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A review of the biology for Pacific saury, *Cololabis saira* in the North Pacific Ocean

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Contents

1. Introduction

Pacific saury, *Cololabis saira*, (hereafter PS) is a small pelagic fish and are distributed from subarctic to subtropical regions of the North Pacific Ocean (Hubbs and Wisner 1980). PS has been traditionally utilized in Japan since at least the 17th century (Fukushima 1979).

The basic biology and ecology of the PS has been extensively studied over the past 60 years (Kosaka 2000); this is fundamental information for stock assessment of this species. Here, we present a brief review on stock identity, spawning ground, maturation process and migration of PS.

2. Stock identity

Some researchers have once suggested that there are at least two seasonal spawning groups in the western North Pacific Ocean: spring-spawning and autumn-spawning groups (Odate 1956, Hotta 1960). However, it is impossible to separate the migration and reproduction processes of these two groups (Fukushima et al. 1990, Suyama 2002). PS had also been divided into three regional subgroups based on their distribution: western North Pacific Ocean, central North Pacific Ocean, and eastern North Pacific Ocean groups (Odate S 1977). PS were scarce in the area from 160°W to the Canadian coast, suggesting that there is a distributional discontinuity between the eastern and central North Pacific Ocean groups (Odate S 1977, Fisheries Research Agency of Japan 2012). Additionally, several differences, such as the number of vertebrae, growth rate, size composition, and parasite fauna and frequency of parasitism (Odate S 1977, Fukushima 1979, Watanabe et al. 1988), were identified between the eastern group and other groups. These facts strongly suggest that the eastern North Pacific Ocean group is independent of the other groups. However, the distribution of PS in the central and western North Pacific Ocean is continuous (Fisheries Research Agency of Japan 2012) and the fish migrate extensively between these areas (Suyama et al. 2012a, Miyamoto et al. 2019); thus, the groups in these areas are homogenous. However, Chow et al. (2009) reported that there was no variance in genetic structure in the PS population from five areas: east China Sea, Sea of Okhotsk, western North Pacific Ocean, central North Pacific Ocean, and eastern North Pacific Ocean.

Hereafter, this review focuses on the fishery biology of PS in the central and western North Pacific Ocean.

3. Early life history

3-1. Spawning ground

PS eggs have filaments that attach to floating objects, such as drifting kelp (Yusa 1960); therefore, it is difficult to conduct a quantitative egg survey of the saury by towing plankton nets. Therefore, the spawning ground of saury has been evaluated in terms of the distribution of larvae and conditions of adults.

The projected spawning ground of PS in the western North Pacific Ocean is summarized in Figure 1. The distribution of saury larvae shifts seasonally from the Kuroshio-Oyashio transitional region in spring and autumn to the Kuroshio region in winter (Odate 1956, 1962, Fukushima et al. 1990, Watanabe and Lo 1989, Watanabe et al. 1997, Watanabe et al. 2003, Iwahashi et al. 2006, Takasuka et al. 2014). It takes approximately two weeks for saury eggs to hatch (Hotta and Fukushima 1963) and this results in disparity between the spawning ground and larval distribution. Iwahashi et al. (2006) projected the spawning ground backcalculating from the distribution and age of larvae in a numerical model; they found that there is a wide range of projected spawning grounds in the Kuroshio-Oyashio transitional region in spring and autumn, and in the Kuroshio region in winter. The distribution of adults almost coincides with the latter region, supporting their expected location of the spawning ground (Hotta 1960, Suyama 2002, Kurita et al. 2002, Meguro et al. 1987, Kurita 2006, Natsume et al. 2009). However, Iwahashi et al. (2006) pointed out that there were some areas left without the estimation in their study due to the lack of feasible larval samplings. For example, the distribution of larvae and spawning adults in the Kuroshio Extension region (east to at least about 160°E) in winter was reported, suggesting the saury spawning ground extend to this region in winter (Kosaka 2000, Fisheries Agency of Japan, Fisheries Research Agency 2012 and 2016). In addition, Baitaliuk et al. (2013) and Odate S (1977) reported the continuous distribution of larvae from 150°E to nearshore area of California in spring and autumn. This suggests that spawning ground extends eastward than area estimated by Iwahashi et al. (2006), although the detail is unknown.

Larval abundance and elevated spawning activity reached a peak during winter in the western North Pacific Ocean (Watanabe and Lo 1988, Kurita et al. 2002). It suggests that the main spawning season of PS is winter season.

