses of the ovaries (Fig. 4b). The northern limit of the horizontal distribution of SKJ larvae was considered to be $\sim 35^{\circ}\text{N}$ (Nishikawa et al., 1985). Larval and juvenile SKJ distribution surveys are needed to determine whether the spawning in Area 1 contributes to recruitment or not.

In Area 2 (Nansei Islands area), SKJ larvae were shown to mainly occur in the 2nd quarter of the year (Nishikawa et al., 1985). However, a recent study reported that SKJ larvae were distributed around Jeju Island ($33^{\circ}22'\text{N}$, $126^{\circ}32'\text{E}$, Fig. 1) in August (Yoon et al., 2015). Ashida and Horie (2015) showed that SKJ spawning occurred around Amami-Oshima (Area 2) from July to September. The present study revealed that the spawning season in Nansei Island area was longer than that reported by Ashida and Horie (2015). Furthermore, spawning capable females appeared near Jeju Island (Fig. 6). The results related to spawning areas and seasons in the Nansei Islands area in this study may explain the results of previous larval surveys and gonad examinations

(Nishikawa et al., 1985; Ashida and Horie, 2015). Spawning capable females suddenly appeared in December (Fig. 4d), when SSTs were higher than 24°C , despite the seasonal decreases in SSTs (Fig. 3b). This phenomenon may be attributed to the migration of spawning capable females. Based on the above discussion, the main spawning season of SKJ in Area 2 occurred from June to October.

In Area 3 (around the Izu and Ogasawara Islands), SKJ larvae are mainly distributed between the 2nd and 3rd quarter of the year (Nishikawa et al., 1985). A previous study revealed that females with $GIs > 6$ appeared between May and September (Masuda and Nihira, 1999). Spawning females were also observed between June and August in Area 3 (Ashida et al., 2013). The spawning season in Area 3, as revealed by this study, may explain the results of previous larval surveys and gonad examinations (Nishikawa et al., 1985; Ashida et al., 2013). Spawning capable females appeared in March in Areas 3 and 4 (Fig. 4f and h). Spawning capable females in Area 3 appeared on the boundary between Areas 3 and 4 in the 1st quarter (Fig. 6). These findings indicate that the appearance of spawning capable specimens in March in Area 3 may have been a result of spawning capable individuals in Area 4 migrating to Area 3. In conclusion, the main spawning season of SKJ in Area 3 as well as in Area 2 occurred from June to September.

Despite the missing data in some months in Area 4 (subtropical WPO), the monthly mean SSTs remained over 24°C and spawning

Table 6

Estimates and standard error of coefficients from generalized linear model analysis of maturity rate in skipjack tuna (*Katsuwonus pelamis*) in subtropical and temperate western Pacific Ocean.

	Female model				Female model			
	Fixed effect		Random effect		Fixed effect		Random effect	
	Intercept	FL	Intercept (Area: Subtropical)	Intercept (Area: Temperate)	Intercept	FL	Intercept (Area: Subtropical)	Intercept (Area: Temperate)
Estimate	−6.3743	0.1207	0.3359	−0.3355	−3.8070	0.0876	0.3167	−0.3180
SE	0.4118	0.0067			0.3959	0.0065		
z-value	−15.480	18.110			−9.616	13.420		
p-value	$p < 0.001$	$p < 0.001$			$p < 0.001$	$p < 0.001$		

SE standard error.

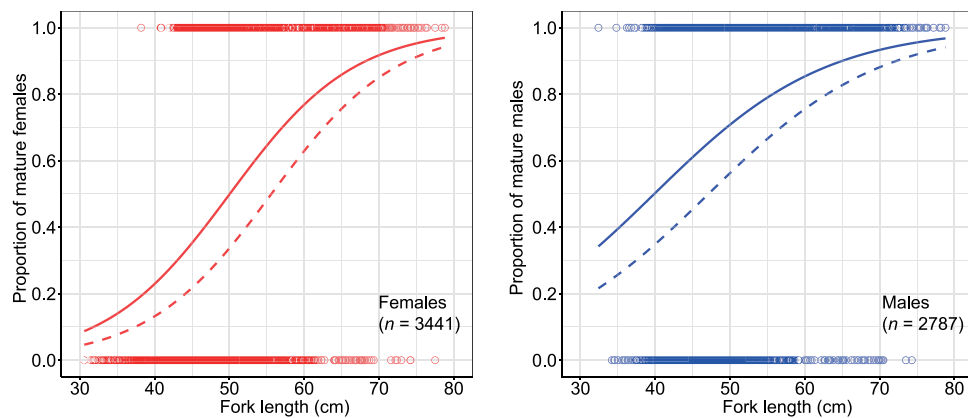


Fig. 7. Relationships between the proportion of female (left panel) and male (right panel) mature skipjack tuna (*Katsuwonus pelamis*) and fork length in the subtropical and temperate western Pacific Ocean (WPO). Solid and dashed lines indicate the subtropical and temperate WPO, respectively.

