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Oceanographic factors affecting interannual recruitment variability of Pacific saury (*Cololabis saira*) in the central and western North Pacific

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Abstract

Pacific saury (*Cololabis saira*) has a short life span of 2 years and tends to exhibit marked population fluctuations. To examine the importance of sea surface temperature (SST) and mixed layer depth (MLD) as oceanographic factors for interannual variability of saury recruitment in early life history, we analyzed the relationship between abundance index (survey CPUE (catch per unit of effort)) of age-1 fish and the oceanographic factors in the spawning and nursery grounds of the previous year when they were born, for the period of 1979–2006, in the central and western North Pacific. Applying the mixture of two linear regression models, the variability in the survey CPUE was positively correlated with previous year's winter SST in the Kuroshio Recirculation region (KR) throughout the survey period except 1994–2002. In contrast, the survey CPUE was positively correlated with the previous year's spring MLD (a proxy of spring chlorophyll *a* (Chl-*a*) concentration) in the Kuroshio-Oyashio Transition and Kuroshio Extension (TKE) during 1994–2002. This period is characterized by unusually deep spring MLD during 1994–1997 and anomalous climate conditions during 1998–2002. We suggest that saury recruitment variability was generally driven by the winter SST in the KR (winter spawning/nursery ground), or by the spring Chl-*a* concentration (a proxy of prey for saury larvae) in the TKE (spring spawning/nursery ground). These oceanographic factors could be potentially useful to predict abundance trends of age-1 saury in the future if the conditions leading to the switch between SST and MLD as the key input variable are elucidated further.

KEYWORDS
chlorophyll, Kuroshio, Kuroshio-Oyashio Transition, mixed layer depth, mixture of regression model, Pacific saury, recruitment, temperature

1 | INTRODUCTION

Pacific saury, *Cololabis saira*, is a major pelagic commercial fish harvested by China, Japan, Korea, Russia, and Taiwan in the northwestern Pacific. Annual catches of saury have fluctuated greatly from 181,000

metric tons (t) in 1998 to 629,000 t in 2014, with an annual average of about 362,000 t during the period 1980–2014 (FAO; http://www.fao.org/fishery/species/3001/en; Accessed on 02/02/2017).

The distribution range of Pacific saury extends in the areas north of 25°N over the entire North Pacific from coast to coast (Hubbs &

Wisner, 1980). This species is an oceanic spawner, so that adults, juveniles, and larvae show a continuous distribution from inshore waters to offshore waters (Watanabe & Lo, 1989). Pacific saury migrate from the subtropical waters to their feeding grounds in sub-arctic regions (Fukushima, 1979), and the spawning season continues from autumn through spring (Watanabe & Lo, 1989). In the western North Pacific, Pacific saury spawn in the Kuroshio-Oyashio Transition region in autumn and spring, and in the Kuroshio region in winter (Watanabe, Kurita, Noto, Oozeki, & Kitagawa, 2003; Watanabe, Oozeki, & Kitagawa, 1997; Figure 1).

Pacific saury have a short life span of 2 years (Suyama, Kurita, & Ueno, 2006) and tend to exhibit marked population fluctuations (e.g., Tian, Akamine, & Suda, 2003; Watanabe et al., 2003). Oceanographic factors in the spawning and nursery grounds of Pacific saury are considered to affect interannual variability of saury recruitment in early life history and accordingly the population dynamics. Tian, Ueno, Suda, and Akamine (2004) hypothesized that the winter sea surface temperature (SST) in the Kuroshio region strongly affects early survival processes and determines the recruitment success and accordingly abundance of Pacific saury. Watanabe (2009) indicated that the SST rise in the Kuroshio-Oyashio Transition region in spring after 1988 could favor survival and the eventual recruitment of the transition region spawned cohorts of Pacific saury. Yasuda and Watanabe (2007) suggested that the winter mixed layer depth (MLD) in the Kuroshio Extension influences the recruitment of Pacific saury because the MLD could regulate the winter chlorophyll *a* concentration (Chl-*a* concentration; a rough proxy of prey for Pacific saury). These studies were conducted using time-series of Japanese commercial fishery-derived abundance index that were collected in the western North Pacific.

On the other hand, time-series of survey-derived abundance index for Pacific saury are available for monitoring of the stock level in the central North Pacific from 1979. So far, this fishery-independent data has not been fully analyzed in relation to saury population dynamics; only a limited period (1998–2006) of time-series data has been analyzed in relation to the Chl-*a* concentration data (Ichii et al., 2017). This study showed that spring Chl-*a* concentration around the Kuroshio Extension and Kuroshio Bifurcation front (KBF) could influence the recruitment of saury during this limited period. However, the influence of spring Chl-*a* concentration prior to 1998 is not certain because the time series of satellite-derived Chl-*a* concentration data are only available from 1998 onwards. We therefore analyzed a longer period of the time-series data (i.e., 1979–2006) to understand Pacific saury recruitment success during early life in relation to the variability of oceanographic factors by including MLD in the present study as a proxy for Chl-*a* concentration.

Specifically, this study addressed the following:

1. comparison of survey-derived abundance index and fishery-derived abundance index to examine consistency between them;
2. examination of the importance of the SST and MLD as oceanographic factors affecting the interannual variability in saury recruitment and;
3. estimation of contribution ratios of the important oceanographic factors for each year using a finite mixture model of linear regressions (Faria & Soromenho, 2010).

It should be noted that, for Pacific saury, catch rates (percentage of catch to stock biomass) were estimated to be less than 12% in the period 1991–2006 (Ueno, Suyama, Nakagami, Mouri, & Ito, 2006), so that there should be less influence of the fishery on the stock even in the low stock years during the study period.

2 | MATERIALS AND METHODS

2.1 | SST and MLD data

We used SST and MLD data from an ocean data assimilation system, MOVE/MRI. COM-WNP (Usui et al., 2006), at monthly intervals during the period of 1980–2006. Data from MOVE/MRI. COM-WNP
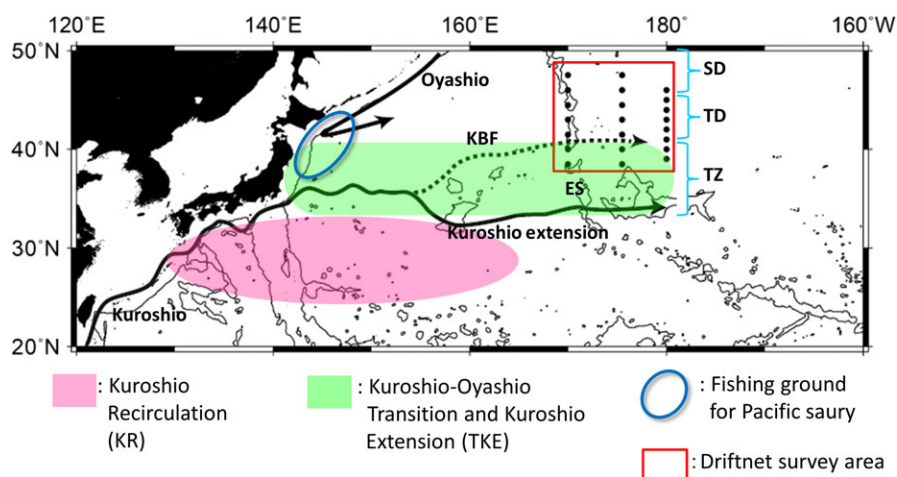