3-2. Larval transportation

The eggs, attached to floating objects such as drifting kelp, are transported by ocean currents until they will hatch; however, few studies have focused on this phase. In addition, it is not clear how the eggs of large stocks of PS are supported by a limited quantity of floating objects (Tanaka and Oozeki 1996).

Small larvae drift in the epipelagic stratum and are passively transported by ocean currents (Odate and Hayashi 1977). It has been suggested that larvae that hatched in the Kuroshio region were transported eastward by the Kuroshio current to the Kuroshio Extension region (Oozeki et al. 2009). Similar results were obtained through virtual particle tracking experiments (Iwahashi et al. 2006, Oozeki et al. 2015). However, the range of larval dispersal in the eastern area of 160°E was limited because of weak currents (Iwahashi et al. 2006, Oozeki et al. 2015). Larvae distributed in this region are considered to hatch in the same region (Iwahashi et al.

2006, Oozeki et al. 2015). Juveniles start to school when they reach 50 mm in size in the rearing condition (Watanabe and Kuji 1991) and spontaneously migrate northward.

3-3. Recruitment variability

Significant annual variation in larval mortality was observed in autumn- and spring-spawning cohorts, while the winter-spawning cohorts were stable. Environmental annual variability in the waters inhabited by saury in spring and autumn (Kuroshio-Oyashio transitional region), such as shifts in the Kuroshio and Oyashio fronts, seems to contribute to the variable mortality of saury in these waters in spring and autumn season (Fukushima et al. 1990, Watanabe et al. 1997, Watanabe et al. 2003). Samples collected during the buoy-tracking surveys indicated that natural larval mortality was estimated at approximately 23–37%/day in the Kuroshio region (Oozeki et al. 2009). However, larval mortality was growth dependent (Nakaya et al. 2011), suggesting that the environmental factors that affect larval growth play a major role in larval survival and recruitment variation. Sea surface temperature, chlorophyll *a* concentration, and biomass of copepodite stage copepods were positively correlated with the growth rate of saury larvae in spring and autumn (Oozeki et al. 2004). The stock size index of saury was positively correlated with the content of spring chlorophyll-*a* (Ichii et al. 2017) and/or temperature (Tian et al. 2003) in its nursery ground (subtropical region in the western North Pacific Ocean). In addition, transportation of larvae to its nursery area is also important for their survival and recruitment to the stock (Oozeki et al. 2015). It is important to elucidate the mechanism that transportation and environmental factors affect larval growth, mortality, and recruitment during their prolonged spawning season in the broad spawning ground.

4. Feeding habits and predators

PS is a zooplankton feeder. It utilizes the transitional zone (the area between subarctic and subtropical fronts) as a feeding ground in spring-summer and increases their weight by feeding on abundant subarctic zooplanktons such as *Neocalanus* copepods and euphausiids (Odate K 1994, Sugisaki and Kurita 2004). Feeding activity decrease after fall (Sugisaki and Kurita 2004, Kurita and Sugisaki 2004) and increased in winter, the spawning season, although it is distributed in an area of poor food conditions in the Kuroshio warm current area. Albacore tuna *Thunnus alalonga*, yellowtail amberjack *Seriola lalandi*, mahi-mahi *Coryphaena hippurus*, striped marlin *Kajikia audax*, salmon shark *Lamna ditropis*, blue shark *Prionace glauca*, minke whale *Balaenoptera acutorostrata*, fur seal *Callorhinus ursinus*, and sea birds such as Sooty shearwater *Puffinus griseus* were reported as predators for PS (Tokai Reg Fish Res Lab 1959, Tanino et al. 1985, Minami et al. 1995, Minami and Ogi 1997, Gould et al. 2000, Tamura and Fujise 2002, Mitani et al. 2006, Davies et al. 2009, Glaser et al. 2015).

5. Growth

PS is two-year lived fish (Suyama et al. 2006a) which grows up to ca. 320 mm in knob length (distance from tip of lower jaw to posterior end of muscular knob on caudal peduncle, Kimura 1956a) and ca. 200 g body weight. The growth schedule of this fish has been estimated by several methods; otolith increments, tank rearing experiment and bioenergetic model.