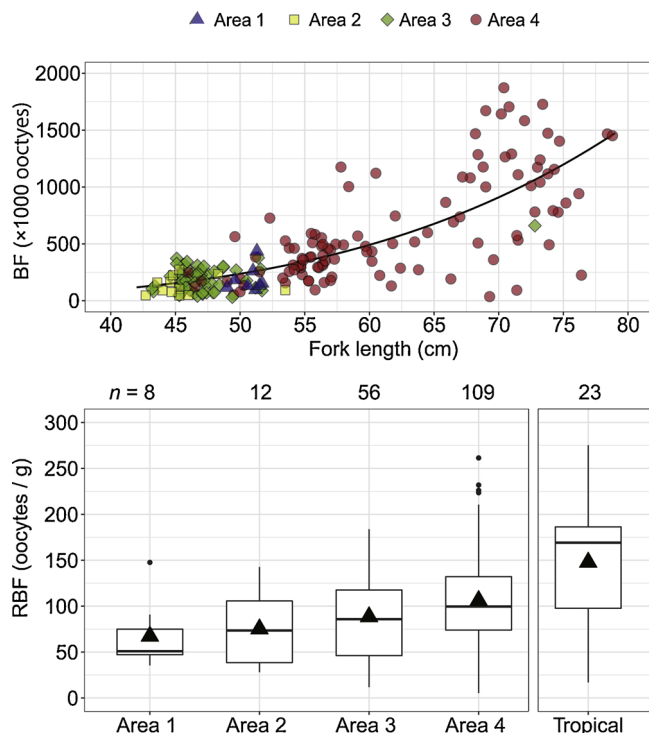


Fig. 8. Relationships between fork length and batch fecundity (BF) (upper), and between relative BF (RBF) (lower) of skipjack tuna (*Katsuwonus pelamis*). Area 1, Kuroshio-Oyashio transition area; Area 2, Nansei Islands area; Area 3, Izu and Ogasawara Islands area; and Area 4, subtropical western Pacific Ocean. The RBF data in the tropical western and central Pacific Ocean (Tropical) were obtained from Ashida et al. (2008). Triangles indicate mean values.

capable females were observed in all sampling months (Figs. 3d and 4h). Females with GIs > 8 were observed year-round in the subtropical WPO (Naganuma, 1979). These findings suggest that spawning occurs in Area 4 throughout the year, which is consistent with the findings of previous larval surveys and gonad examinations (Ueyanagi, 1969; Naganuma, 1979; Nishikawa et al., 1985). Additional sampling is required between June and August to more accurately describe the spawning season of SKJ in subtropical WPO.

4.3. Latitudinal difference in length at maturity

According to previous studies, the minimum size at maturity of SKJ is 39–40 cm FL in females and 35.5–37.6 cm FL in males (Simmons,

1969; Naganuma, 1979; Matsumoto et al., 1984; Stéquent and Ramcharrun, 1996; Ashida et al., 2010, 2013, 2017; Ashida and Horie, 2015). These findings suggest that the minimum size at maturity of SKJ does not vary geographically.

The FL_{50} in the tropical WCPO was estimated to be 47.9 and 50.3 cm FL in females (Ashida et al., 2008, 2017), respectively, and 40.7 cm FL in males (Ashida et al., 2010). The age at FL_{50} in these studies was estimated to be between 0.8–1.3 years based on the growth model for SKJ (Tanabe et al., 2003). The estimated FL_{50} s for males and females in the temperate WPO were slightly larger than those in the subtropical WPO and tropical WCPO (Fig. 7). In addition, the estimated age at FL_{50} in the temperate WPO corresponded to 1.6 years in females and 1.1 years in males. These findings implied that the SKJ at 50% maturity in WCPO may be slightly older in higher latitudinal areas.

