



Biological interactions potentially alter the large-scale distribution pattern of the small pelagic fish, Pacific saury *Cololabis saira*

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ABSTRACT: We aimed to understand the effect of biological interactions on the distribution of small pelagic fishes. Surveys were conducted during 2003–2019 using sea surface trawl nets in the western and central North Pacific Ocean, covering an area between 143° E and 165° W, to estimate the distributions of 4 small pelagic fishes: Pacific saury *Cololabis saira*, Japanese sardine *Sardinops melanostictus*, chub mackerel *Scomber japonicus*, and Japanese anchovy *Engraulis japonicus*. These species are potential competitors, as they all occupy a similar niche. Japanese anchovy was abundant during 2003–2012, while Japanese sardine and chub mackerel were abundant during 2013–2019. Only Pacific saury was distributed throughout the survey area, while the others occurred within the area west of 180° longitude (WA). Pacific saury and its potential competitors showed adjacent distributions, with a slight overlap along sea surface temperature gradients in the WA. This distribution pattern remained even when Japanese sardine expanded its distribution to colder waters and increased in abundance after 2013, resulting in a shift in the distribution of Pacific saury to colder waters and a period of high densities of Japanese sardine. Such a distribution shift of Pacific saury was not observed in the area east of 180° longitude, where no Japanese sardine was observed. These results suggest the possibility that biological interactions such as inter-species competition can be an important factor in determining the distribution of small pelagic fishes.

KEY WORDS: Biological interaction · Competition · Pelagic region · Small pelagic fish · Species distribution

1. INTRODUCTION

Biological interactions are potentially important factors in determining large-scale species distributions (Guisan & Thuiller 2005). However, determining the effect one species has on the distribution of another is difficult because species distributions are affected by a multitude of environmental factors, and in many cases, these environmental and biological

factors cannot be separated (Guisan & Thuiller 2005, Elith & Leathwick 2009). To date, research on this topic has largely focused on the terrestrial realm (e.g. terrestrial plants: Leathwick & Austin 2001; pocket mice: Anderson et al. 2002; owls: Yackulic et al. 2014), with limited research undertaken in the ocean (but see Robinson et al. 2011, Morfin et al. 2012, Kleisner et al. 2016, Pinsky et al. 2020). The information on species distributions in the ocean, especially

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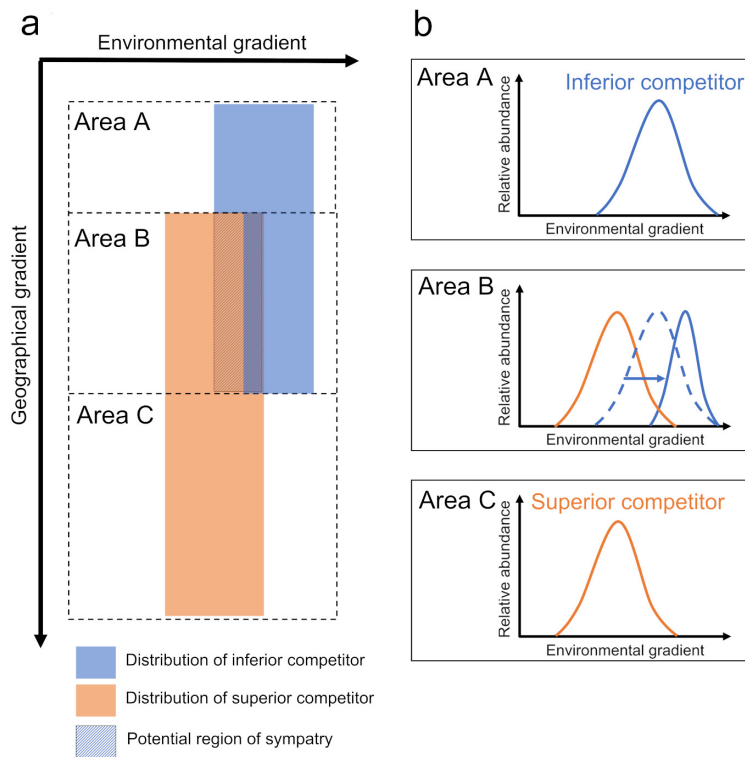


Fig. 1. (a) Schematic of the distribution pattern of the target species pair and (b) expected response of a species to an environmental gradient in areas A, B, and C in (a). If one species competitively excludes another from areas that both could potentially inhabit (i.e. area B), then the inferior competitor would be predicted to inhabit different environmental conditions in biogeographic regions where the other species is not present (area A) in comparison with the conditions it inhabits in regions where both species exist (area B). Conversely, the superior competitor would be predicted to inhabit similar environmental conditions regardless of the presence or absence of the inferior competitor in a region (areas B and C)

in the pelagic region, is much scarcer than that available for terrestrial regions because pelagic regions are harder to sample than terrestrial environments (Robinson et al. 2011, Record et al. 2018). Thus, little progress has been made on this topic in the ocean because of limited data on species distributions and the stringent conditions that data sets must satisfy to show the effects of biological interaction (Robinson et al. 2011).