Otolith increments of PS has been used in many studies of growth. Suyama et al. (2006a) used the otolith annual ring and found age-0 and age-1 fish can be divided at the body length of ca. 290 mm in autumn season. The daily formation of otolith increments was evaluated by tank rearing experiments (Watanabe and Kuji, 1991). Watanabe et al. (1988) and Suyama et al. (2015) described growth trajectory using otolith daily increments. They fitted body length and daily age data derived from field samples to the Gompertz growth curve. These two studies showed similar patterns of growth (Fig. 2a, Table 1). On the other hand, Nakaya et al. (2010) derived the growth curve during 340 days after hatching under laboratory condition. Estimated asymptotic body length in Nakaya et al. (2010) was smaller than others (Fig. 2) because they use only age-0 fish.

Growth trajectory was also estimated using bioenergetics/ecosystem coupled model called NEMURO.FISH (Ito et al. 2004, Ito et al. 2007). This model calculates the time-change of body length/weight (i.e., growth) as the difference of income and consumption of energy in the fish body. Giving the information of north-south migration and feeding conditions in each area (Kurita and Sugisaki, 2004, Sugisaki and Kurita, 2004), Ito et al. (2007) successfully reconstructed the growth pattern of PS similar to other studies. In addition, they found that the PS growth ceases during winter because of the energy expenditure for its spawning and the poor prey condition in the subtropical spawning ground.

Some researchers focused on the geographical difference in PS growth. Pacific sauries in the western North Pacific Ocean grow faster than those in central and eastern North Pacific Ocean waters (Watanabe et al. 1988, Suyama et al. 2012). Suyama et al. (2012b) reported faster growth in sauries distributed west of 160°E than east of 170°E.

Kosaka (2000) and Suyama et al. (2015) reported the relationship between knob length and body weight (Fig. 2b, Table 1).

6. Maturation

6-1. Spawning pattern, fecundity and spawning duration

The oocyte development pattern of PS is asynchronous developmental type and is considered to lay eggs multiple times during a single spawning season (Hatanaka 1955, Sato 1981, Kosaka 2000, Suyama 2002, Suyama et al. 2016). Though their spawning season lasts from September to next June (Watanabe and Lo

1989), the individual spawning period is considered to be shorter than the entire spawning season. However, we do not know the actual spawning duration of a wild individual. Under rearing conditions, spawning lasted for five months, but the actual individual spawning period could be about three-four months (Suyama et al. 2016). Suyama (2002) reported that there was no clear relationship between batch fecundity and body length, and the batch fecundity of PS as ca. 2000 per a female. Several papers reported similar pattern (Kubo 1954, Hatanaka 1956). As PS is regarded as an income breeder (most of the energy allocated to egg production is derived from the food consumed during spawning; Kurita 2003), the total number of spawned eggs vary depending on the food availability in the spawning ground.

Suyama (2013) estimated the total number of spawned eggs per fish per one spawning season (supposed as 4 months) as 47000-18000 from the results of tank rearing experiments. In these experiments, the size of spawners coincided to that of age-0 fish (ca. 25-27 cm).

6-2. Seasonal change of maturity size

The knob length at first maturity varies among seasons; the size gets smaller during main spawning season, winter (Hatanaka et al. 1953, Hatanaka 1955, Kosaka, 2000, Kurita 2001). The smallest size of PS maturity was 260 - 287 mm in autumn (September to December), and 270 - 294 mm in spring (Hatanaka et al. 1953, Hatanaka 1955, Kurita 2001, Suyama 2002, Kurita 2006, Huang and Huang 2015). On the other hand, Hatanaka et al. (1953) reported the minimum length of maturity in winter (January and February) as 254 mm, although they pointed out the possibility of missing the smaller samples because of the catchability of fishing gear. Suyama (2002) observed the developmental stages of oocytes of year-round samples and found the knob length of smallest matured female fish was 253 mm in winter. Kurita (2001) observed the developmental stages of oocytes and revealed minimum length was ca. 210 mm in winter. Kosaka (2000) also reported that PS start maturing at ca. 220 mm KnL in winter (January to March) estimated by gonadosomatic index (GSI).

Tank rearing experiments clearly showed the first maturation of PS. Nakaya et al. (2010) showed the minimum size of females that matured (GSI of > 1) was 234.7 mm KnL (310 days after hatch). Suyama et al. (2006b) reported that PS can start spawning within half year after hatching at the length of ca. 234 mm under high temperature condition in the tank (ca. 19 °C).