FIGURE 1 Survey areas and major oceanographic regions in the North Pacific Ocean. Solid circles enclosed by red box indicate locations of driftnet survey sites. The bottom contours at 4,000 m are illustrated

KBF: Kuroshio Bifurcation Front   ES: Emperor Seamounts
SD: Subarctic domain TD: Transition Domain   TZ: Transition Zone

are available only from 1980 onwards. MLD is defined as the depth where the density is 0.125 kg/m³ higher than that at the surface. The ocean data assimilation system comprises an ocean general circulation model (MRI.COM; Tsujino et al., 2011) and a variational analysis scheme. The horizontal resolution is variable: 1/10° from 117°E to 160°E, and 1/6° from 160°E to 160°W, zonally; and 1/10° from 15°N to 50°N, meridionally. Details of this assimilation system was explained in Usui et al. (2006).

Regarding MLD, the data are less reliable before 1992 because of the unavailability of the satellite sea-surface-height data. However, as mentioned in the Results, MLD data from 1993 onward is relevant to our study because the significant correlations between MLD and the survey CPUE and between Chl-a and spring MLD observed during 1993–2006 and 1998–2006 respectively, were used in the analysis to derive the results. Therefore, the reliability of MLD data before 1992 may not be crucial to our study.

2.2 | Chl-a concentration and net primary production data

We used Sea-viewing Wide Field-of-view Sensor (SeaWiFS) level-3 binned monthly 9 km resolution Chl-a concentration data for 1998–2006. These data are available from NASA Goddard Space Flight Center, Ocean Biology Processing Group (2014): http://oceandata.sci.gsfc.nasa.gov/SeaWiFS/L3BIN. Accessed on 02/02/2017.

Monthly Net Primary Production (NPP) was estimated by the Vertically Generalized Production Model (VGPM) (Behrenfeld & Falkowski, 1997) using 9 km resolution SeaWiFS.r2014 Chl-a concentration, cloud-corrected incident photosynthetically active radiation (PAR) and AVHRR SST data for 1998 and 2006. Euphotic depths used for the NPP estimation were calculated from SeaWiFS Chl-a concentration data following Morel and Berthon (1989). The generic mapping tools (GMT) software package was used to produce contour lines depicting the distribution of anomaly of NPP.

2.3 | Driftnet survey and commercial fishery data

To reveal interannual changes in abundance of Pacific saury, we examined catch and effort data from a driftnet survey conducted in the central North Pacific initially by Hokkaido University (HU) from 1979 to 1999 (Hokkaido University, 1980–2000) and then continued by the National Research Institute of Far Seas Fisheries (NRIFSF) from 2001 to 2006 (Ichii et al., 2011). The data were collected annually from July to August at nearly fixed sites along primarily a 175°30′E longitudinal transect and also along 170°E and 180° longitudinal transects during some years between 38°30′N and 47°30′N (Ichii et al., 2017) that passed through the Subarctic Domain and Transition Region (Transition Domain and Zone; Figure 1). For each driftnet site, 49 to 134 net panels were deployed in the evening and retrieved the following morning at sunrise. Each panel was 50 m long and 7 m deep. Survey driftnets used by HU comprised of commercial mesh nets (stretched mesh size: 112 to 118 mm) and a nonsize selective net ensemble (18 mesh sizes from 19 to 157 mm, see

Takagi, 1975). Driftnets used by the NRIFSF comprised of commercial mesh nets (115 mm mesh) and a non-size selective net ensemble (12 mesh sizes from 48 to 157 mm).

We examined age-1 (1 year old) Pacific saury, which were defined as individuals with knob length ≥28 cm considering Suyama et al. (2006). It may be noted that Suyama et al. (2006) examined Pacific saury caught from September to November and defined age-1 fish as individuals with knob length ≥29 cm. As our survey was conducted from July to August, we used "knob length ≥28 cm" based on the age-length relationship of Pacific saury (Ueno, Suyama, Nakagami, Naya, & Ito, 2008). Since age-1 Pacific saury (saury hereafter) were effectively collected using mesh sizes, 33–48 mm, the survey driftnet CPUE (catch per unit of effort; abundance index) was calculated as the number of saury per driftnet panel of these meshes. Following Ichii et al. (2017), we consider that there should be no need to standardize the survey driftnet CPUEs (survey CPUE hereafter) because the survey was principally conducted in fixed months and locations, which cover the latitudinal occurrence range of the study species in summer, using the same sampling method (i.e., driftnet).

The driftnet survey was not conducted in 2000, thus survey CPUE in this year was estimated from the fishery abundance index for saury by using a linear regression between the survey CPUE and the fishery abundance index, which is presented in the Results section. The fishery abundance index (the number of age-1 fish migrating into the fishing ground) is defined as the sum of mean CPUE (the number of age-1 fish per haul) for 0.5° × 0.5° latitude longitude grid at 10 day intervals throughout the fishing ground (35°N–48°N, 140°E–160°E) and fishing season (August–December) (Naya, Nakagami, Suyama, & Ueno, 2011, 2012). For calculation of this index, catch in number of all fish was converted from the catch in weight of all fish using mean body weight and based on body length frequency and by applying the age-length key, catch in number of age-1 fish was estimated for each 10 day. Both survey CPUE and the fishery abundance index were natural log (ln) transformed to satisfy the assumption of normality and homogenous variance.

2.4 | Correlation analysis

To identify regions and seasons related to recruitment variability of saury, we examined the spatial distribution of correlation coefficients of ln (survey CPUE +1) with oceanographic factors, i.e., SST and MLD. Because the survey CPUE is the index of age-1 fish, we used SST and MLD data of the previous year when age-1 fish were born, to elucidate the influence of oceanographic factors on their recruitment during early life. In the correlation analyses, SST and MLD are interpolated to a 1° × 1° horizontal resolution.

2.5 | Mixture model of linear regressions

As mentioned in the Introduction, two oceanographic factors, i.e., winter SST or spring MLD, in the spawning/nursery grounds are considered to influence interannual change in the survey CPUE of the

following year. We used the long-term time-series data on these two factors in the present study. For the purpose of estimating the contribution ratio of each factor to survey CPUE variability of the following year, we used two component mixture of linear regression model as follows:

$$y_t = \begin{cases} \beta_{01} + \beta_{11}x_{1(t-1)} + \beta_{21}x_{2(t-1)} + \varepsilon_{1t} & \text{with probability } \pi_1 \\ \beta_{02} + \beta_{12}x_{1(t-1)} + \beta_{22}x_{2(t-1)} + \varepsilon_{2t} & \text{with probability } \pi_1 \end{cases} \quad (1)$$

where y_t is ln(survey CPUE$_t$ +1) of year t; $x_{1(t-1)}$ and $x_{2(t-1)}$ are winter SST and spring MLD, respectively, of year $t-1$; β_{ij} are regressions coefficients ($i = 0, 1, 2$; $j = 1, 2$); π_j are mixing probabilities ($\sum_{j=1}^{2} \pi_j = 1$); and $\varepsilon_{jt} \sim N(0, \sigma_j^2)$ where σ_j^2 is the residual variance. Both x_{1t} and x_{2t} are standardized to have a mean of zero and a standard deviation of one.