Data sets satisfying the following conditions are required for studying the effects of biological interaction between 2 species by separating environmental and biological factors (Fig. 1). First, there should be partially overlapping distributions of target species and other species along environmental gradients. Such adjacent distributions with a slight overlap, also known as a 'parapatric distribution' (Bull 1991), suggest the potential for biological interaction between

the 2 species. Second, the data set must contain both co-occurrences and areas where only the target species occur. Fulfillment of these conditions would allow a comparison of the distribution patterns of the target species along an environmental gradient with and without potential competitors (Anderson et al. 2002). This comparison can help determine the effects of biological interactions on species distributions based on significant differences between the distribution patterns along the environmental gradient (Guisan et al. 2017). Such approaches are often used in studies on the small-scale distribution of aquatic organisms, such as in riverine ecosystems (e.g. Sone et al. 2001), but have rarely been applied to large-scale areas such as the pelagic realm due to lack of data (Robinson et al. 2011).

Pacific saury *Cololabis saira*, Japanese anchovy *Engraulis japonicus*, Japanese sardine *Sardinops melanostictus*, and chub mackerel *Scomber japonicus* are potential species subject to biological interactions in a pelagic ecosystem. See Table 1 for the general characteristics of these species. All 4 species are small pelagic fishes that are mainly distributed in the central and western North Pacific Ocean and are commercially and ecologically important. The general seasonal migration pattern among the species is similar (Yatsu 2019). They generally spawn in subtropical waters from winter to spring (Takasuka et al.

2008, Kanamori et al. 2019, Fuji et al. 2021). The Kuroshio–Oyashio transition zone and some sub-arctic waters are important feeding grounds for the adults and juveniles during summer (Okazaki et al. 2019, Miyamoto et al. 2022). All 4 species share habitats of similar depth in the pelagic ocean (shallower than 20 m) during summer (Wada & Kitakata 1982, Inagake & Hirano 1983, Kamimura et al. 2021). The primary food of Pacific saury in the central and western North Pacific Ocean during summer is mesozooplankton, in particular *Neocalanus* copepods (Miyamoto et al. 2020). Japanese sardine and chub mackerel also feed on *Neocalanus* copepods (Sato et al. 1968, Yoshida 1987). Japanese sardine and Japanese anchovy are filter feeders and are less selective of environmental prey communities (Yamamoto & Katayama 2012). Therefore, these fish species have the potential for sharing prey items and are consid-

ered potential resource competitors (Iizuka 1987, Matsuda et al. 1991). In particular, the impacts of Japanese sardine on growth, body condition, and population dynamics of other species have attracted the attention of many researchers because the abundance of Japanese sardine has shown drastic iterative boom-and-bust cycles, dominating other species during population booms. For example, it has been speculated that Pacific saury and Japanese sardine compete for the large copepods *Neocalanus* spp., and the enormous feeding pressure of Japanese sardine induced by their high abundance in the 1980s could have significantly reduced the abundance of *Neocalanus* spp. (Tadokoro et al. 2005), possibly reducing the growth of individual Pacific saury (Ito et al. 2007). Kamimura et al. (2021) investigated annual changes in the body condition of chub mackerel and found that the higher the density of Japanese sardine, the lower the body condition of chub mackerel. Nakayama et al. (2018) showed that Japanese sardine affect the population dynamics of Japanese anchovy, as suggested by convergent cross-mapping. However, it is not known how these interspecific relationships affect their distribution. Hsu et al. (2021) indicated that the observed interannual changes in the distribution of Pacific saury could not be completely explained by measurable environmental factors, such as sea surface temperature (SST) alone, and speculated that the influence of some biological factors such as competition with Japanese sardine might be an additional determinant of Pacific saury distribution.