6-3. Maturation schedule for each seasonal cohort considering growth and maturation size

PS has long spawning season (Suyama 2002), suggesting the several seasonal cohorts. Many studies suggested the autumn, winter and spring spawn cohorts to describe the whole picture of PS population dynamics (e.g., Fukushima et al. 1990, Watanabe et al. 2003). Kurita et al. (2002) and Suyama (2002) conceptually described the schematic images of growth and maturity schedules of each seasonal cohorts (Fig. 3). They estimated that autumn and winter cohorts joined spawning in their second winter as age-0 fish because they have enough time to grow to smallest size at maturity until the next winter. On the other hand, spring cohort does not reach to that length up to winter and skip the second winter without spawning, keeping on growing until next autumn. In the third spawning season, all cohorts join to spawning as age-1 fish. In summary, age-1 fish and a part of age-0 fish (autumn and winter cohorts) spawn in main spawning season (winter). Only age-1 fish spawns in the other spawning season (autumn and spring).

6-4. Maturation and environmental factors

The main environmental factors affecting attainment of maturity is water temperature. Kurita (2006) reported that the maturation status of this species is related to sea surface temperature (SST), noting that almost all females were actively spawning in areas of high SST (>18 °C), whereas no females were spawning in low SST zones (<13 °C). Under rearing experiments, maturation was suppressed in the water temperature less than 12 °C (Suyama 2013).

6-5. Percentage of matured fish

As we mentioned in 6-3, all age-1 fish would get matured in the last spawning season. On the other hand, a part of age-0 fish would get matured in their first year. It is difficult to get the reasonable value of maturity ratio of age-0 PS population because of following reasons. First, maturation status varies spatio-temporary depending on environmental factors such as temperature (Kurita 2006). Second, the individual spawning duration of this asynchronous maturing fish (ca. 5 months in maximum) is shorter than whole spawning season of this species (10 months) (Suyama et al. 2016). In addition, it is difficult to confirm the spawning experience of individuals that have passed considerable time after spawning because spawning record (post ovulatory follicle is usually used as an index) disappears immediately (within several days) in case of PS (Suyama 2002). Thus, the rate of spawning fish at a certain moment does not much with the maturation rate of whole spawning season. To overcome this problem, Suyama et al. (2016) developed a new method to detect past spawning experience of PS that remain longer period after its spawning. Then Suyama et al. (2019) applied this method to the filed samples derived in the Japanese biomass survey in June and July. The rate of spawned fish varied from ca. 10 to 100 % according to longitudinal areas. The ratio was higher in the western than eastern area. The ratio also considerably fluctuated by years.

7. Distribution and migration

Detailed, and broadly covered age-specific distribution patterns of PS is only known in June and July (Fig. 4). The spatial distributional patterns were clearly different between age-0 and age-1 fish, that is, age-0 fish tend to distribute in eastern areas than age-1. Accordingly, in most years the percentage of age-0 fish increased as we go east and reach in high abundance beyond 180˚ (Kidokoro et al. 2017, Fuji et al. 2018; Fig. 4).

The migration of age-1 PS is summarized in Figure 5. Age-1 fish is mainly distributed from 150°E to 180° in the North Pacific Ocean (Fisheries Research Agency in Japan 2012). Age-1 fish is mostly distributed in the Kuroshio-Oyashio transitional region (approximately 35°N–40°N), gradually migrating northward with the warm water extension during the spring/early summer season (Fukushima 1979, Tameishi 2000). Main schools drastically migrate northward and reach ca. 45°N, the southern part of Oyashio region, after July. The age-1 fish then remain in the subarctic water, which is characterized by a high abundance of prey organisms, such as *Neocalanus* copepods and *Euphausia pacifica*, leading to high feeding activity and energy storage until August (Kurita 2003, Kurita and Sugisaki 2004, Sugisaki and Kurita 2004). Age-1 fish start to migrate westward along with the offshore Oyashio front after autumn, in order from the west to the east of their distribution during the spring/early summer season (Yasuda and Watanabe 1994, Suyama et al. 2012a, Miyamoto et al. 2019). Simultaneously, the fish move southward, coincident with the southward shift of the offshore Oyashio front (Huang et al. 2007). Consequently, fish migrate south-westward from the subarctic offshore area during the autumn/winter season. PS distributed in the area at 150°E–160°E (the western limit of their distribution range during the spring/early summer season) appear in the eastern area of Hokkaido in September and then reach the Kuroshio region (south of Honshu island) in October or November (Kimura 1956b, Kosaka and Tanno 1984, Iwahashi et al. 2006). Fish distributed in the area around 180° (the eastern limit of their main distribution range during pre-fishing season) during spring/early summer arrive in the offshore area of Sanriku Coast in November or December (Suyama et al. 2012, Miyamoto et al. 2019). On the other hand, some schools remain in the offshore area after November, without south-eastward migration (Huang et al. 2007, Fisheries Agency of Japan, Fisheries Research Agency 2009, Tseng et al. 2011). The southward migration route in autumn around the Japanese coast is dependent to the location of the offshore Oyashio front in early autumn. When the offshore front is positioned north (south), the fishing grounds were formed relatively nearshore (offshore) (Yasuda and Watanabe 1994). PS migrates through not only the area near the Japanese coast, but also the high sea around 170°E (Huang et al. 2007). After January, most of the age-1 fish are distributed in the Kuroshio region and Kuroshio Extension region (to the south of 35°N) and actively spawn (Fukushima 1979, Fisheries Agency of Japan, Fisheries Research Agency 2012,2015).