Given a set of independent observations $y_1, y_2, \ldots, y_n$, corresponding to predicator values (x_{10}, x_{20}), $(x_{11}, x_{21}), \ldots, (x_{1(n-1)}, x_{2(n-1)})$, the complete set of the mixture model, $\theta = (\pi_1, \pi_2, \beta_{01}, \beta_{11}, \beta_{21}, \beta_{02}, \beta_{12}, \beta_{22}, \sigma_1^2, \sigma_2^2)$, can be estimated by maximizing the log-likelihood:

$$L(\theta \mid y_1, y_2, \ldots, y_n) = \sum_{t=1}^{n} \log\left(\sum_{j=1}^{2} \pi_j \emptyset_j(y_t \mid x_{1(t-1)}, x_{2(t-1)})\right) \quad (2)$$

where $\emptyset_j(y_t \mid x_{1(t-1)}, x_{2(t-1)})$ denotes the density of an univariate Gaussian distribution with mean $(\beta_{0j} + \beta_{1j}x_{1(t+1)} + \beta_{2j}x_{2(t-1)})$ and variance σ_j^2. $t = 1$ and $t = n$ correspond to the year of 1981 and 2006, respectively, because MLD data are available from 1980 onward.

A standard tool to find a maximum likelihood solution for the mixture model is the EM (Expectation–Maximization) algorithm. The EM algorithm iterates two steps of E (for expectation) and M (for maximization) until convergence. Let $\theta^{(r)}$ be estimate of the parameters after the rth iteration.

On the $(r + 1)$th iteration, the E-step of the EM algorithm involves the calculation of the Q-function, which is the expectation of the complete-data log-likelihood conditional on the current parameter estimates and the observed data,

$$Q(\theta, \theta^{(r)}) = \sum_{t=1}^{n} \sum_{j=1}^{2} w_{jt}^{(r)} \log(\emptyset_j(y_t \mid x_{1(t-1)}, x_{2(t-1)})) \quad (3)$$

where

$$w_{jt}^{(r)} = \frac{\pi_j^{(r)} \emptyset_j(y_t \mid x_{1(t-1)}, x_{2(t-1)})}{\sum_{j=1}^{2} \pi_j^{(r)} \emptyset_j(y_t \mid x_{1(t-1)}, x_{2(t-1)})} \quad (t = 1, \ldots, n; \quad j = 1, 2) \quad (4)$$

is the estimate of the posterior probability that the tth observation belongs to the jth component of the mixture after the rth iteration ($r = 1, \ldots, R$). The converged $w_{jt}^{(R)}$ corresponds to the contribution ratio.

The M-step updates the estimate $\theta^{(r+1)}$ that maximizes the Q-function with respect to θ. It is equivalent to computing the sample proportion and the weighted least-squares estimates when performing a weighted regression of $y_1, y_2, \ldots, y_n$ on (x_{10}, x_{20}), (x_{11}, x_{21}), $\ldots, (x_{1(n-1)}, x_{2(n-1)})$ with weights $w_{j1}, w_{j2}, \ldots, w_{jn}$ ($j = 1, 2$) (Faria & Soromenho, 2010).

3 | RESULTS

3.1 | Comparisons of survey CPUE and fishery abundance index trends

Driftnet survey CPUE and the fishery abundance index for saury showed similar interannual variations from around 1990 onward (Figure 2). We constructed a linear regression equation between them for the period of 1991–2006, except 2000 when the driftnet survey was not conducted:

$$\begin{aligned} \ln(\text{survey CPUE} + 1) &= 1.583 \ln(\text{fishery abundance index}) \\ &- 1.716 \ (r = .90, \ p < .001) \end{aligned} \quad (5)$$

Using Equation 5, we estimated the survey CPUE for 2000.

On the other hand, the survey CPUE and the fishery abundance index showed different variation patterns during the 1980s. The fishery abundance index tended to deviate downward from the correlation relationship in Equation 5 (Figure 2). This suggests the possibility of under-estimation in the fishery abundance index during this period.

3.2 | Winter SST in the Kuroshio recirculation

We examined the spatial distribution of the correlation coefficients between time series data of survey CPUE and SST. A high positive correlation coefficient occurred between survey CPUE in the period 1981–1993 and winter (January–March) SST in the period 1980–1992 in the Kuroshio Recirculation region (KR) (Figure 3a). The area enclosed by a yellow rectangle (25°N–33°N, 135°E–165°E) is area of the high positive correlations in the KR within the meridional extent of the SST range (16–22°C) for the winter larval habitat (Watanabe et al., 1997). Regarding the zonal extent of the rectangle, western and eastern boundaries are defined based on Watanabe et al. (2003), Oozeki et al. (2007), and Oozeki, Okunishi, Takasuka, and Ambe (2015). Time-series of the winter SST data for the period 1980–1992 in this region and those of the survey CPUE in the
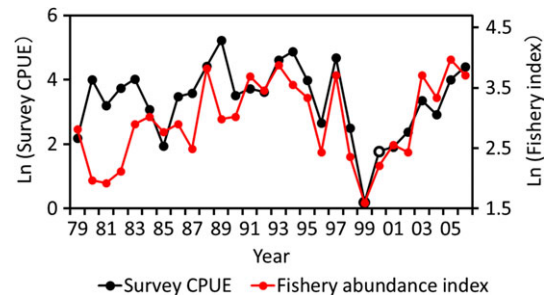

FIGURE 2 Interannual variations in survey driftnet CPUE (No. of age-1 fish per driftnet panel) and the fishery abundance index (migration index of No. of age-1 fish). Both survey CPUE and the fishery abundance index were natural log (ln) transformed to satisfy the assumption of normality and homogenous variance. Survey CPUE for 2000 (open circle) was estimated using the linear regression between survey CPUE and the fishery abundance index

