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ORIGINAL ARTICLE

Biology

Geographical variation in spawning histories of age-1 Pacific saury *Cololabis saira* in the North Pacific Ocean during June and July

Satoshi Suyama[1] · Hitomi Ozawa[2,4] · Yasutoki Shibata[1] · Taiki Fuji[1,5] · Masayasu Nakagami[1,6] · Akio Shimizu[3]

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Abstract

We examine geographical differences in percentages of age-1 Pacific saury *Cololabis saira* with previous spawning experience collected from 143°E to 165°W during June and July of 2013 and 2014. Previous spawning experience of fish was determined using a new histological method involving Victoria blue (VB)-positive ovarian arterioles. We also compared the radius of the otolith annual ring (ROA), which indicates fish body size at the beginning of the breeding season, with the incidence of previous spawning experience. A generalized linear model was used that treats the occurrence of fish with VB-positive arterioles as a response variable, following the Bernoulli distribution of probability p_i, where longitude, latitude, body length, ROA in age-1 fish, year (2013 or 2014), sea surface temperature, and days elapsed from a survey starting date, are used as fixed effect terms. An estimated regression coefficient of longitude was negative while that of ROA was positive, meaning that the probability of previous spawning increases with a latitudinal progression west, and with increased ROA. Our results suggest that differences in the percentage of previously spawned fish in different geographic areas are caused by differences in body length at the beginning of the breeding season.

Keywords Age · Otolith · Spawning experience · Arterioles · Ovary · North Pacific Ocean

Introduction

Pacific saury *Cololabis saira* are widely distributed in subarctic to subtropical regions of the North Pacific Ocean, from the coast of Japan to the western coastal waters of North America (Hubbs and Wisner 1980). This species is caught commercially by Japan, Russia, Korea, China, Taiwan, and Vanuatu, with total landings fluctuating over the last 20 years from 180,973 tons in 1998 to 631,094 tons in 2014 [The Food and Agriculture Organization; http://www.fao.org/fi/statist/statist.asp (Accessed 1 November 2018)]. Prior to 2000, the catch by Japan accounted for more than 80% of the total world catch, but this has since dropped to approximately 30% given increased recent foreign catches, concomitant with an expansion of fishing grounds and periods. Japanese and Russian fishing vessels mainly catch Pacific saury in their exclusive economic zone from August to December, whereas Taiwanese, Chinese and Korean fishing vessels operate in more eastern areas, mainly in the high seas west of 165°E from June to December (Huang et al. 2007; Huang 2010; Tseng et al. 2013, 2014).

✉ Satoshi Suyama
suyama@affrc.go.jp

1 Tohoku National Fisheries Research Institute, Japan Fisheries Research and Education Agency, Hachinohe Station, 25-259, Shimomekurakubo, Same, Hachinohe, Aomori 031-0841, Japan

2 Faculty of Fisheries Sciences, Hokkaido University, 3-1-1, Minato, Hakodate, Hokkaido 988-8501, Japan

3 National Research Institute of Fisheries Science, Japan Fisheries Research and Education Agency, 2-12-4 Fukuura, Yokohama, Kanagawa 236-8648, Japan

4 Present Address: Ministry of Agriculture, Forestry and Fisheries, 1-2-1, Kasumigaseki, Chiyoda, Tokyo 100-8950, Japan

5 Present Address: The National Research Institute of Far Seas Fisheries, Japan Fisheries Research and Education Agency, 2-12-4 Fukuura, Yokohama, Kanagawa 236-8648, Japan

6 Present Address: National Research Institute of Fisheries Science, Japan Fisheries Research and Education Agency, 2-12-4 Fukuura, Yokohama, Kanagawa 236-8648, Japan

Improved international management of Pacific saury resources is increasingly necessary. Age at maturity data are important for fisheries management (e.g., Domínguez-Petit et al. 2017), but they are difficult to obtain for Pacific saury. This species has a short 2-year life span, with age-1 fish developing an annual ring that forms mainly in winter (Hotta 1960; Suyama 2002). The body length frequency distributions and age composition of caught fish fluctuate annually (Suyama et al. 2006). Spawning occurs over a long time and wide area (Watanabe and Lo 1989), with a breeding season that extends over 10 months from September to June. Spawning grounds shift with season; spawning occurs from the Oyashio–Kuroshio transitional waters off northeastern Japan in autumn and in spring, but moves to the Kuroshio Current region in winter (Watanabe and Lo 1989). Fish spawn multiple times and have asynchronous oocyte development (oocytes in many stages of development occur simultaneously in active ovaries) (Hatanaka 1955; Kosaka 2000; Suyama 2002; Kurita 2006; Suyama et al. 2016a). Rearing experiments suggest the spawning period of an individual fish extends for a maximum of 6 months (Suyama et al. 2016a). Hereafter, we describe the spawning duration for the population of Pacific saury as the 'breeding season,' and the spawning duration for each individual as the 'spawning period.'

Because of differences in the spawning period of individuals, fish that are about to spawn, are spawning, and those that have recently spawned (which cannot readily be distinguished from immature fish) can all be collected in the same month (Kurita 2006). To clarify maturation rate based on the occurrence of spawning fish, extensive investigations over a long period of time are required. However, in a species with a breeding season lasting 10 months, with a spawning ground spread over a wide area throughout the North Pacific Ocean, this is very difficult.

Spawning fish body length (BL), the distance from the tip of the lower jaw to the posterior end of the muscular knob on the caudal peduncle (Kimura 1956), varies in different spawning areas and breeding seasons (Hotta 1960; Kosaka 2000; Sugama 1957). The minimum BL of spawning fish collected from Japanese fishing grounds is about 25 cm (Hatanaka 1955); however, individuals collected outside the fishing grounds or season can spawn at about 20 cm (Hotta 1960; Kosaka 2000; Sugama 1957). Based on their body length, these smaller fish could be age-0 (Kurita et al. 2004; Nakaya et al. 2010; Nemoto et al. 2001; Suyama et al. 1992, 1996, 2011; Watanabe et al. 1988) — that is, they have commenced spawning within 1 year of hatching. Minimum maturation size seems to vary according to spawning area and month. Some fish do commence first spawning in the latter half of age-0 (Hatanaka 1955; Kosaka 2000), but it is not known whether all or only some individuals of this age spawn. If fish do not commence first spawning during this breeding season, they would do so in the next breeding season. As Pacific saury growth varies in different locations (Suyama et al. 2012a) and hatch periods (Kurita et al. 2004; Nemoto et al. 2001), maturation rate in each age-class might be influenced by several factors, such as growth rate, hatch period, or location. We consider the hatching period, growth rate, and age at first spawning to be very closely related in Pacific saury, but the fact that spawning occurs over such a long period and wide area made it difficult to determine exactly how these three factors were related.