Although knowledge on the migration of age-0 fish is limited, it is known that age-0 saury migrates northward during the spring/summer season and southward during the autumn/winter season (Kosaka 2000). The age-0 fish migration tends to lag behind that of the age-1 fish (Yasuda and Kitagawa 1996). During the northward (southward) migration season, age-0 fish are dense in the southern (northern) area (Fukushima 1979, Meguro et al 1987). Suyama et al (2012a) detected the difference in radius of otolith annual ring in fish collected between the areas east of 160°E and west of 170°E. These differences considered to be caused by the difference of the growth rate in both area in the first year (Suyama et al. 2012b). The geographical difference in ROA in age-1 fish suggested the fish that grow up in the eastern and western areas do not mix, do not largely east-westward migration in their first year.

8. Natural mortality

Several studies revealed out the mortality during larval-juvenile stage. For example, Watanabe et al. (2003) estimated the daily instantaneous mortality rate for each seasonal cohort as 0.060-0.107. However, information of adult natural mortality is scarce. Matsumiya and Tanaka (1976) tried to estimate the mortality during autumn season using fishing statistics, although they pointed out the difficulty of reasonable estimation because of unignorable immigration and emigration of fish school in the fishing ground. Some researchers utilize the equation suggested by Tanaka (1960) to estimate the natural mortality from longevity of PS (Oozeki et al. 1998, Watanabe et al. 2006, Suyama et al. 2015). Suyama et al. (2015) used 2 years as the longevity of PS and estimated the natural mortality as 1.25 per year. Nakayama et al. (2019) calculated several natural mortality estimators for PS on trial and found that estimators distributed relatively high range, between 1.71 and 2.75.

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10. Table and figures

Table 1 Growth curves and length-weight relationships of Pacific saury.

	Equation	Reference
Growth curve	$\mathrm{KnL} = 5.95\exp\left(\left(\frac{0.0504}{0.0128}\right)\left(1 - e^{(-0.0115(t-5))}\right)\right)$	Watanabe et al. (1988)
	$\mathrm{KnL} = 277.1\exp\left(-\exp\left(-0.015(\mathrm{t} - 83.8)\right)\right)$	Nakaya et al. (2010)
	$\mathrm{KnL} = 305.8\exp\left(-\exp\left(-0.01196(\mathrm{t} - 112.1)\right)\right)$	Suyama et al. (2015)
Length–Weight relationship	$\mathrm{BW} = 0.0017KnL^{3.3216}$	Kosaka (2000)
	$\mathrm{BW} = 0.0022KnL^{3.2315}$	Suyama et al. (2015)