The distribution patterns of these 4 small pelagic fish species satisfy the aforementioned conditions (Fig. 1), and therefore they are suitable candidates for studying the effects of biological interactions on their distributions in the pelagic region, as described below. The main spawning grounds of the species other than Pacific saury are the subtropical waters around the Kuroshio current along the southern coast of Japan in winter and spring (Takasuka et al. 2008, Kanamori et al. 2019). The spawning ground of Pacific saury extends farther eastward than that of the other 3 species (Fuji et al. 2021). Because of geographical differences in their spawning grounds, Pacific saury have a different distribution pattern than the other 3 species (see Table 1). All 4 species coexist in the area west of 180° longitude (hereafter 'WA'), while only Pacific saury is distributed in the area east of 180° longitude (hereafter 'EA') in the North Pacific Ocean (Murase et al. 2012, Takagi et al. 2013, Hashimoto et al. 2019, 2020). In addition, environmental conditions (e.g. SST) within the range of

the Pacific saury and the other 3 species partially overlap, although Pacific saury tends to prefer colder waters than the other 3 species (see Table 1). Therefore, it is possible to infer the effects of biological interactions on Pacific saury distributions by comparing the distribution patterns of Pacific saury along certain environmental gradients between the WA (where biological interactions between Pacific saury and other species included in this study could occur) and the EA (where no biological interaction is expected). Conversely, Japanese sardine, chub mackerel, and Japanese anchovy show similar environmental preferences and often occur sympatrically (e.g. Murase et al. 2012). Since there are no areas in which only one of these species is found, it is difficult to infer the effect of biological interaction on the distributions among these species. Therefore, in this study, we focused on evaluating the effect of biological interactions with respect to Japanese sardine, chub mackerel, and Japanese anchovy on the distribution pattern of Pacific saury.

SST seems to be the most representative environmental variable that affects the distribution of small pelagic fish (Dambach & Rödder 2011, Melo-Merino et al. 2020). Various environmental factors have been examined as determinants of distribution in Pacific saury and other species. Many studies have described the characteristics of Pacific saury habitat (location of fishing ground) using abiotic factors, such as SST and its horizontal gradient (SSTG), sea surface height (SSH), sea surface salinity (SSS), and others, as well as biotic factors such as chlorophyll *a* concentration (chl *a*) and net primary production (e.g. Tseng et al. 2013, Chang et al. 2019, Hua et al. 2020, Hsu et al. 2021). In recent years, some studies have compared the relative importance of various environmental variables on Pacific saury distribution and found that SST and SSTG are more influential than other factors (Chang et al. 2019, Liu et al. 2022, Xing et al. 2022). Hence, we focused on the distribution pattern of Pacific saury and other species along the SST gradient in this study because SST is one of the most important factors explaining the distribution of not only Pacific saury (e.g. Liu et al. 2022, Xing et al. 2022) but also other marine species including chub mackerel, Japanese sardine, and Japanese anchovy (Dambach & Rödder 2011, Murase et al. 2012, Yasuda et al. 2014, Muko et al. 2018, Hashimoto et al. 2019, Melo-Merino et al. 2020).

Over the past 20 yr, important changes in the biomass and distribution patterns of Japanese sardine, chub mackerel, and Japanese anchovy have been

observed in the North Pacific Ocean (Yatsu 2019). The biomass of Japanese anchovy was higher during the 2000s and decreased thereafter. By contrast, chub mackerel and Japanese sardine showed low biomass during the 2000s, and the biomass of these 2 species increased drastically from the 2010s onward. This situation offers us the opportunity to infer species-specific effects of biological interactions on the distribution of Pacific saury by comparing the distribution patterns of Pacific saury under various densities of potential competitors.

Based on our current understanding of substantial stock fluctuations of small pelagic fishes and associated changes in their distributions, we propose the following scenario and hypothesis regarding the effect of competition on the distribution of small pelagic fishes. The distribution patterns of small pelagic fishes along gradients of SST vary greatly with rapid stock fluctuations. In addition, consistent with the 'Basin model' (MacCall 1990), a positive relationship between abundance and the distributional range is observed for many pelagic fishes, including the target species of this study (Barange et al. 2009, Yatsu 2019). Increasing densities are associated with increased competition for food and a decrease in the ambient water temperature at which optimal fish growth is achieved (Elliott 1975). Therefore, during periods of increasing stock sizes, the thermal preference is expected to occur at lower temperatures as the feeding environment deteriorates due to density-dependence (Swain & Kramer 1995). Here, we examined if biological interactions with Japanese sardine, chub mackerel, and Japanese anchovy lead to density-dependent changes in the distribution of Pacific saury, using the framework suggested by Anderson et al. (2002). Specifically, we hypothesized a negative relationship between the center of distribution of Pacific saury relative to SST and the density of potential competitors, which would suggest that the distribution of Pacific saury may be altered by biotic interactions.