Species like Pacific saury with asynchronous oocyte development have postovulatory follicles (POF) or atretic oocytes that originate from yolked oocytes during or after spawning (Barbieri et al. 1994; Hunter and Macewicz 1985a, b; Hunter et al. 1986; Karlou-Riga and Panas 1996; Suyama et al. 2016a), which might provide evidence of previous spawning activity. However, these spawning indicators typically disappear immediately or soon after spawning. For example, POF in anchovy disappear within days, and atretic yolked oocytes within weeks, limiting the use of either to identify previous spawning experience in any individual. However, females of Pacific saury that had spawned up to 6 months previously, that had completely resorbed their POF or atresia oocyte from the yolked oocyte, retained Victoria blue (VB)-positive arterioles in their ovaries, whereas fish that had not spawned did not (Suyama et al. 2016a). As such, VB staining might enable identification of maturation rate in asynchronous spawning fish like Pacific saury.

The Tohoku National Fisheries Research Institute (TNFRI) has routinely performed stock assessment surveys from near the coast of Japan to 165°W during the months of June and July (Suyama et al. 2016b). Pacific saury occur widely throughout the survey area during this time, after which age-1 fish commence a westward migration, with most reaching the Japanese fishing ground east of 150°E in the fishing season from August to December (Suyama et al. 2012b, Miyamoto et al. 2019). During two of these surveys (2013 and 2014) we collected and examined ovaries of Pacific saury from over a wide geographic area, and for each fish determined the presence or absence of VB-positive arterioles. Collecting Pacific saury during these surveys enabled collection of individuals from the western half of this species' distribution, for it is otherwise more widely distributed throughout the year (Suyama et al. 2012a, b); no comparable opportunity exists for us to collect specimens over such a large area, within such a short period of time. Additionally, the months during which these surveys occurred corresponded with the end of the Pacific saury breeding season, when all fish that would have matured in the current breeding season have or are in the process of finishing spawning. Using these collections, we inferred the percentage of fish that had spawned in the first breeding season, their geographical variation, and differences in their size at the beginning of the breeding season, based on otolith annual ring radius details.

Materials and methods

Trawl survey

Pacific saury were collected between 143°E and 165°W using surface trawl nets towed from RV *Hokko-maru* (143–163°E) and the training vessel *Hokuho-maru* (167°E–165°W) during June and July of 2013 and 2014. The surface trawl (NST-99) was manufactured by Nichimo Co. Ltd. Net width during trawling on *Hokuho-maru* was 24.0 m, and on *Hokko-maru* 34.7 m; headline height varied between 20 and 25 m; net length was 90 m; maximum and minimum stretched mesh sizes were 15,189 mm and 16.7 mm, with a innner cod-end mesh-size of 18 mm (Ueno et al. 2017). The entire head rope, including wingtips, floated near the surface; the net was towed at 4–5 knots for 1 h during daytime. Samples were collected from 124 (36°09–48°35′N and 143°09′E–164°58′W) stations in 2013 and 121 (37°01–46°24′N and 143°58′E–164°58′W) stations in 2014. The survey region was divided into six areas each spanning 10° of longitude: 140°E–150°E, 150°E–160°E, 160°E–170°E, 170°E–180°, 180°–170°W, and 170°W–160°W; these were denoted A140E, A150E, A160E, A170E, A170 W, and A160 W, respectively (Table 1, Fig. 1).

Fish were sorted from the catch, immediately frozen, and transported to the laboratory. BL was measured to the nearest 0.1 cm. When the total number of fish caught at a station was less than 100, all fish were measured; otherwise a random sample (100–434 fish) was measured. From these results and the ratio of the total number of caught fish and the number of measured fish, total catch in each 0.5-cm size class at each sampling station and longitudinal area was estimated. When the total number of Pacific saury caught at any station was less than 80, all fish was sexed, and for females the ovarian weights (OW) were measured to the nearest 0.01 g; otherwise a random sample of 80 fish was sorted from the catch, measured and sexed, and the OW of any females weighed (Table 1).

Age determination and otolith radius measurement

After measuring BL, otoliths were extracted. The right otolith was embedded in epoxy resin and the incidence of an annual ring determined using light microscopy following Suyama et al. (2012a, b). Because formation of the annual ring commences in September (Suyama et al. 2011) and is completed by the spring of the following year, during our survey period age-1 fish already had an annual ring (Suyama et al. 2012a, b). After annual ring identification, the radius of the ring (ROA) was measured from the otolith core to the area where ring formation commenced. Otolith images were captured on a computer at 32 × magnification; the ROA was calculated using image analysis software (Image × Earth 3.0, Kikuchi Optical Co. Ltd., Nagano, Japan). The breeding season started in September (Watanabe and Lo 1989), ROA is an indicator of BL at the beginning of the breeding season.

Ovary samples

As BL of both age-1 fish in June and July (Suyama et al. 2012b) and spawning individuals usually exceeded 25 cm, the ovaries that we collected were mainly from age-1 fish. However, ovaries from some age-0 fish less than 25 cm were also collected, as we could not discount the possibility that these fish had previous spawning experience. In total, ovaries from 622 fish from 25 sampling stations (40°53–48°35′N and 154°59′E–165°01′W) in 2013, and 262 fish from 11 sampling stations (39°43–44°29′N and 158°58′E–165°00′W) in 2014, were examined (Table 2, Fig. 1).

Immediately after capture, one of a fish's two ovaries was extracted and fixed for 3–7 days in Bouin's solution, then transferred to 70% ethanol. Fish bodies were frozen, then transported to the laboratory where their BL (to nearest 0.1 cm) was measured. Fish were aged and their ROA measured. Because of right otolith abnormality, the left otolith of 10 fish (seven in 2013 and three in 2014) was examined; ROAs of these otoliths were not measured.

Ovarian histology

Two serial histological (using standard paraffin techniques) sections of 8–10 μm were taken from the mid-part of each ovary. The first section was stained with VB solution (Wako Pure Chemical Industries, Osaka, Japan) and unoxidized Azocarmine G solution (Wako Pure Chemical Industries) to enable ovarian arteriole analysis (Suyama et al. 2016a). However, as VB-positive arterioles are often not detected in spawning fish (Suyama et al. 2016a), the second section was stained with Mayer's hematoxylin and eosin-Y (H&E) to examine oocyte developmental stage and the presence of atretic oocytes and/or POF (Hunter and Macewicz 1985a, b).

Stained arterioles were observed under a microscope at maximum magnifications of 400 × or 1000 ×. In the first slide, numbers of deeply and clearly stained VB-positive arterioles were counted across complete cross-sections. In the second slide, individuals with yolked oocytes (yolk-accumulating oocytes to ovulated stages), POF and/or alpha and beta stages of atresia from yolked oocytes, were identified as either spawning or recently spawned fish (Hunter and Macewicz 1985a, b).