Schaefer and Fuller (2019) noted that the observed latitudinal variation in maturity size was probably a result of the environmental differences among the home range distribution of spatially-discrete stocks. As confirmed by SKJ tagging experiments in WPO, a portion of SKJ adults of a specific size (i.e., FL > 40 cm) seasonally migrate between subtropical and temperate WCPO (Yasui and Mori, 1985; Tashiro and Uchida, 1989; Nihira, 1996; Aoki et al., 2017). The observed horizontal movement of SKJ in the subtropical and temperate WPO may indicate that the stock in the subtropical and temperate WCPO is not spatially-discrete. The estimated FL_{50} of yellowfin tuna and albacore were also reported to be longer in higher latitudinal areas (Itano, 2000; Farley et al., 2014). In albacore, the proportion of mature females varies with latitude due to the different geographical distributions of mature and immature fish (Farley et al., 2014). Itano (2000) pointed out that lower mean SSTs in spawning areas and relatively short spawning seasons may delay maturity in yellowfin tuna. The percentage of mature fish was different in each SST class in this study (Fig. 2). In addition, monthly changes of SST differed, especially between the temperate (Areas 1, 2 and 3) and subtropical WPO (Area 4). The results of the present study imply that the proportion of mature fish is also affected by the SSTs. Therefore, the observed geographical differences in the FL_{50} of SKJ in the subtropical and temperate WPO may be a result of the migration and distribution of mature fish as well as the variations in the environmental conditions of each spawning area.

4.4. Geographical differences in batch fecundity

The RBF (mean \pm SD) estimated in this study for all the WPO areas were lower than in the tropical WCPO (147.8 ± 65.1 oocytes/g; Ashida et al., 2008; Fig. 8) and western Indian Ocean (140 ± 64 oocytes/g, Grande et al., 2014). In the EPO, the mean RBF of SKJ was reported to be 54.9 oocytes/g (Schaefer and Fuller, 2019). Food availability and SST have been shown to affect the BF or relative egg

Table 7

Monthly variations in the spawning fraction (SF) and revised SF (Rev-SF) of skipjack tuna (*Katsuwonus pelamis*) in four areas in subtropical and temperate western Pacific Ocean.

	Area 1			Area 2			Area 3			Area 4		
	<i>n</i>	SF	Rev-SF	<i>n</i>	SF	Rev-SF	<i>n</i>	SF	Rev-SF	<i>n</i>	SF	Rev-SF
Jan	nd	nd	nd	0	nd	nd	0	nd	nd	33	0.45	0.58
Feb	nd	nd	nd	0	nd	nd	0	nd	nd	95	0.28	0.55
Mar	nd	nd	nd	0	nd	nd	12	0.25	0.33	56	0.38	0.64
Apr	nd	nd	nd	0	nd	nd	3	0.00	0.00	62	0.44	0.63
May	0	nd	nd	2	0.00	0.00	3	0.00	0.00	4	1.00	1.00
Jun	4	0.25	0.25	39	0.62	0.67	24	0.33	0.46	nd	nd	nd
Jul	10	0.30	0.30	43	0.44	0.44	123	0.67	0.77	nd	nd	nd
Aug	20	0.20	0.50	67	0.58	0.58	83	0.37	0.43	nd	nd	nd
Sep	1	0.00	0.00	41	0.29	0.29	31	0.13	0.13	49	0.24	0.27
Oct	0	nd	nd	14	0.21	0.29	0	nd	nd	24	0.17	0.50
Nov	0	nd	nd	3	0.00	0.00	0	nd	nd	102	0.33	0.43
Dec	nd	nd	nd	7	0.43	0.43	nd	nd	nd	nd	nd	nd
Total	35	0.23 (4.38)	0.40 (2.50)	216	0.46 (2.16)	0.48 (2.10)	279	0.46 (2.16)	0.54 (1.86)	425	0.34 (2.95)	0.52 (1.94)

Area 1, Kuroshio-Oyashio transition area; Area 2, Nansei Islands area; Area 3, Izu and Ogasawara Islands area; Area 4, subtropical western Pacific Ocean; *n*, number of mature fish; nd, no data. Values in parentheses indicate the spawning intervals.

production of indeterminate spawning fish that utilize the income breeding strategy (Takasuka et al., 2005; Margulies et al., 2007; Zudaire et al., 2013; Yoneda et al., 2014). The present study showed that the RBF of SKJ varied in each sampling area and a weak correlation was observed between RBF and SST. The geographical differences observed in the RBF of SKJ may suggest that the energy investment for reproduction in individuals may change depending on the existing oceanographic conditions, such as water temperature and food availability, in each spawning area.

4.5. Geographical difference in the spawning fraction

The estimated total SF in all sampling areas in this study were lower than for SKJ in the tropical WCPO (0.50–0.55; Ashida et al., 2008, 2017) and South Pacific Ocean (0.85; Hunter et al., 1986). In the temperate WPO (Areas 1, 2, and 3), an increase in the monthly SF was observed in boreal summer (Table 7). These findings imply that the seasonal fluctuations in SF and Rev-SF in female SKJ in the temperate WPO may have occurred in response to seasonal variations in SST.