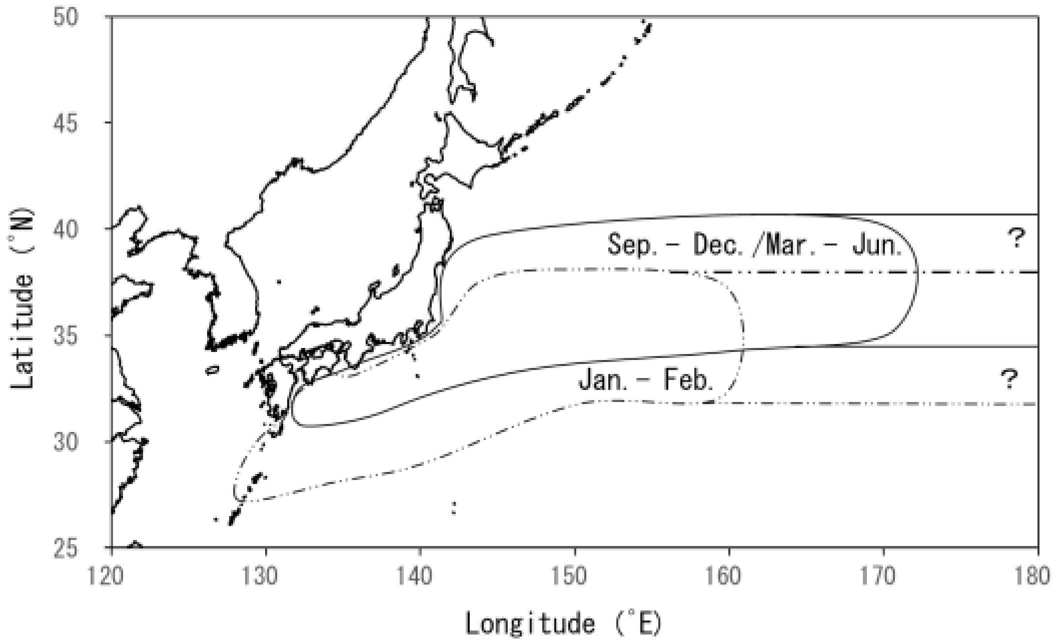

Figure 1. Schematic image of seasonal spawning ground of Pacific saury in the western North Pacific Ocean. The eastern boundaries of seasonal spawning grounds are unknown.

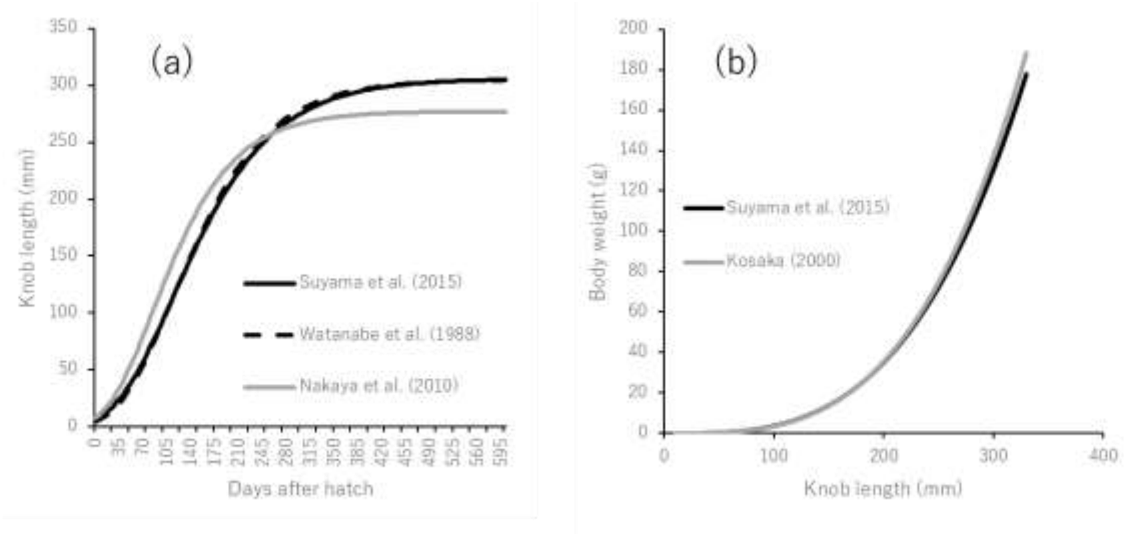

Figure 2. (a) Growth curves of Pacific saury suggested by Watanabe et al. (1988), Nakaya et al. (2010) and Suyama et al. (2015). (b) Length-Weight relationships suggested by Kosaka (2000) and Suyama et al. (2015).