Table 1 Pacific saury (PS, *Cololabis saira*) sampling records and comparison of body length (BL), radius of annual ring (ROA) of otolith, and ovary weight (OW)

	Area						
	140–150°E	150–160°E	160–170°E	170°E–180°	180–170°W	170–164°W	All areas
2013							
Survey duration	8–12 July	23 June–2 July	12–22 June	17–28 June	26 June–7 July	4–13 July	12 June–13 July
N stations	15	24	21	22	18	25	125
N stations PS caught	4	9	10	15	12	15	65
N PS caught	66	7451	11,487	10,738	11,398	13,727	54,867
Estimated *N* of age-0	43	3999	5	1039	4282	7874	17,245
Estimated *N* of age-1	24	3452	11,482	9699	7114	5853	37,623
Percentages of age-1 (%)	35.6%	46.3%	100.0%	90.3%	62.4%	42.6%	68.6%
Measured BL (cm) of age-1							
N	22	385	700	1080	510	388	3063
Mean (SD)	30.2 (0.8)	29.6 (0.9)	29.1 (1.1)	28.8 (1.2)	28.7 (1.5)	29.5 (1.4)	29.0 (1.3)
Min–max	28.7–31.2	26.7–31.7	25.7–32.4	24.7–32.2	25.9–33.3	26.1–33.1	24.7–33.3
BL (cm) for histological observations of age-1							
N	0	60	95	167	74	91	487
Mean (SD)	–	30.2 (0.95)	29.2 (1.24)	28.6 (1.26)	28.9 (1.48)	29.8 (1.38)	29.2 (1.39)
Min–max	–	27.8–31.7	26.5–31.9	25.7–31.8	25.9–32.1	26.4–32.9	25.7–32.9
Measured ROA (mm) of age-1							
N	22	381	699	1077	510	388	3055
Mean (SD)	0.57 (0.05)	0.57 (0.06)	0.56 (0.06)	0.55 (0.06)	0.53 (0.05)	0.51 (0.06)	0.55 (0.06)
Min–max	0.47–0.68	0.41–0.82	0.36–0.76	0.40–0.79	0.39–0.66	0.36–0.73	0.36–0.82
ROA (mm) for histological observations of age-1							
N	0	56	95	164	74	91	480
Mean (SD)	–	0.58 (0.07)	0.57 (0.06)	0.54 (0.06)	0.52 (0.06)	0.52 (0.06)	0.55 (0.06)
Min–max	–	0.42–0.82	0.36–0.70	0.41–0.68	0.40–0.65	0.38–0.73	0.36–0.82
Measured OW (g) of age-1							
N	10	218	381	618	302	232	1761
Mean (SD)	4.11 (3.02)	0.67 (0.24)	0.54 (0.24)	0.45 (0.17)	0.46 (0.44)	0.55 (0.52)	0.53 (0.47)
Min–max	0.83–9.28	0.25–1.65	0.11–1.96	0.07–1.38	0.17–6.02	0.04–3.28	0.04–9.28
OW (g) for histological observations of age-1							
N	0	60	95	167	74	91	487
Mean (SD)	–	0.67 (0.24)	0.44 (0.19)	0.41 (0.16)	0.54 (0.74)	0.61 (0.62)	0.50 (0.43)
Min–max	–	0.29–1.65	0.11–1.08	0.21–1.38	0.20–6.02	0.10–3.28	0.10–6.02
2014							
Survey duration	13–15 July	27 June–5 July	12–26 June	15 June–16 July	5–11 July	25 June–3 July	12 June–15 July
N stations	8	23	21	31	18	20	121
N stations PS caught	0	12	14	19	12	12	69
N PS caught	0	2858	11,195	16,141	5854	13,984	50,032
Estimated *N* of age-0	0	315	379	5601	5359	13,597	25,251
Estimated *N* of age-1	0	2543	10,816	10,540	495	387	24,781
Percentages of age-1 (%)	–	89.0%	96.6%	65.3%	8.5%	2.8%	49.5%
Measured BL (cm) of age-1							
N	0	565	553	815	202	92	2227
Mean (SD)	–	30.4 (0.91)	29.7 (0.99)	29.4 (1.08)	30.2 (1.11)	30.2 (1.20)	29.8 (1.1)
Min–max	–	27.6–33.0	27.1–32.9	26.3–33.0	27.7–33.2	28.0–34.7	26.3–34.7
BL (cm) for histological observations of age-1							
N	0	20	60	86	31	40	237
Mean (SD)	–	30.6 (1.05)	29.8 (0.99)	29.6 (0.98)	29.9 (1.07)	30.7 (1.27)	30.0 (1.13)
Min–max	–	28.5–32.7	27.9–32.9	27.5–32.5	28.4–32.6	28.5–34.7	27.5–34.7

Table 1 (continued)

	Area						
	140–150°E	150–160°E	160–170°E	170°E–180°	180–170°W	170–164°W	All areas
Measured ROA (mm) of age-1							
N	0	565	552	813	202	91	2223
Mean (SD)	–	0.60 (0.06)	0.59 (0.06)	0.56 (0.06)	0.55 (0.06)	0.54 (0.06)	0.58 (0.06)
Min–max	–	0.40–0.81	0.40–0.79	0.35–0.77	0.41–0.73	0.38–0.69	0.35–0.81
ROA (mm) for histological observations of age-1							
N	0	20	60	84	31	39	234
Mean (SD)	–	0.61 (0.08)	0.59 (0.06)	0.57 (0.05)	0.53 (0.06)	0.55 (0.06)	0.57 (0.06)
Min–max	–	0.45–0.80	0.48–0.71	0.48–0.75	0.41–0.65	0.38–0.69	0.38–0.80
Measured OW (g) of age-1							
N	0	295	327	435	92	70	1219
Mean (SD)	–	0.73 (0.37)	0.57 (0.21)	0.60 (0.59)	0.75 (0.57)	0.92 (1.00)	0.65 (0.51)
Min–max	–	0.24–4.05	0.20–2.14	0.20–7.12	0.17–4.02	0.30–6.55	0.17–7.12
OW (g) for histological observations of age-1							
N	0	20	60	86	31	40	237
Mean (SD)	–	0.89 (0.33)	0.56 (0.23)	0.54 (0.28)	0.46 (0.21)	0.96 (0.84)	0.64 (0.45)
Min–max	–	0.54–1.85	0.20–1.81	0.20–1.90	0.26–1.38	0.34–4.00	0.20–4.00