(a) ## Spatial correlation for CPUE and winter SST
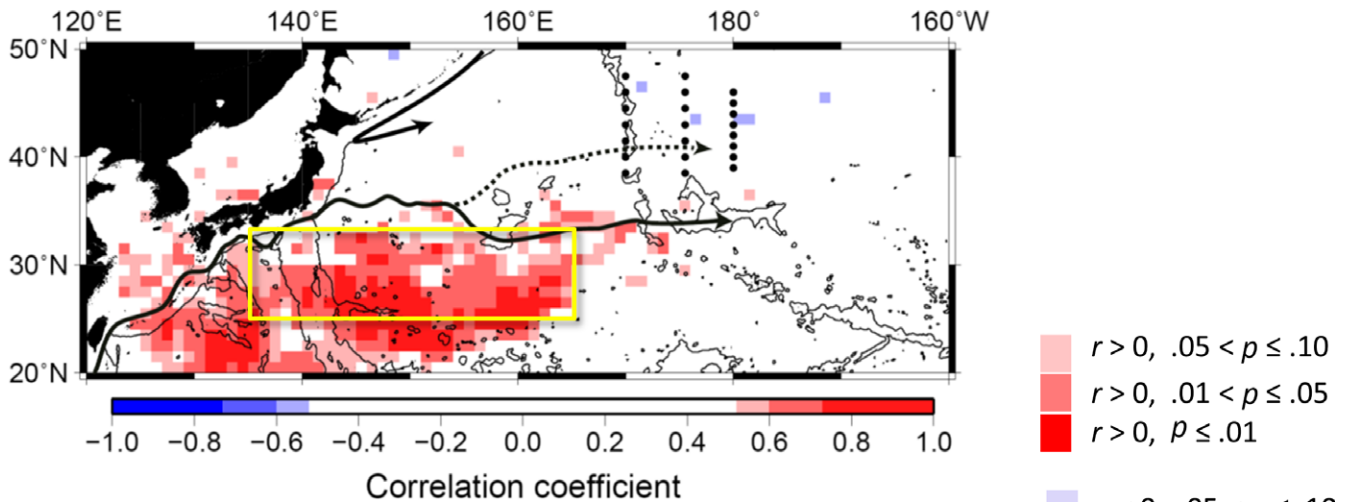
(b) ## Spatial correlation for CPUE and spring MLD
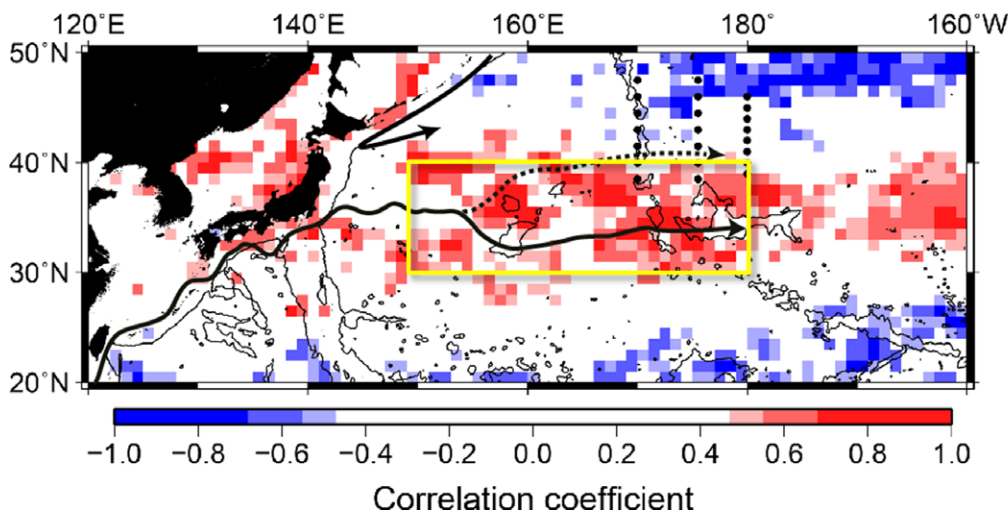

FIGURE 3 (a) Distribution of the correlation coefficient between survey CPUE during the period 1981–1993 and winter (January–March) sea surface temperature (SST; °C) during the period 1980–1992. (b) Distribution of the correlation coefficient between survey CPUE during the period 1994–2006 and spring (April–May) mixed layer depth (MLD; m) during the period of 1993–2005. Saury were 1 year old (age-1), and hence SST and MLD for the previous year were compared with the year of CPUE. Note that the correlation coefficients (r) are shown based on the 90%, 95%, and 99% confidence intervals (t test $df = 11$ for [a] and [b]). In each panel, region enclosed by a yellow rectangle is area for correlation analysis. See text for details

period 1981–1993 were compared and a significant positive correlation was observed between them with $r = .79$ ($p = .001$) (Figure 4a).

3.3 | Spring MLD in the transition and Kuroshio extension

We examined the spatial distribution of the correlation coefficients between time series data of survey CPUE and MLD. A high positive correlation coefficient occurred between survey CPUE in the period 1994–2006 and spring (April–May) MLD in the period 1993–2005 in

the Kuroshio-Oyashio Transition and Kuroshio Extension (TKE), especially the area enclosed by a yellow rectangle (30°N–40°N and 150°E–180°) in Figure 3b. This region is characterized by KBF and Emperor Seamounts corresponding to the potential spring nursery grounds for saury in terms of the SST range (12–20°C) for their larval habitat (Watanabe et al., 1997). Time series data of the spring MLD for the period 1993–2005 in this region and those of the survey CPUE in the period 1994–2006 were compared and a significant positive correlation was observed between them with $r = .83$ ($p < .001$) (Figure 4b).
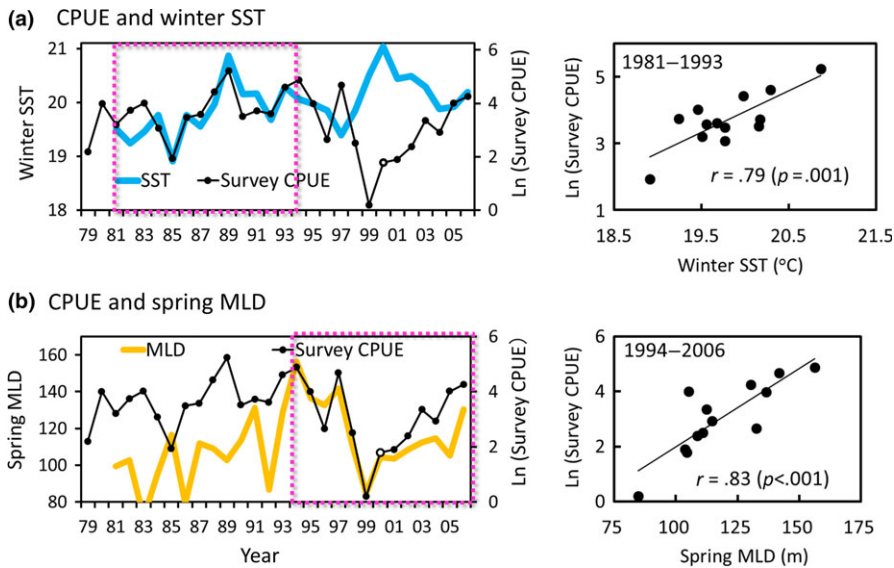
FIGURE 4 (a) Time series of survey CPUE and winter (January to March) SST (°C) in the Kuroshio Recirculation region (KR) as enclosed by the yellow rectangle in Figure 3a. (b) Time series of survey CPUE and spring (April to May) MLD (m) in the Kuroshio-Oyashio Transition and Kuroshio Extension (TKE) as enclosed by the yellow rectangle in Figure 3b. Note that the SST and MLD lag 1 year behind the CPUE. In right panels, *r* denotes the correlation coefficient, and *p* denotes the probability value only for the period shown within a pink dashed rectangle in left panels

We also examined distribution of spring NPP in relation to the area of high positive correlation between the survey CPUE and the spring MLD. The TKE is characterized by the highest productivity during spring in the pelagic region of the North Pacific although magnitude of interannual variation in the productivity was large (Figure 5a,b); low productivity in 1998 and higher productivity in 2005 corresponded with low and high survey CPUE in the following year, respectively.