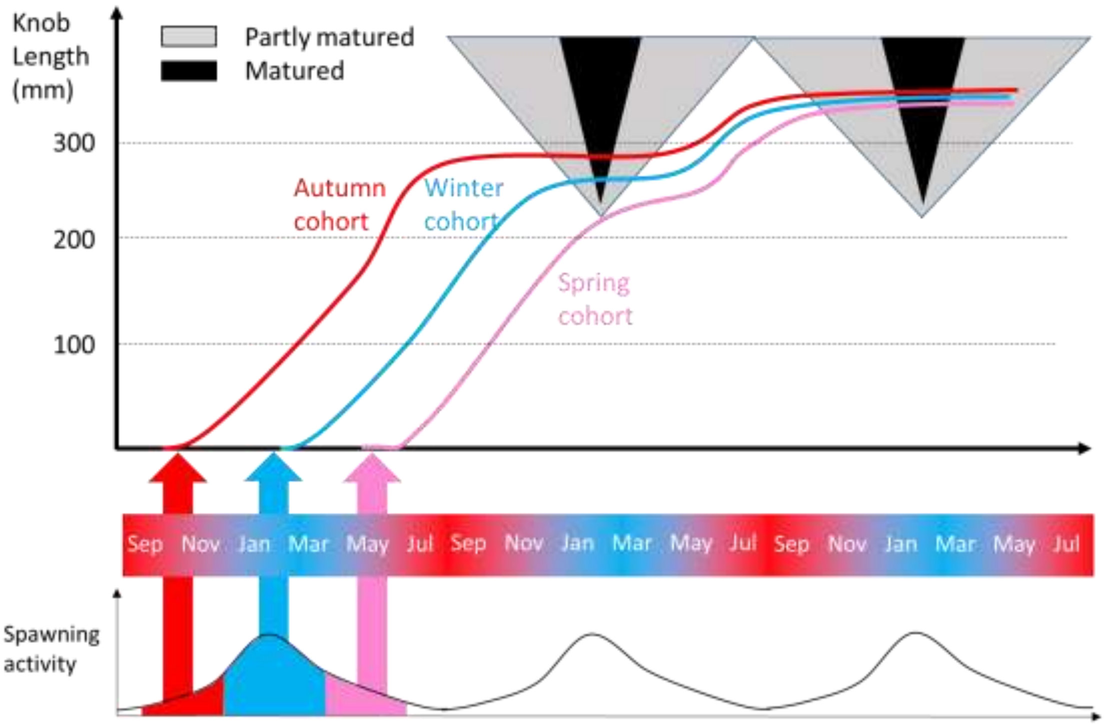

Figure 3. Schematic image of growth and maturity schedules of Pacific saury for each seasonal cohort, redrawn from Kurita et al. (2002) and Suyama (2002).