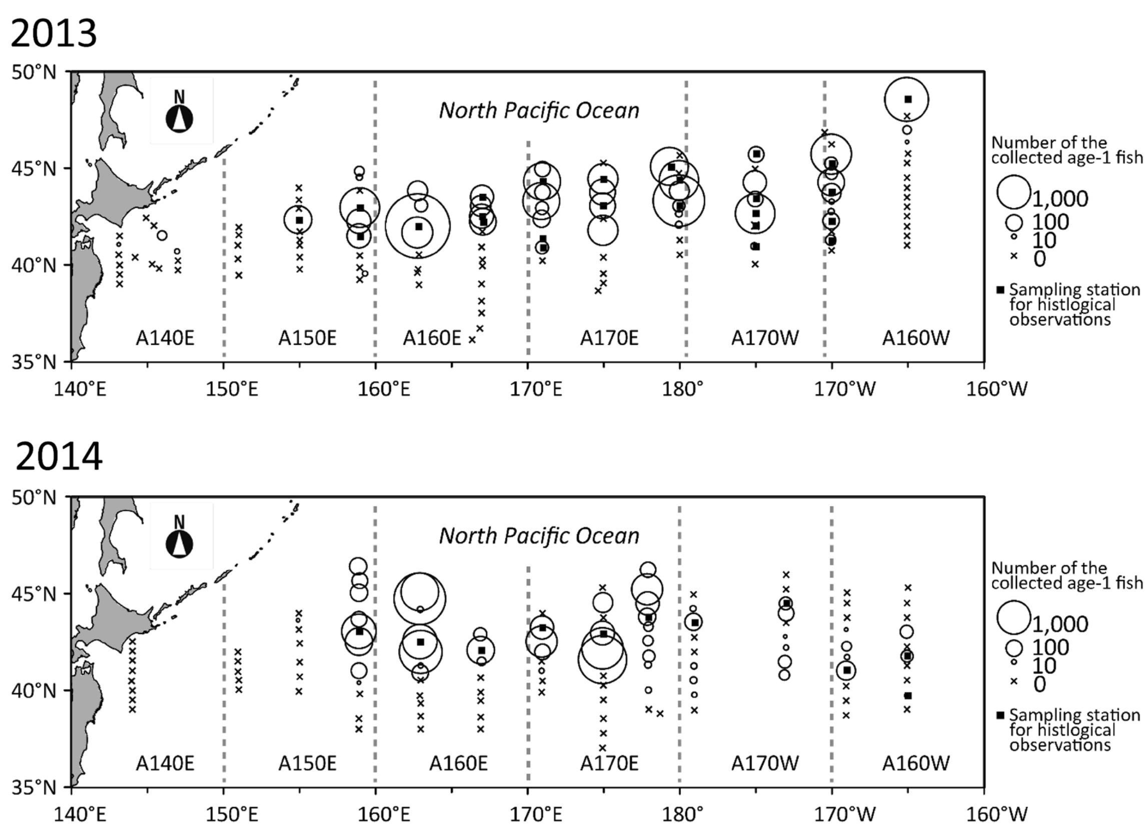

Fig. 1 Sample stations and numbers of age-1 Pacific saury *Cololabis saira* in the North Pacific off Japan, June and July, 2013 and 2014. *White circles* and *crosses* depict the numbers of fish caught; *solid squares* depict sampling stations for histological observations of ovarian arterioles and maturation stages

Table 2 Coordinate and summary statistics for Pacific saury *Cololabis saira* age, and ovarian stage

Sampling date	Sampling location			*N* observed (all)		*N* observed (age-0)		*N* observed (age-1)		VB-positive individuals		*N* fish with yolked oocytes	
	Latitude	Longitude	SST (°C)	*N*	BL (range) (cm)	*N*	BL (range) (cm)	*N*	BL (range) (cm)	*N*	Mean *N* of VB	Age-0	Age-1
2013													
15 June	42°13′N	167°06′E	10.4	20	26.5–30.3	0		20	26.5–30.3	8	11.4	0	1
15 June	42°30′N	167°02′E	7.9	30	27.1–30.5	0		30	27.1–30.5	13	13.2	0	1
16 June	43°30′N	167°02′E	8.2	25	27.1–29.9	0		25	27.1–29.9	5	10.0	0	0
17 June	44°19′N	171°00′E	7.9	25	26.9–31.0	0		25	26.9–31.0	6	24.7	0	0
18 June	41°22′N	170°59′E	14.3	24	22.6–31.0	5	22.6–24.6	19	26.0–31.0	3	14.3	0	1
19 June	41°59′N	162°50′E	11.9	20	30.0–31.9	0		20	30.0–31.9	16	19.8	0	0
19 June	40°53′N	171°01′E	14.7	23	23.0–32.0	10	23.0–25.8	13	27.0–32.0	7	26.4	0	0
24 June	41°27′N	159°00′E	13.8	20	28.6–31.7	0		20	28.6–31.7	13	17.0	0	1
24 June	43°04′N	174°58′E	8.9	25	26.9–31.8	0		25	26.9–31.8	7	6.9	0	1
25 June	42°57′N	159°00′E	10.8	20	27.8–30.6	0		20	27.8–30.6	11	8.0	0	0
25 June	44°25′N	174°59′E	8.6	25	26.0–30.8	2	26.0–26.9	23	26.8–30.8	0		0	0
26 June	45°03′N	179°26′E	9.2	25	27.6–31.2	0		25	27.6–31.2	1	6.0	0	0
27 June	44°23′N	179°59′E	9.0	24	26.0–30.5	0		24	26.0–30.5	1	24.0	0	0
28 June	42°18′N	154°59′E	11.8	20	29.8–31.4	0		20	29.8–31.4	19	24.8	0	1
28 June	43°04′N	179°59′E	11.0	24	20.0–31.0	11	20.0–25.5	13	25.7–31.0	0		0	0
1 July	40°57′N	174°59′W	15.8	17	22.4–31.4	13	22.4–27.0	4	31.0–31.4	3	9.7	0	3
2 July	42°02′N	174°59′W	14.0	1	31.0	0		1	31.0	1	8.0	0	1
2 July	43°26′N	174°58′W	11.7	23	25.4–29.4	1	25.4	22	25.9–29.4	1	4.0	0	0
2 July	42°40′N	175°00′W	13.4	50	22.4–32.1	28	22.4–28.1	22	26.4–32.1	3	6.7	0	0
3 July	45°45′N	174°57′W	9.7	25	27.1–31.2	0		25	27.1–31.2	0		0	0
5 July	45°14′N	169°59′W	11.6	25	27.3–31.0	0		25	27.3–31.0	0		0	0
6 July	43°45′N	170°00′W	14.5	30	20.5–31.0	14	20.5–27.3	16	26.4–31.0	1	4.0	0	1
7 July	42°15′N	170°00′W	15.6	42	16.6–32.9	34	16.6–28.4	8	30.2–32.9	4	32.5	0	2
8 July	41°14′N	170°00′W	18.3	19	25.5–31.6	17	25.5–28.1	2	30.0–31.6	0		0	2
13 July	48°35′N	165°01′W	10.4	40	26.8–32.1	0		40	26.8–32.1	3	15.0	0	3
Subtotal				622	16.6–32.9	135	16.6–28.4	487	25.7–32.9	126		0	18
2014													
14 June	42°03′N	166°59′E	9.4	30	27.9–31.5	0		30	27.9–31.5	21	24.2	0	0
15 June	43°14′N	171°00′E	8.8	30	27.5–31.0	0		30	27.5–31.0	19	43.3	0	0
21 June	42°55′N	175°00′E	10.3	29	27.9–31.2	0		29	27.9–31.2	11	41.3	0	0
24 June	42°30′N	162°58′E	9.9	30	29.1–32.9	0		30	29.1–32.9	26	28.4	0	0
28 June	41°02′N	169°00′W	13.6	30	27.1–33.0	3	27.1–28.7	27	28.5–33.0	14	30.8	0	2
29 June	43°02′N	158°58′E	11.4	20	28.5–32.7	0		20	28.5–32.7	20	85.6	0	1