Generally, random sampling may lead to a biased estimation of SF when the duration of spawning markers, such as POF, germinal vesicle migration, and hydrated oocytes, is less than 24 h (Ganias, 2012). Because of the fast degeneration of POFs in the ovary, the SF estimates based on the POF method tend to be underestimated with regards to the sampling time when the final maturational process of oocytes (i.e., germinal vesicle migration or hydrated oocytes) is observed in the ovary (Ashida et al., 2008, 2017). Ashida et al. (2017) highlighted the advantage of the Rev-SF method, i.e., the time of capture does not need to be considered because this index uses all spawning traits, such as POFs, germinal vesicles, and hydrated oocytes. A significant difference was observed between the total SF and Rev-SF in Areas 3 and 4. Furthermore, large differences between the SF and Rev-SF were observed in some sampling months (Table 7). Of the total specimens in the spawning capable phase (*n* = 486), 203 specimens possessed migrated germinal vesicles or hydrated oocytes in the ovary (Table 2). Therefore, the findings of the present study suggested that the SF estimates based on the POF method were biased, presumably due to the degeneration of POF and the lack of specimen capture data.

4.6. Geographical differentiation in *Kn*

The *Kn* in Area 1 (Kuroshio-Oyashio transition area) was the highest among all areas in this study. The crude fat and fatty acid reserves in SKJ have been shown to differ among areas, and a positive correlation

was found between the quantity of crude fat and the latitudinal position of fishing sites in the Kuroshio-Oyashio transition area (Saito et al., 1997; Takagi and Katase, 2006). According to Aoki et al. (2017), the estimated energy intakes and expenses in SKJ differ according to the habitat; with the net energy intake being the highest in the Kuroshio-Oyashio transition area. Generally, net energy is allocated to growth, egg production, and storage (Lambert et al., 2003). The RBF, SF, and duration of the spawning season were lower in Area 1 than in the other areas, which suggests that the energy investment for reproduction in Area 1 was relatively low compared to the other areas. These findings suggest that the significantly high *Kn* in Area 1 may have been a result of the relationship between a high net energy input and a low energy investment for reproduction.

5. Conclusion

Geographical differences in the reproductive traits of SKJ in WPO were observed, and the spawning potential per individual in the temperate WPO was lower than in the subtropical WPO and tropical WCPO (Table 8). This conclusion suggests that the reproductive investment of spawning fish in high latitudinal areas may be lower than in subtropical and tropical waters because of shorter durations of favorable oceanic conditions for spawning. SKJ utilize the income breeding strategy, i.e., spawning individuals can adjust their reproductive investment in response to environmental factors. In addition to the impacts of geographical and oceanic differences, variations and adjustments of reproductive investment in SKJ may be one of the main explanatory factors for the observed variation in reproductive traits of this species. The relationship between reproductive traits and internal or external factors need to be analyzed in future studies to clarify the mechanisms involved in the observed geographical differences in reproductive traits.

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Table 8
Summary of reproductive traits of skipjack tuna (*Katsuwonus pelamis*) in the western Pacific Ocean (WPO), western and central Pacific Ocean (WCPO), eastern Pacific Ocean (EPO), and western Indian Ocean (WIO).

	Temperate WPO				Subtropical WPO		Tropical WCPO	EPO	WIO
	Area 1		Area 2		Area 3		Area 4		
	Area 1	Area 2	Area 2	Area 3	Area 3	Area 4			
Minimum size at maturity in females (cm FL)		40.9*	40.9*			38.2	40.0	nd	nd
FL ₅₀ in females (cm FL)		55.6*	55.6*			50.0	49.8, 50.3	46.9–56.0	42.0, 43.5
Total SF (Rev-SF) in spawning season	0.23 (0.40)	0.46 (0.48)	0.46 (0.48)	0.46 (0.54)	0.34 (0.52)		0.5 (0.49–0.57), 0.85	0.21–0.85	nd
RBF (mean ± SD, oocytes/g BW)	67.2 ± 36.7	71.2 ± 39.8	71.2 ± 39.8	88.4 ± 43.1	106 ± 50.6		147.8 ± 65.1	54.9	140.0 ± 64.0
Minimum size at maturity in males (cm FL)		32.4*	32.4*			36.2	35.5	nd	nd
FL ₅₀ in males (cm FL)		47.1*	47.1*			39.8	40.7	nd	43.5
Reference		This study	This study			This study	Hunter et al. (1986); Ashida et al. (2007, 2008, 2010, 2017)	Schaefer and Fuller (2019)	Stéquent and Ramcharrun (1996); Grande et al. (2014)

Area 1, Kuroshio-Oyashio transition area; Area 2, Nansei Islands area; Area 3, Izu and Ogasawara Islands area; Area 4, subtropical area; BW, body weight; FL, fork length; FL₅₀, size at 50% maturity; nd, not determined; RBF, relative batch fecundity; SF, spawning fraction. The value marked with asterisk was estimated using the data in Area 1, 2 and 3.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishres.2019.105352>.

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