It may be noted that there was a significant positive correlation between time series data of spring Chl-*a* concentration and spring
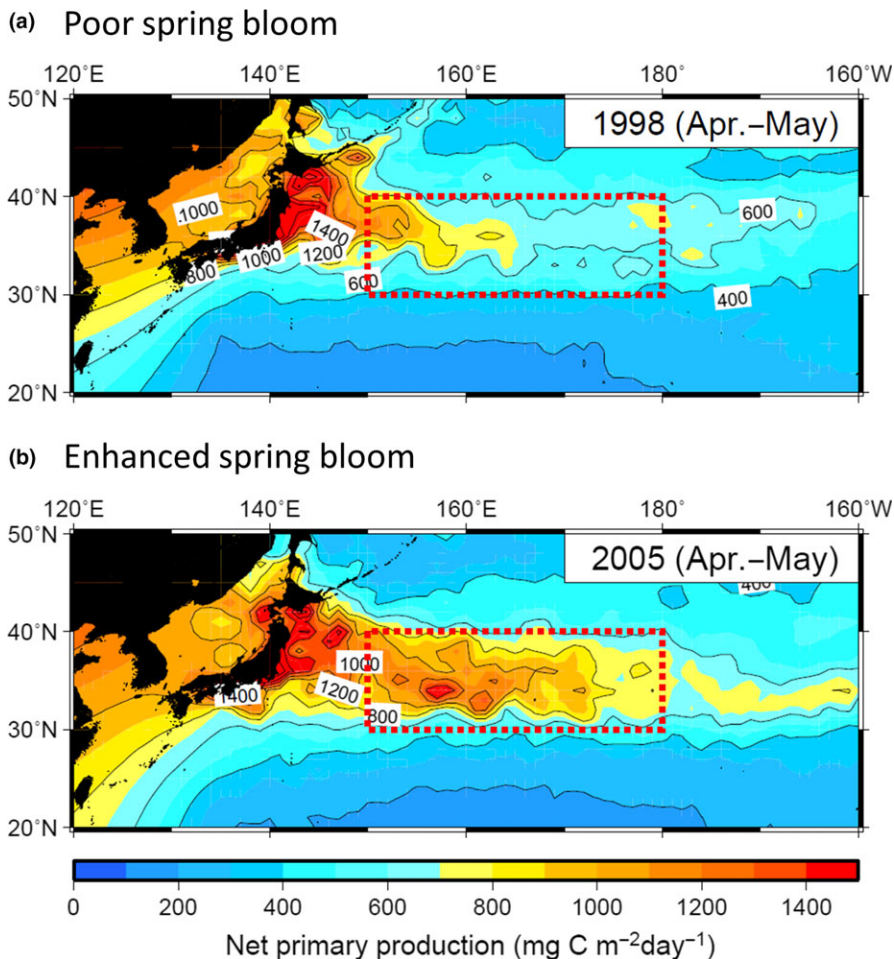

FIGURE 5 Distribution of net primary productivity (NPP; mg C m^{-2}/day) in the North Pacific during spring (April to May) in 1998 (a) and 2005 (b). The region of high correlation coefficient between survey CPUE and the spring MLD shown in Figure 3b is depicted as a red dashed rectangle

MLD in the TKE during the period of 1998–2006 ($r = .90$, $p < .001$) (Figure 6). Therefore, we considered spring MLD as a proxy of Chl-a concentration in this region.

3.4 | Contribution ratios of winter SST and spring MLD to interannual variability of survey CPUE

We applied the two component mixture of the linear regression model. In the mixture models, the Bayesian information criterion (BIC) is recommended to determine appropriate number of components (i.e., linear regressions) (Fraley & Raftery, 1998). The BIC suggested that the mixture model of two linear regressions was substantially better than the single linear regression model (BIC = 83.32 and 88.13, respectively) in the case of our study.

The two component mixture of linear regression model was fitted to the time series data during 1981–2006. The two estimated linear lines were as follows:

1 linear regression 1 (line 1; Figure 7a):

$$\ln(\text{survey CPUE}_t + 1) = 3.785^* + 0.623^*\text{SST}_{t-1} - 0.200\,\text{MLD}_{t-1}$$

2 linear regression 2 (line 2):

$$\ln(\text{survey CPUE}_t + 1) = 2.483^* - 0.199\,\text{SST}_{t-1} + 1.207^*\text{MLD}_{t-1}$$

where t is year; explanatory variables (SST_{t-1} and MLD_{t-1}) are standardized to have mean zero and variance one; and * indicates significant coefficient at a significant level of 0.1% (Table 1). Thus, the survey CPUE has a significantly positive correlation with the previous year's winter SST in line 1 while with that of the previous year's spring MLD in line 2.

Hence we can estimate contribution ratios of the winter SST in the KR and spring MLD in the TKE to the interannual variability of the survey CPUE from probabilities that line 1 and line 2 represent, respectively. The estimates of overall contribution ratio of line 1 ($\hat{\pi}_1$; i.e., contribution of the winter SST) and line 2 ($\hat{\pi}_2$; i.e., contribution of the spring MLD) throughout the survey period were calculated as 0.67 and 0.33, respectively. In terms of their interannual variabilities, contribution ratio of line 1 ($\hat{w}_{1t}$) tended to be dominant in 1981–1993 and 2003–2006, while contribution ratio of line 2 ($\hat{w}_{2t}$) was dominant in 1994–2002 (Figure 7b).

4 | DISCUSSION

4.1 | Comparisons of survey CPUE and the fishery abundance index trends

The survey CPUE, which was collected in the central North Pacific, significantly correlated with the fishery abundance index, of the western North Pacific, from around 1990 onward (Figure 2). This implies that both survey CPUE and the fishery abundance index were comparable during the period because both indices potentially reflect on population abundance of saury. However, in the 1980s, they showed different interannual patterns with
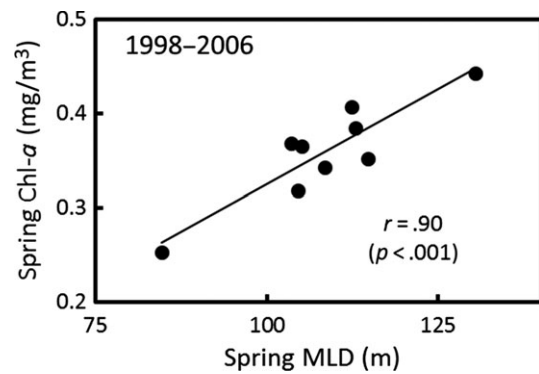