Table 2 (continued)

Sampling date	Sampling location		SST (°C)	N observed (all)		N observed (age-0)		N observed (age-1)		VB-positive individuals		N fish with yolked oocytes	
	Latitude	Longitude		N	BL (range) (cm)	N	BL (range) (cm)	N	BL (range) (cm)	N	Mean N of VB	Age-0	Age-1
30 June	39°43′N	165°00′W	16.3	1	26.4–26.4	1	26.4–26.4	0		0		0	0
1 July	41°46′N	165°01′W	13.8	30	26.1–34.7	17	26.1–28.0	13	30.1–34.7	9	23.1	0	4
5 July	44°29′N	172°58′W	10.5	2	29.6–30.0	0		2	29.6–30.0	0		0	0
9 July	43°29′N	179°00′W	11.4	30	27.5–32.6	1	27.5–27.5	29	28.4–32.6	5	42.6	0	0
15 July	43°46′N	177°58′E	13.1	30	25.5–32.5	3	25.5–27.4	27	27.5–32.5	16	75.9	0	2
Subtotal				262	25.5–34.7	25	25.5–28.7	237	27.5–34.7	141		0	9
Total				884	16.9–34.7	160	16.9–28.8	724	27.5–34.7	267		0	27

BL (body length), *N* (number), *SST* (sea surface temperature), *VB* (Victoria blue)

Statistical analysis

We used a generalized linear model where the ith ($i=1, \ldots, N$; where N is total number of age-1 fish observed) occurrence of a fish with VB-positive arterioles was treated as a response variable ($y_i=1$ if ith fish has VB-positive arteriole, otherwise $y_i=0$). The response variable follows the Bernoulli distribution of probability p_i, where longitude (LONG), latitude (LAT), BL, ROA of age-1 fish, year (2013 or 2014), sea surface temperature (SST), and elapsed days from a starting date of the survey (DAY), were used as fixed effect terms. Here, the starting date of the survey was set as 14 June (i.e., elapsed days for 15 June 2013 and 14 June 2014 were treated as two and one, respectively). The model formula is: $y_i \sim \text{Bernoulli}\left(p_i\right)$,

$$\text{logit}\left(p_i\right) = \alpha + \beta_1\text{LONG}_i + \beta_2\text{LAT} + \beta_3\text{ROA}_i + \beta_4\text{BL}_i + \beta_5 z_i + \beta_6\text{SST}_i + \beta_7\text{DAY}_i,$$

where α and β_{1-7} are parameters to be estimated. Year was treated as a categorical variable ($z_i=0$ if ith year $=2013$, $z_i=1$ otherwise). Longitude and latitude were treated as continuous variables. Westings were converted to eastings (e.g., 170°W was converted to 190°E). Because of high collinearity, interaction terms among the seven fixed terms were not included in the model. Model selection using Akaike information criterion (AIC) (Akaike 1974) was carried out. The statistical software R (https://www.R-project.org/. Accessed 27 June 2018) and a function "glm" were used.

Differences in mean ROA between groups (e.g., comparison between ROA of fish with and without VB-positive arterioles, or ROA of fish with VB-positive arterioles, in 2013 and 2014) were assessed using analysis of variance followed by Tukey's multiple comparisons tests. Significant differences were determined at the 5% level.

Results

Age composition and BL range of age-1 fish

A total 54,813 Pacific saury were caught at 64 of 124 stations (39°04–48°35′N and 143°10′E–164°58′W) in 2013, and 50,032 individuals at 69 out of 121 sampling stations (37°01–46°24′N and 154°59′E–165°00′W) in 2014. Of these, 37,589 (68.6%) were estimated age-1 fish in 2013, and 24,781 (49.5%) in 2014. The minimum BL of age-1 fish was 24.7 cm in 2013, and 26.3 cm in 2014 (Table 1, Fig. 2).

Of 622 fish in 2013 from which ovaries were examined, 487 were classified as age-1; BL ranged 25.7–32.9 cm. The remaining fish (135 individuals; BL 16.9–28.8 cm) were classified age-0. Of the 262 fish in 2014 for which ovaries