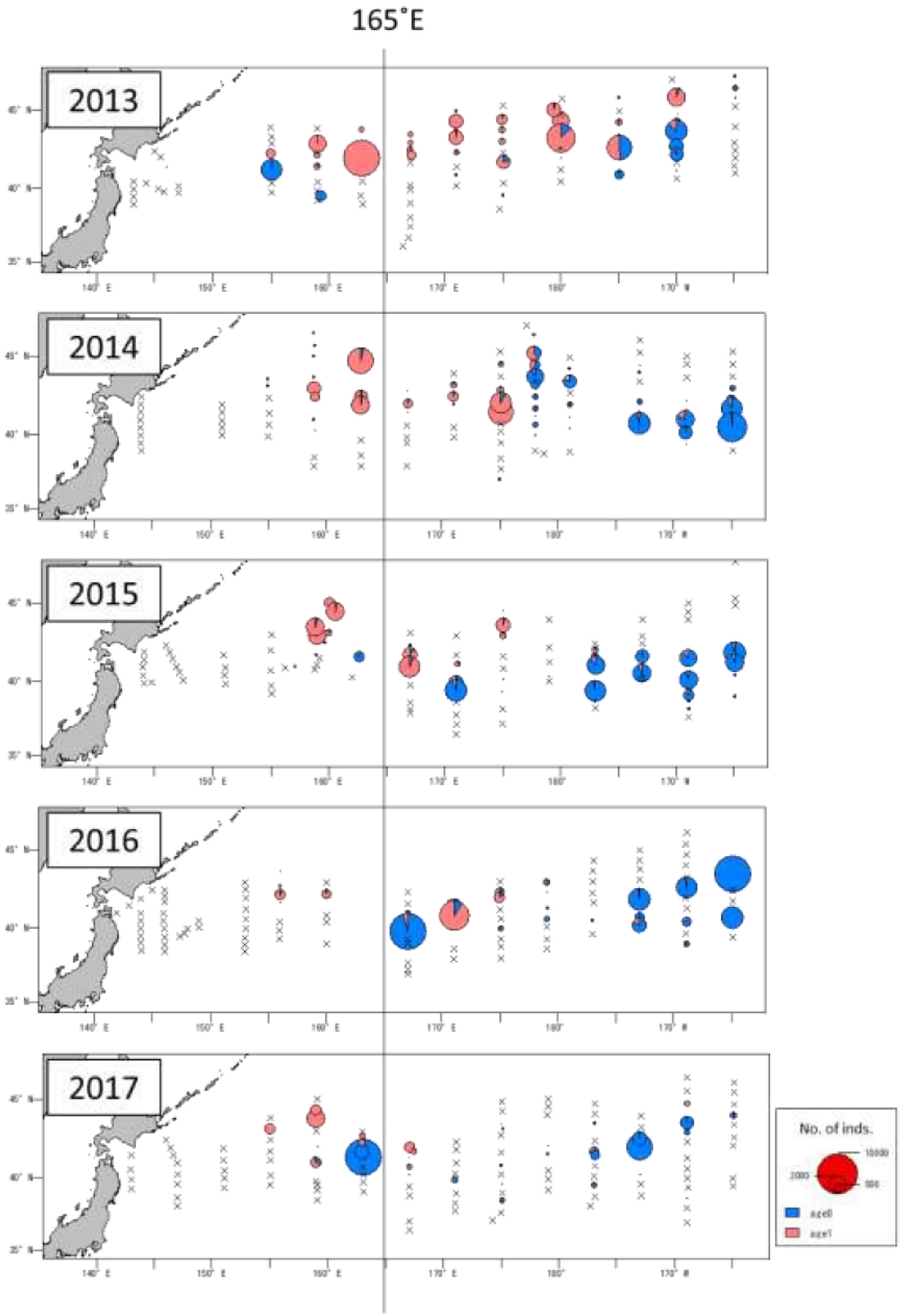

Figure 4. The results of biomass surveys using sea surface trawl net in recent 5 years.

The size of circle shows the number of collected saury in each sampling station.

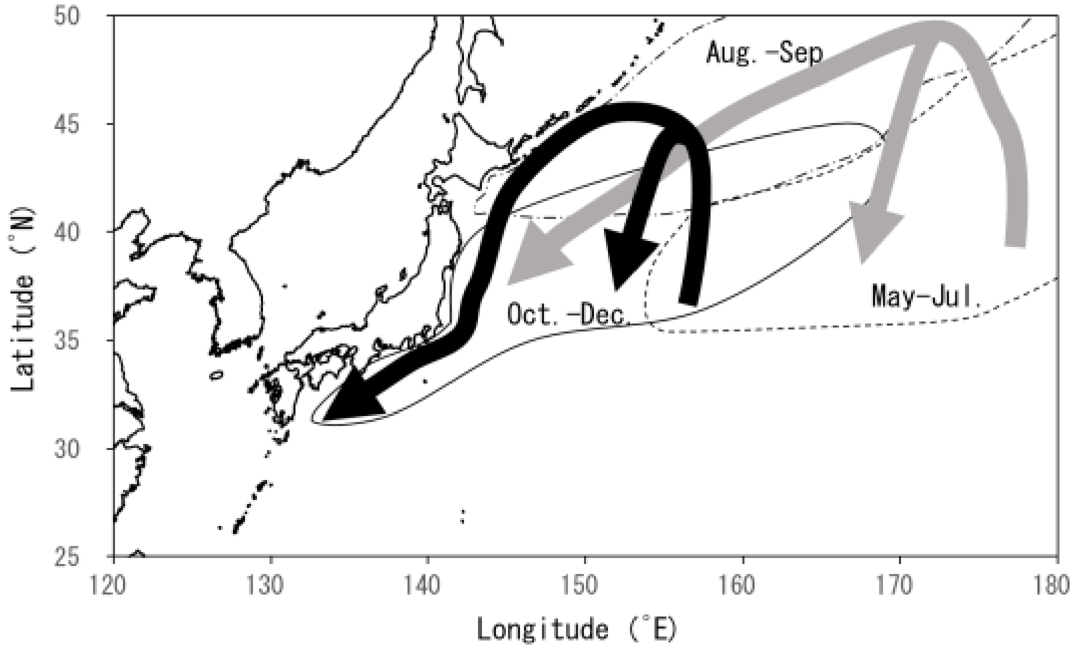

Figure 5. Schematic image of migration of age- 1 Pacific saury in the western North Pacific Ocean during spring-autumn season. Black and grey arrows show the projected migration route of fish distributed in the western and eastern limit of their distribution range during the northward migration season (May-July), respectively. The main distribution range is indicated for each season.