FIGURE 6 Relationship between spring Chl-a concentration (mg/m^3) and spring MLD (m) in the Kuroshio-Oyashio Transition and Kuroshio Extension (TKE) during 1998–2006

downward tendency of the fishery abundance index. Yasuda and Watanabe (1994) found that the average distances of saury fishing grounds varied interannually in the range from 60 to 300 km off the nearest coast of northern Japan. This interannual variation was closely associated with the meridional shift of the offshore Oyashio front (OOF) in the pre-fishing season (August). In the years 1981–1986 the average distances of fishing grounds from the coast were as far as 200–300 km mostly along the offshore Oyashio branch. This period approximately corresponds to the southward shift of the OOF during 1983–1987. Once the OOF shifted north after 1988, the average distances of fishing grounds returned to a 100–150 km level mostly along the coastal Oyashio branch. Yasuda and Watanabe (1994) indicated that these spatial changes in the saury distribution clearly reflect on the distribution density in the fishing grounds. When the OOF shifted north, saury migrate to the coastal area, whereas when the OOF shifted south, they do not migrate to the coastal areas, but disperse in extensive offshore areas. Thus, when major fishing grounds occurred offshore, the distribution density in the fishing grounds tended to be low, causing downward tendency of the fishery abundance index. Such an offshore-ward shift of fishing grounds occurred only in the 1980s during the period of the investigation, 1973–2009 (Naya et al., 2012). Therefore, it is suggested that the survey CPUE tended to show a similar interannual variability with the fishery abundance index except for 1981–1987 when the oceanographic conditions in the western North Pacific caused the major fishing grounds to be formed with less dense distribution in the offshore areas, rather than the fishing grounds being formed in the coastal areas.

4.2 | Important oceanographic factors for recruitment

RPS (recruitment per spawner) would have been a more robust index to have insight into the recruitment variability and to assess the effect of environment on such variability. However, we were not able to find the time series of RPS before 2002; furthermore, the
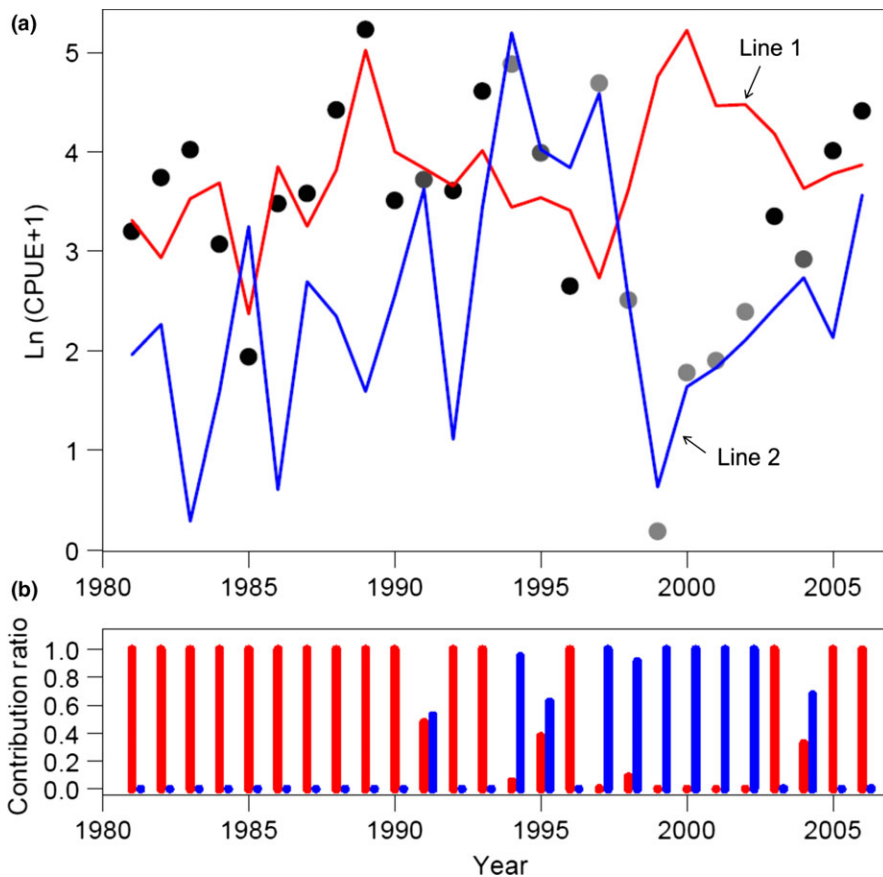
FIGURE 7 (a) The survey CPUE data with fitted regression lines of the two component mixture model to the winter SST and spring MLD data during 1981–2006. Red (line 1) and blue (line 2) lines are fitted regression lines using the BIC-selected coefficients for winter SST and for spring MLD, respectively. Solid circles denote the survey CPUEs whose colors indicate the strength of the link with line 1 and line 2 (Deep black is strongly linked with line 1 whereas grey color is linked with line 2). (b) Contribution ratios of line 1 (red bar) and line 2 (blue bar) to interannual variability in the survey CPUE. See text for details

TABLE 1 Estimated parameters for two component mixture of linear regression fitted to the data set of survey CPUE, winter SST and spring MLD

	Estimate	SE	p value
Line 1			
β_{01} (Intercept)	3.785	0.141	<.001
β_{11} ($SST_{(t-1)}$)	0.623	0.147	<.001
β_{21} ($MLD_{(t-1)}$)	−0.200	0.172	.879
Line 2			
β_{02} (Intercept)	2.483	0.108	<.001
β_{12} ($SST_{(t-1)}$)	−0.199	0.105	.971
β_{22} ($MLD_{(t-1)}$)	1.207	0.095	<.001

See text for details.

RPS time series estimated since 2003 onward are insufficiently reliable due to lack of robust age-structured stock assessment model. Thus we could not use RPS in the present study. Instead of RPS, we used the survey CPUE which reflects recruitment fluctuations as mentioned earlier. We believe that our study, which does not use RPS, would be adequately meaningful. With the availability of the reliable RPS data in the future, further analysis should be undertaken in conjunction with such data.

Tseng et al. (2013) identified preferred habitat for saury in the northwestern Pacific using fishery data and indicated that the oceanographic conditions such as SST and Chl-a concentration could influence their migration pattern and resultantly their spatial distribution, e.g., the formation of fishing grounds. This suggests a possibility that the survey CPUE might be determined by the migration process, rather than by the recruitment variability. To examine this possibility, we compared the survey CPUE with SST and with Chl-a concentration in the survey region during the survey period (July–August) of the same year and found no correlation between them for any of the periods examined. Therefore, we suggest that the survey CPUE may be determined by recruitment not by the migration process.

The survey CPUE was estimated to be linked with the previous year's winter SST in the KR (winter spawning/nursery ground) in 1981–1993 and 2003–2006, and with the previous year's spring MLD in the TKE (spring spawning/nursery ground) in 1994–2002 (Figure 7). Furthermore, MLD was considered as a proxy of spring Chl-a concentration in the TKE (Figure 6), which will be discussed in detail later. Hence, we suggest that recruitment variability of saury was affected by winter SST in the KR, or spring Chl-a concentration in the TKE.