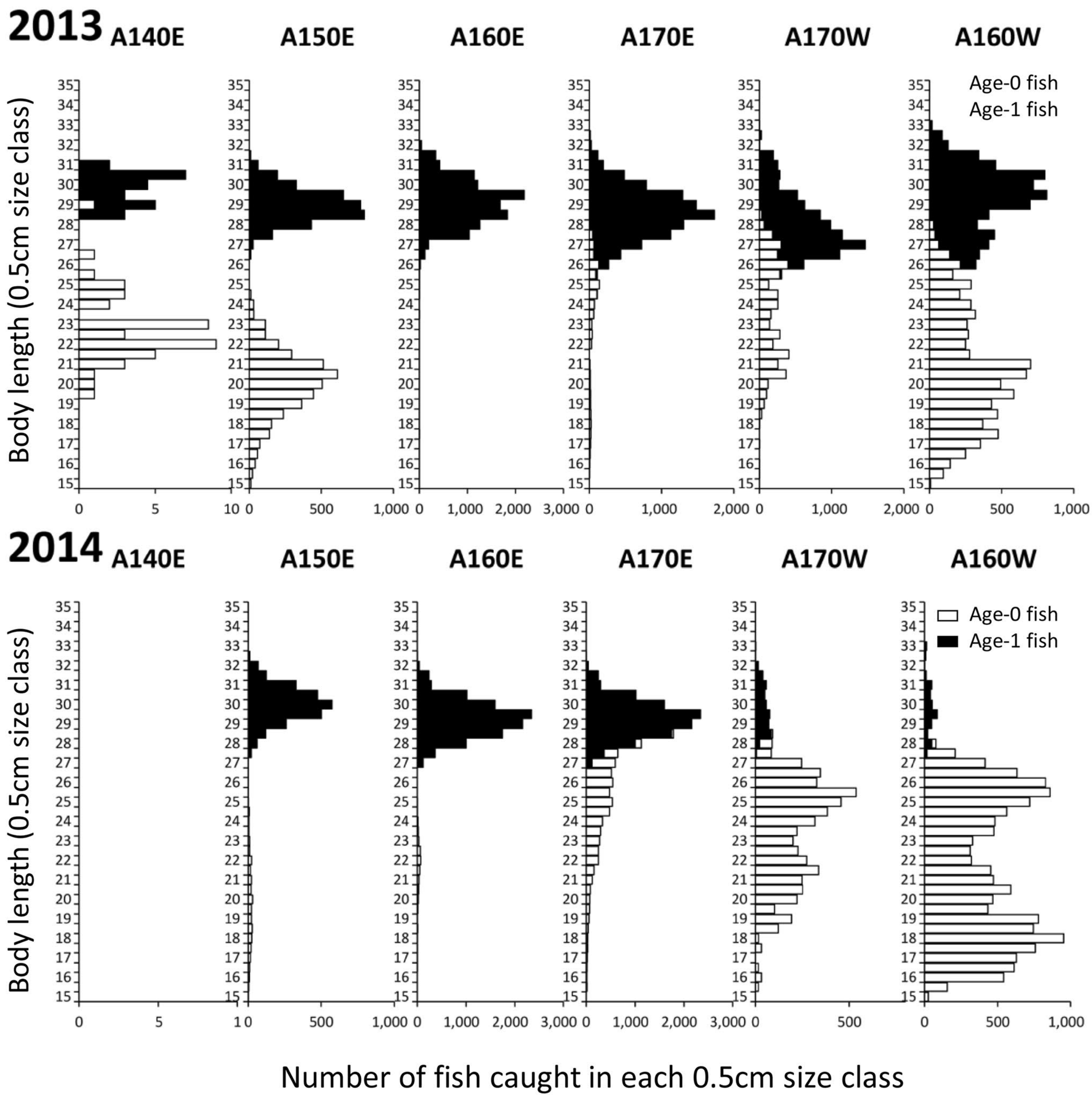

Fig. 2 Size compositions of Pacific saury *Cololabis saira* collected by surface trawl in 10° longitudinal areas in June and July in 2013 (*upper*) and 2014 (*lower*)

were examined, 237 of them were classified as age-1; BL ranged 27.5–34.7 cm. The remaining fish (25 individuals; BL 25.5–28.7 cm) were classified as age-0.

Occurrence of VB-positive arterioles

Whereas no age-0 fish had VB-positive arterioles, 126 (25.9%) of 487 age-1 fish in 2013 (BL 26.4–32.9 cm) and 141 (59.5%) of 237 age-1 fish in 2014 (BL 27.9–34.7 cm), did. BL in fish lacking VB-positive arterioles ranged 25.7–31.7 cm in 2013 and 27.5–31.9 cm in 2014 (Table 2).

The percentages of age-1 fish with VB-positive arteriolesin 2013 were highest at 150°E (71.7%), with 44.2%, 15.0%, 10.8%, and 8.8% in areas A160E, A170E, A170 W, and A160 W, respectively. All age-1 fish collected in 2014 had VB-positive arterioles in area A150E, but the ratio

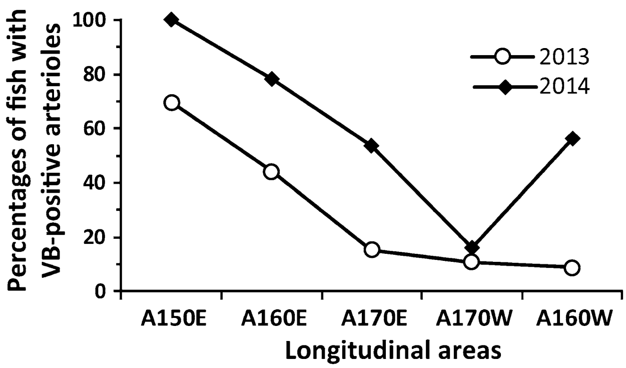

Fig. 3 Percentages of Pacific saury *Cololabis saira* with Victoria blue (VB)-positive arterioles in each longitudinal area in 2013 and 2014

decreased in eastern areas (78.3%, 53.5%, and 16.1% at A160E, A170E, and A170 W, respectively). Exceptionally, 57.5% of fish had VB-positive arterioles in area A160 W, which was higher than values in areas A160E, A170E, or A170 W (Fig. 3).

Occurrence of yolked oocytes, POF and atresia from yolked oocytes

No age-0 fish collected in 2013 or 2014, caught in June or July, had yolked oocytes, POF, or atresia from yolked oocytes. A minority of age-1 fish [18 (3.7%) in 2013 and 9 (3.8%) in 2014] had yolked oocytes, atretic oocytes that originated from yolked oocytes, and/or POF (Tables 2, 3). Seven of 18 fish in 2013 and one of nine fish in 2014 lacked VB-positive arterioles, though they had yolked oocytes and/or atretic oocytes originating from yolked oocytes. All but one of these fish were sampled in the western area. POF

Table 3 Fish with yolked oocytes and/or atretic oocytes originating from yolked oocytes

Individual number	Year	Sampling location				BL (cm)	OW (g)	N of VB-P	Yolked Oocyte	Atretic Oocyte from yolked oocyte	POF
		Sampling date	Latitude	Longitude	SST (°C)						
13611	2013	15 June	42°13′N	167°06′E	10.4	28.6	1.02	10	−	+	−
13639	2013	15 June	42°30′N	167°02′E	7.9	29.5	0.70	36	−	+	−
13675	2013	18 June	41°22′N	170°59′E	14.3	31	1.38	26	−	+	−
13727	2013	24 June	43°04′N	174°58′E	8.9	29.1	1.05	8	−	+	−
13124	2013	24 June	41°27′N	159°00′E	13.8	30.1	1.65	2	+	+	−
13072	2013	28 June	42°18′N	154°59′E	11.8	30	0.63	0	−	+	−
13854	2013	1 July	40°57′N	174°59′W	15.8	31.1	6.02	0	+	+	+
13856	2013	1 July	40°57′N	174°59′W	15.8	31.4	1.30	4	+	+	−
13857	2013	1 July	40°57′N	174°59′W	15.8	31.4	2.74	18	+	+	+
13877	2013	2 July	42°02′N	174°59′W	14.0	31	1.30	8	−	+	−
131024	2013	6 July	43°45′N	170°00′W	14.5	30.5	0.98	4	+	+	−
131051	2013	7 July	42°15′N	170°00′W	15.6	32.9	1.59	3	+	+	−
131052	2013	7 July	42°15′N	170°00′W	15.6	31.5	3.08	0	+	+	−
131031	2013	8 July	41°14′N	170°00′W	18.3	30	2.66	0	+	+	+
131040	2013	8 July	41°14′N	170°00′W	18.3	31.6	2.64	0	+	+	−
131102	2013	13 July	48°35′N	165°01′W	10.4	31	1.40	0	+	+	+
131109	2013	13 July	48°35′N	165°01′W	10.4	31.6	3.28	0	+	+	+
131134	2013	13 July	48°35′N	165°01′W	10.4	31	3.00	34	+	+	−
14071	2014	29 June	43°02′N	158°58′E	11.4	32	1.85	237	+	+	−
14382	2014	28 June	41°02′N	169°00′W	13.6	31.4	1.32	42	+	+	−
14392	2014	28 June	41°02′N	169°00′W	13.6	31.3	2.20	7	+	+	−
14452	2014	1 July	41°46′N	165°01′W	13.8	34.7	4.00	53	+	+	−
14457	2014	1 July	41°46′N	165°01′W	13.8	30.8	3.20	0	+	−	+
14465	2014	1 July	41°46′N	165°01′W	13.8	32.3	3.24	3	+	+	−
14470	2014	1 July	41°46′N	165°01′W	13.8	31.2	1.28	11	−	+	−
14585	2014	15 July	43°46′N	177°58′E	13.1	29	1.90	83	+	+	−
14595	2014	15 July	43°46′N	177°58′E	13.1	32.5	1.84	92	−	+	−