To test for effects of biological interactions on the distribution of Pacific saury, we compared the distribution of this species relative to the abiotic environment (i.e. SST) under various conditions of density and distribution of potential competitors (Japanese sardine, chub mackerel, Japanese anchovy). Long-term trawl surveys covering a wide area of the central and western North Pacific Ocean facilitated these comparisons. We initially examined the species-specific distribution patterns to confirm that they met the necessary conditions suggested by Anderson et al. (2002). We then examined annual changes in

species-specific distributions to confirm that the distributional pattern changed with density. Finally, we tested for significant correlations between a potential competitor's density and SST preference of Pacific saury using a linear regression approach to provide evidence that biological interactions affect the distribution of Pacific saury.

2. MATERIALS AND METHODS

2.1. Survey protocol and environmental data

Surveys were conducted in June and July from 2003–2019 using sea surface trawl nets (NST-99, Nichimo; Ueno et al. 2004) to evaluate the distribution of small pelagic fishes in the central-western North Pacific Ocean. The maximum and minimum mesh sizes of this net were 15.18 m and 16.7 mm, respectively. The surveys covered an area between 33° 59' N–48° 51' N and 141° 58' E–164° 51' W (Fig. 2, Table 1). The survey season coincided with the northward feeding migration of the target species (Yatsu 2019). The surveys were designed to cover the habitat of Pacific saury based on SST during this season (8–18°C; Meguro et al. 1987, Hashimoto et al. 2020; see Table 2, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m704p099_supp.pdf). These surveys also covered most of the habitats of the other 3 species (Murase et al. 2012, Okunishi et al. 2012, Hashimoto et al. 2019).

Sampling stations were set along survey lines at 4° longitude intervals in the survey area (Hashimoto et al. 2020). The northernmost station along each survey line was placed in water $\leq 9^{\circ}\text{C}$, which is the limit of the distribution of Pacific saury during the early summer season (Meguro et al. 1987). No Pacific saury were caught at the end of each survey line, confirming the edge of its distribution. There was, however, a case where the northernmost station could not be determined under the condition of SST $\leq 9^{\circ}\text{C}$ in the area west of 158° E. Specifically, the northern limits of survey lines in that area were constrained by inaccessible waters off Hokkaido and the Kuril Islands (Ueno et al. 2017). The extent of area restriction for each survey line varied depending on the location of nearby islands, and more restriction was expected in the western part of the area (Fig. 2). Surface trawls were towed at more than 100 sampling stations every year except 2011, and density data from a total of 2099 stations, covering a range in SSTs from 6.3–23.3°C, were eventually used for analysis (Table 2, Fig. S1). Surface trawls were towed

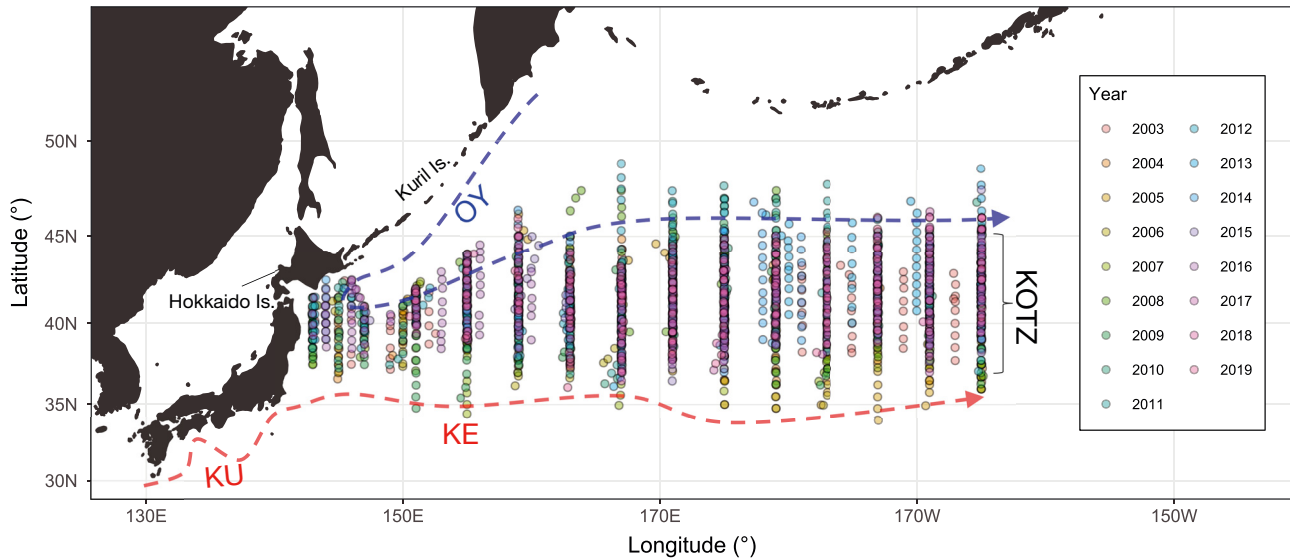


Fig. 2. Survey area and sampling stations. Broken blue line with arrow: general position of the Oyashio Current (OY); broken red line with arrow: general position of the Kuroshio (KU) and Kuroshio Extension (KE). The Kuroshio–Oyashio transition zone (KOTZ) is the area between OY and KU/KE