Tian et al. (2004) suggested the importance of winter SST in the Kuroshio region for recruitment variability based on long-term time series data from 1951 to 2000 (Table 2). Our result is similar to this in that winter SST in the KR tends to be important until the mid-1990s. Watanabe (2009) indicated the importance of spring SST in Kuroshio-Oyashio Transition for the period around 1988/1989 when the rise in the spring SST was associated with the increase in fishery

TABLE 2 Summary information on potential oceanographic factors and periods being suggested to affect recruitment of Pacific saury

Studies	Possible oceanographic factors affecting recruitment	Study periods	Periods when the oceanographic factors are suggested to affect recruitments
Tian et al. (2004)	Winter SST in Kuroshio region	1951–2000	1951–2000
Watanabe (2009)	Spring SST in Kuroshio-Oyashio Transition	1978–2005	1988–1991
Yasuda and Watanabe (2007)	Winter MLD in Kuroshio Recirculation	1955–2000	1955–2000
This study	Winter SST in Kuroshio Recirculation	1981–2006	1981–1993 and 2003–2006
This study	Spring MLD in Kuroshio-Oyashio Transition and Kuroshio Extension	1981–2006	1994–2002

CPUE but not of importance during 1999–2004 when the rise in spring SST was associated with the decline in fishery CPUE. Our result is similar to this in that SST in the spawning and nursery ground was less important during the mid-1990s–early 2000s. Regarding Yasuda and Watanabe (2007), the relationship between fishery CPUE and winter MLD in the KR was less clear throughout the study period of 1955–2000. Hence, it is difficult to compare between Yasuda and Watanabe (2007) and our result.

A principal factor determining recruitment variability is considered to be the growth rate in early life stages (Bailey & Houde, 1989; Houde, 1987). SST directly affects growth of saury larvae because an increase in SST enhances the growth rate (Oozeki & Watanabe, 2000). In the Kuroshio Current occurrence and density during early life stages of saury are also reported to be largely determined by SST (Takasuka et al., 2014). Chl-*a* concentration may support zooplankton production as food for saury larvae (Oozeki, Watanabe, & Kitagawa, 2004) and hence an increase in Chl-*a* concentration may also promote faster growth. Miller, Crowder, Rice, and Marschall (1988) suggested that fast-growing larvae are larger than slow-growing larvae and thus less vulnerable to predators (the bigger-is-better hypothesis). Therefore, fast-growing larvae may have a survival advantage and contribute more to elevate recruitment.

Recently a bioenergetics model has been constructed to be coupled to a lower trophic level ecosystem model, i.e., NEMURO (North Pacific ecosystem model for understanding regional oceanography) for sardine (Okunishi, Yamanaka, & Ito, 2009) and saury (Ito, Okunishi, Kishi, & Wang, 2013). As future perspectives, such an ecosystem-based bioenergetics model should be used to investigate the responses of saury to variabilities in SST and Chl-*a* concentration for further insight.

4.3 | Oceanographic features of the areas of correlations

Area for significant positive correlations between the survey CPUE and SST in the KR approximately corresponds to formation region for Subtropical Mode Water (STMW), which occurs between 20°N and 35°N, i.e., the subtropical region, and between 130°E and 180° (Kumamoto et al., 2014). This could be the reason that the correlation area is distributed more southward beyond the winter habitat of saury larvae, but the meridional extent of the SST range for the larval habitat occurs only north of 25°N (Figure 3a).

Area for significant positive correlations between the survey CPUE and MLD in the TKE is patchy and occurred mainly in the offshore region (Figure 3b). As for being patchy, it is probably because this region is characterized by extensive meanders and mesoscale eddies of tens to hundreds of kilometers scales in diameter. The occurrence of the high positive correlation area offshore can be attributed to the different trend in the interannual variation of MLD between the inshore and offshore regions. In the inshore region, MLD is considered to be strongly influenced by the interaction between Kuroshio and Oyashio Currents, whereas in the offshore region by the wind stress. Such diverse trend in MLD variability plausibly resulted in the different trend in interannual variability in Chl-*a* concentration.

4.4 | Relationship between MLD and Chl-*a* concentration

The significant positive correlation between MLD and Chl-*a* concentration in spring ($r = .90$, $p < .001$) in the TKE (Figure 6) can be mostly attributed to the two endpoints, i.e., the deepest (the highest) and the shallowest (the lowest) MLD (Chl-*a* concentration). Lack of the significant correlations between MLD and Chl-*a* concentration in their medium-range values ($r = .44$, $p = .32$) could be due to the possibility that the relationship between MLD and nutrient entrainment, as well as between nutrient entrainment and Chl-*a* concentration may not form perfect linear functions. However, Figure 6 indicates that the very deep and shallow values of MLD may represent the very high and low Chl-*a* concentration, respectively. If so, we can consider that the deep and shallow values of MLD during 1993–1998 (Figure 4b) may reflect the high and low levels of Chl-*a* concentration. Furthermore, as for the period of 1999–mid-2000s when SeaWiFS Chl-*a* concentration data are available, there was the significant positive correlation between the SeaWiFS Chl-*a* concentration in the TKE in spring and the survey CPUE of the following year (Ichii et al., 2017). Therefore, we can assume plausibility of the meaningful correlation between the survey CPUE and spring Chl-*a* concentration in the TKE during 1993–mid-2000s.

Positive correlation between MLD and spring Chl-*a* concentration in the TKE suggests that the food environment for saury larvae could be better in the deep MLD and worse in the shallow MLD in spring in the region. This implies that deeper MLD in spring may entrain more nutrients to the surface layer and accordingly enhance

Chl-*a* concentration. According to Shiozaki et al. (2014), the critical depth in that region is 150–200 m in spring. Considering that the maximum spring MLD is 156 m (Figure 4b), spring mixing may not inhibit photosynthesis, but enhance it by entrainment of nutrients.

Yasuda and Watanabe (2007) suggested that in the case of the KR in winter, the food environment for saury larvae could be better in the shallow MLD and worse in the deep MLD. Their suggestion is based on a negative correlation between MLD and Chl-*a* concentration in winter in the region, which is in contrast to the positive correlation between them in spring in the TKE as demonstrated in our study. Such different correlations of MLD and Chl-*a* concentration between Yasuda and Watanabe (2007) and our study is probably explained by the long-lasting spring bloom. In both the TKE and KR, spring bloom starts with the mixed layer shoaling in March and lasts until May (Shiozaki et al., 2014). A simulation study in the same region suggests that nutrients that winter MLD entrained are used up by mid-April (Nishikawa et al., 2013). Thus, from April to May, which is the season we focused on, it is plausible that the entrained nutrients by spring vertical mixing are used. Observational studies also reported that a volume of entrained nutrients in spring in that region is comparable to a volume of consumed nutrients in spring (Kaneko, Yasuda, Komatsu, & Itoh, 2012; Kaneko, Yasuda, Komatsu, & Itoh, 2013). For that reason, we considered that the spring MLD plays a more important role than that of the winter MLD, especially in the latter half of the bloom period.