BL body length, *OW* ovary weight, *N of VB-P* detected number of VB-positive arterioles, *POF* post ovulate follicle, present (+) or absent (−)

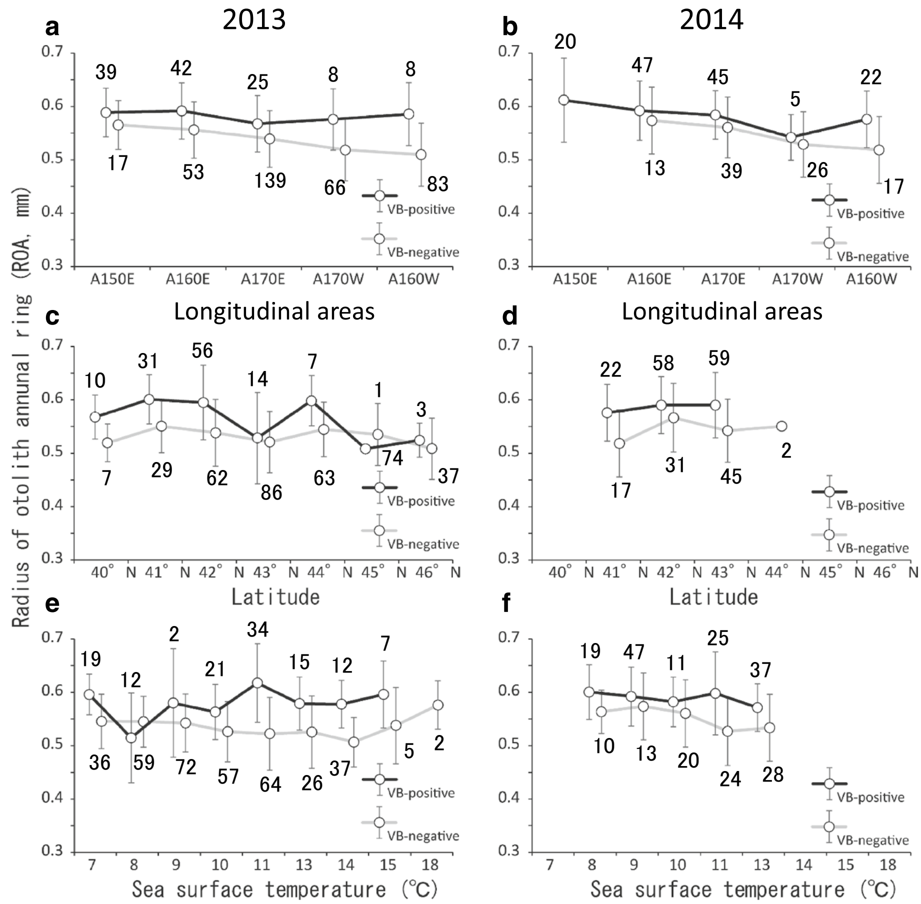

Fig. 4 Relationship between the mean radius (± SD) of the annual ring (ROA) in Pacific saury *Cololabis saira* otoliths, and incidence of Victoria blue (VB)-positive and VB-negative ovarian arterioles, for different latitudinal (**a**, **b**) and longitudinal (**c**, **d**) areas, and SST (**e**, **f**), off the coast of Japan in 2013 (*left*) and 2014 (*right*). *Numbers* denote numbers of fish analyzed

Table 4 Estimated parameters from GLM

Variables	Parameters	Estimates	SE	*P* value
Intercept	α	− 0.073	4.956	0.988
LONG	β_1	− 0.085	0.012	< 0.01
LAT	β_2	− 0.374	0.091	< 0.01
ROA	β_3	5.061	1.989	0.0109
BL	β_4	0.921	0.106	< 0.01
z	β_5	0.997	0.220	<0.01

SE standard error

were detected from five individuals in 2013 and one in 2014; all fish had yolk accumulating oocytes.

Geographic variation in percentages of fish with VB-positive arterioles and ROA

Comparisons of mean ROA in different latitudinal and longitudinal areas and SST, with VB-positive and negative ovarian arterioles are shown in Fig. 4. After model selection, SST and DAY were dropped from the model of best fit. Estimated parameters are shown in Table 4. Calculated *P* values of all parameters are less than 0.05. The longitude (β_1) estimated regression coefficient is negative, while that of ROA (β_3) is positive, meaning the probability of previous spawning increased with a progression west, and as ROA increased. The effect of year (β_5) was different from zero ($P < 0.05$), which suggests that its probability differs between years (Table 4, Fig. 4).

ROA comparison between fish with and without VB-positive arterioles

Mean ROA of all age-1 fish in 2014 [0.57 ± 0.065 mm: mean ± SD, 95% confidence interval (0.563, 0.579)] was higher than that for 2013 [0.55 ± 0.06 mm (0.540, 0.551)]. Mean ROA of fish with VB-negative arterioles in 2014 [0.55 ± 0.06 mm (0.533, 0.559)] was also higher than that for 2013 [0.53 ± 0.06 mm (0.526, 0.538)], but differences were not detected in fish with VB-positive arterioles between 2013 [0.58 ± 0.07 mm (0.572, 0.596)] and 2014 [0.59 ± 0.06 mm (0.578, 0.597)] (Fig. 5).

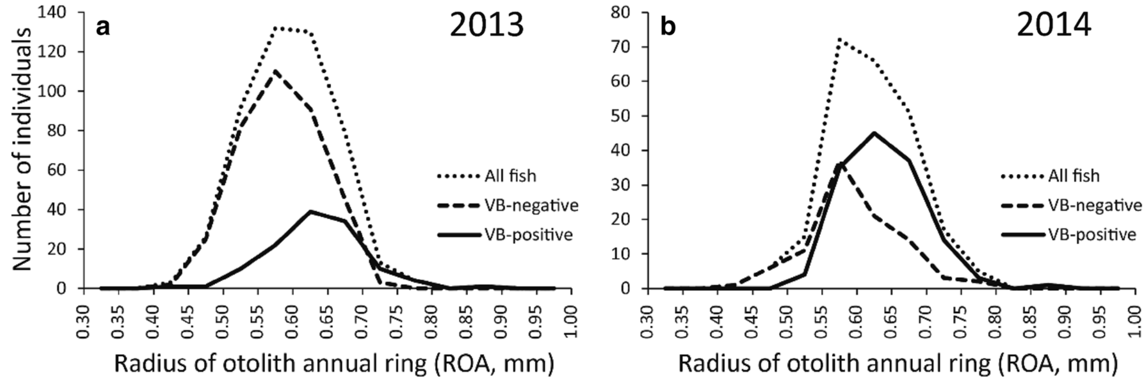

Fig. 5 Size comparison of the radius of the annual ring (ROA) in otoliths for each 0.25-mm size class of Pacific saury *Cololabis saira* caught in 2013 and 2014. *Dotted*, *solid* and *broken lines* depict all fish, fish with Victoria blue (VB)-positive, and VB-negative ovarian arterioles, respectively

Discussion

The incidence of fish with VB-positive arterioles varied according to age and/or collection area. Because variation in the incidence of VB-positive arterioles is caused by differences in the spawning history of an individual fish (Suyama et al. 2016a), the presence of VB-positive arterioles is considered to indicate past spawning experience. As June and July are at the end of the breeding season that commenced the September of the previous year, our results demonstrate age-0 fish do not spawn in the first breeding season in which they hatched. All individuals with VB-positive arterioles are age-1 fish, indicating that some Pacific saury spawn in the second breeding season.

The incidence of fish with VB-positive arterioles also related to ROA. The likelihood of VB-positive arterioles occurring in fish with larger ROA was high, which suggests that BL at the beginning of the breeding season was important for initiation of maturation in their first year. Therefore, BL composition at the beginning of the breeding season, determined by annual and geographical changes in main hatching periods and/or growth rate, influences the percentage of fish that will spawn (Fig. 6). The difference in ROA between eastern and western survey areas was observed every year; Suyama et al. (2012a) inferred that these differences in the ROA were not caused by differences in hatch period, but by differences in growth rate. We consider that a fish's first spawning in the second breeding season, at an age of almost 1 year, is determined mainly by growth rate during the first year.

During both years, both the percentage of fish with VB-positive arterioles and mean ROA were high in the western area, and low in the eastern area. Mean ROA of all age-1 fish was greater in 2014 than in 2013, and the percentages of fish with VB-positive arterioles were also higher in 2014.

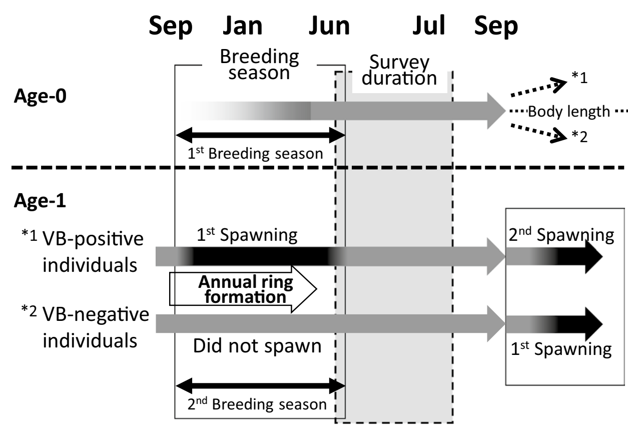

Fig. 6 Schematic of differences in Pacific saury *Cololabis saira* past spawning experience with and without Victoria blue (VB)-positive ovarian arterioles. "Breeding season" and "spawning period" refer to spawning duration for the population, and spawning duration for each Pacific saury individual, respectively. Breeding season traverses years, from September of one year to June of the following year (*square with solid line*). Because age-0 fish lack spawning experience in the first breeding season [i.e., from hatching to survey commencement in June or July (*gray square with broken line*)], they lack VB-positive ovarian arterioles. Some individuals that spawn (*thick black band*) in the second breeding season appear as age-1 fish with VB-positive ovarian arterioles during the survey. Individuals that do not spawn in the second breeding season lack VB-positive ovarian arterioles

However, the mean ROA of fish with VB-positive arterioles in 2013 and 2014 did not differ significantly, and their 95% confidence intervals overlapped. Mean ROA was greater in western than eastern areas, as previously reported by Suyama et al. (2012a, b), which suggests geographical differences in maturation rate occur annually. Differences in zooplankton abundance might contribute to high western-latitude growth rates and the percentage of fish with previous spawning experience; however, information on Pacific saury diet is available for coastal areas only (Taka et al. 1982; Odate 1994; Sugisaki and Kurita 2004). Surveys comparing the important species making up the Pacific saury's diet and the relative abundances of these species in the western and eastern parts of the survey area would be helpful for identifying the causes of geographical variation in growth until age at first spawning.

We considered that geographical differences in growth rates of first year fish would be reflected in the different ROA of age-1 fish, and differences in the percentage of age-1 fish with spawning experience. Our results suggest that age-0 fish do not migrate widely, though Suyama et al. (2012b) reported most age-1 Pacific saury had migrated from east of 160°E to near the coast of Japan from June to December. Larvae and juveniles are abundant in southern waters off Honshu each year during winter (Watanabe and Lo 1989; Takasuka et al. 2014), identifying the importance of this region as a winter spawning ground. Such wide latitudinal migrations have been validated only in age-1 fish (Suyama et al. 2012b, Miyamoto et al. 2019). However, we considered that some larger age-0 fish in the eastern area might possibly migrate to western areas to spawn; in contrast most age-0 fish that do not spawn in their first year do not migrate west. Consequently, the proportion of mature fish in the second breeding season would increase in western areas, and the percentage of age-1 fish with spawning experience during the survey would increase. To determine relationships between maturity and migration in age-0 fish, we should compare otolith growth increments between eastern and western areas, and age-1 fish collected the following year in both areas.

It is unknown how long VB-positive arterioles remain after spawning, though rearing experiments suggest they might persist for 6 months (Suyama et al. 2016a). The breeding season of Pacific saury might continue more than 10 months. We believe that VB-positive arterioles are retained for a long time, probably throughout a current breeding season, because the percentage of individuals with VB-positive arterioles was high in individuals with large ROA. During the migration to southern spawning grounds, larger fish generally arrive first, and start spawning earlier (Fukushima 1979); they would also finish spawning earlier. As the incidence of VB-positive arterioles was high in fish with a large ROA, VB-positive arterioles may persist in individuals that finish spawning early. Furthermore, although individuals with yolked oocytes were common at eastern longitudes, which suggests a spawning delay, the percentage of fish with VB-positive arterioles was low. As such, the reason for low percentages of individuals with VB-positive arterioles in eastern regions might be because of a lack of spawning experience, rather than their disappearance.

The TNFRI has performed stock assessment surveys in the area extending from near the coast of Japan to 165°W during June and July since 2003 (Suyama et al. 2016b). Pacific saury abundance off the Japanese coast to 162°E decreased suddenly after 2010 from levels experienced from 2003 to 2009, and has remained low on the Japanese coast and offshore regions to the west of 165°W. Because percentages of spawned age-1 fish were high in western areas, a decrease in their abundance means total maturation rate also decreased in the first year. Annual changes in Pacific saury distributions in June and July might affect total maturation rates in the first year. Further investigation of geographical variation in maturation rates of age-1 Pacific saury is required when abundance levels in western areas increase to those experienced from 2003 to 2009.

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