4.5 | Dominant seasonal cohort for recruitment

Saury have a long spawning period from autumn through spring. It is generally suggested that the most important season for spawning of saury is winter and the most important area is the Kuroshio region because of the occurrence of the highest ratio of mature adults and the highest spawning density (Kurita, 2001). Watanabe and Lo (1989) also pointed out that winter was the most active spawning season using larval catch data during 1973–1986. Furthermore, Tian et al. (2004) suggested that the winter-spawned cohort (winter cohort) is considered to be usually dominant in recruitment and consequently winter oceanic conditions, SST in the KR, in particular, could affect early survival and determine the recruitment success of saury. Our study supports the general dominance of the winter cohort in recruitment in 1981–1993 and 2003–2006, assuming that the winter SST substantially influenced the winter cohort, rather than the spawned cohorts of the other two seasons. This assumption will be discussed later.

On the other hand, Watanabe et al. (1997, 2003) pointed out the importance of the spring-spawned cohort (spring cohort) on interannual fluctuations. This is because the early life parameters such as the daily growth and mortality rates and resulting recruitment are generally stable under the stable conditions in the subtropical Kuroshio Current in winter but tend to vary under variable conditions in the transition region in spring. Such variability in the spring recruitment can influence the overall recruitment when the spring cohort dominates the overall recruitment. In our study, the

period of 1994–2002 may correspond to such a period, assuming that the spring MLD could have a substantial influence on the spring cohort, rather than on the spawned cohorts of the other two seasons. This assumption will also be discussed later.

Regarding autumn oceanographic factors, they showed no correlation with the survey CPUE for any of the periods examined. This can be attributed to the least favorable oceanographic conditions in autumn among the three spawning seasons (Watanabe et al., 1997). In the TKE during the autumn, (i) zooplankton biomass is lower than that in spring (Odate, 1994), and (ii) SST is lower than in winter in the KR. As a result, the growth rate of autumn larvae was at a minimum and their mortality was highest, leading to a minimum production of juveniles of autumn-spawned cohort (autumn cohort) among the three seasonal cohorts (Oozeki et al., 2004). Hence, contribution of the autumn cohort to the recruitment is considered to be minimal (Watanabe et al., 1997).

4.6 | Possibilities for winter SST and spring Chl-*a* concentrations to influence recruitment of the other season spawned cohorts

There are possibilities that the winter SST in the KR and the spring Chl-*a* concentration in the TKE may directly or indirectly influence the recruitment of cohort spawned in the other seasons apart from the ones cited earlier. As for the winter SST, there is a possibility of its direct and indirect influence on the autumn and spring cohorts, respectively. Regarding the direct influence, some hatched larvae in the TKE in autumn may be transported to the KE in winter, given the variability in transport processes of saury larvae leading to their broad dispersal (Oozeki et al., 2015). The transported autumn cohort may then be directly affected by the winter SST in the KR. However, assuming the minimal contribution of the autumn cohort to the recruitment (Watanabe et al., 1997), the influence of the winter SST on the autumn cohort may be less important for determining the overall recruitment level.

Regarding the indirect influence of the winter SST on the spring cohort, the winter SST in the KR can affect biological production and subsequent prey availability for the spring cohort in the TKE. Specifically, at first winter SST may influence the nutrient and Chl-*a* concentrations through physical processes such as vertical mixing within the KR. Then, lateral transports of nutrients and Chl-*a* concentration from the KR to the TKE due to currents might influence the biological production in the TKE and consequently the prey environments for the spring cohort. So far there has been no report that suggests the importance of laterally transported water from the KR in winter for spring biological production in the TKE. Considering that nutrients and Chl-*a* concentrations are generally low in the KR (e.g., Shiozaki et al., 2014), their contribution to biological production in the TKE might be limited.

As for the spring Chl-*a* concentration in the TKE, direct influence on the winter cohort is considered to occur when this cohort migrates northward from the KR to the TKE for feeding in spring. The influence of spring Chl-*a* concentration on the winter cohort,

however, may not be strong enough to determine the recruitment of this cohort. This is because there was a tendency of a negative correlation between the winter SST in the KR and the spring MLD in the TKE during 1993–2006 ($r = -.54$, $p < .05$). This indicates that years when the winter SST in the KR is high (generally favorable for growth), the spring Chl-*a* concentration in the TKE tends to be low (less favorable for growth), and vice versa. In other words, the two oceanographic factors tend to work in the opposite directions for growth and hence if the recruitment of the winter cohort is strongly affected not only by the winter SST but also by the spring Chl-*a* concentration, the relationship between the survey CPUE and the winter SST should be less apparent throughout the study period.

Therefore, at this stage, we consider that winter SST in the KR and spring Chl-*a* concentration in the TKE would substantially influence the recruitment of the winter cohort and spring cohort, respectively, as compared with their influences on recruitment of spawned cohorts of the other seasons.

4.7 | Potential causes for low contribution of winter recruitment between mid-1990s and early 2000s

Our study implies a low contribution ratio of the winter recruitment in 1994–2002 (Figure 7b). There may be two possible reasons for this. Firstly, the spring MLD was distinctly deep in the TKE in 1994–1997 (Figure 4b), suggesting the extraordinary high spring Chl-*a* concentration there. Hence, such an enhanced Chl-*a* concentration (food availability for saury larvae) in spring in the TKE could promote the increase in recruitment of the spring cohort as compared to the winter cohort.

Secondly, there is a possibility that the winter food availability was very poor in the KR during the period between late 1990s and early 2000s, leading to poor recruitment of the winter cohort as saury larvae require some amount of food at their first feeding stage to survive. This possibility was supported by Aita, Yamanaka, and Kishi (2007) and Megrey et al. (2007), as during the period of the 1990s and the early 2000s (especially around 1998/1999), the abundance of small zooplankton and phytoplankton was speculated to be historically low in the Kuroshio region using the NEMURO model.

It may also be noted that the period 1998–2002 corresponded to the 1997/1998 regime shift and subsequent anomalous climate conditions in the western and central North Pacific (Bond, Overland, Spillane, & Stabeno, 2003; Yamanishi, 2012; PICES, 2005). These climate conditions were characterized by a prominent warm anomaly south of 40°N extending from the coast of Asia to about 150°W. This tendency of high SST was observed in the KR (Figure 4a). On the other hand, a similar level of high SST in winter was also observed in the KR around 1988, but with very high values of the survey CPUE. This period corresponds to the 1988/1989 regime shift associated with relatively enhanced biological production in winter in the Kuroshio/tropical region (Yatsu et al., 2008). Hence, the possible large contrast in winter recruitment in spite of similar SST between the two periods could be attributed to the inferred contrast in food availability for saury larvae between the 1988/1989 and 1997/1998.

Our findings suggested that oceanographic factors such as the winter SST in the KR and spring MLD in the TKE could be potentially useful to predict the abundance trends of age-1 saury if the switching criteria between SST and MLD as input variable are further elucidated. This remains a future challenge.

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