for a target duration of 1 h during daytime at 4–5 knots. At some sites (3% of the stations), towing duration was reduced to 30 min to avoid breaking the net due to a large catch. The bottoms of vertical openings of the nets were 20–25 m deep to cover the main habitat depths of the 4 small pelagic fishes dur-

ing the survey season (Wada & Kitakata 1982, Inagake & Hirano 1983, Murase et al. 2012, Kamimura et al. 2021). The swept area was calculated as the product of the horizontal opening width and the towing distance between net setting and hauling. Our methodology for surface trawl surveys follows com-

Table 1. Biological information for small pelagic species included in this study

	Pacific saury	Japanese sardine	Chub mackerel	Japanese anchovy
Longevity and maximum size	2 yr, 35 cm, 200 g	7 yr or more, 24 cm, 140 g	7 yr or more, 40 cm, 800 g	3 yr, 13 cm, 25 g
Feeding behavior	Particulate feeder (Hotta & Odate 1956)	Filter feeder (Yoshida 1955)	Particulate feeder	Particulate feeder and filter feeder (Uotani 1985)
Prey items	Copepods, especially <i>Neocalanus</i> spp. (Miyamoto et al. 2020), euphausiids (Sugisaki & Kurita 2004)	Phytoplankton, copepods such as <i>Neocalanus</i> spp., euphausiids (Iizuka 1987, Yoshida 1987, Okazaki et al. 2019)	Copepods such as <i>Neocalanus</i> spp., euphausiids, anchovy (Sato et al. 1968, 1975)	Copepods, phytoplankton, mysids, amphipod (Sato et al. 1968, Okazaki et al. 2019)
Trophic position	Trophic position of chub mackerel is higher than Japanese sardine and Japanese anchovy (Iizuka 1987, Ohshimo et al. 2016)			
Habitat temperature during summer	8–17°C (Meguro et al. 1987)	10–17°C (Kondo 1988)	Warmer than 10°C (Hashimoto et al. 2019)	Mainly 10–21°C (Murase et al. 2012)
Habitat depth during summer	10–15 m (Wada & Kitakata 1982)	10–20 m (Inagake & Hirano 1983)	Shallower than 20 m (Kamimura et al. 2021)	12–28 m (Murase et al. 2012)
Main longitudinal distribution range	Japanese coast to 165°W (Hashimoto et al. 2020)	West of 180° longitude (Takagi et al. 2013)	West of 180° longitude (Hashimoto et al. 2019)	West of 180° longitude (Murase et al. 2012)
Spawning ground	Waters around Kuroshio and Kuroshio Extension (Fuji et al. 2021)	Coastal waters around Kuroshio (Takasuka et al. 2008)	Coastal waters around Kuroshio (Kanamori et al. 2019)	Coastal waters around Kuroshio (Takasuka et al. 2008)

monly used methods (e.g. Nøttestad et al. 2016, Murphy et al. 2021). Sea surface water was collected using a bucket at each station to measure SST (°C) with a bar thermometer.

Catches were sorted on board, the number of individuals of each species was recorded after each tow, and body lengths were measured in the laboratory. Median body lengths (size ranges) of collected Pacific saury, Japanese sardine, chub mackerel, and Japanese anchovy during surveys were 29.4 (27.0–36.5), 10.5 (2.9–22.4), 14.2 (2.4–40.2), and 8.1 (2.0–15.3) cm, respectively (Fig. S2). The density (no. km⁻²) of these small pelagic fishes at each sampling station was calculated by dividing the number of fish caught by the swept area.

2.2. Data analysis

Pacific saury comprises age-0 and age-1 fish because of their 2 yr lifespan (Suyama et al. 2006), and the species' distribution pattern is age-dependent during summer (Meguro et al. 1987). The trawl net used for the surveys could not capture smaller age-0 fish due to mesh size selectivity (Hashimoto et al. 2020). Therefore, in this study, only the data of age-1 Pacific saury (>27 cm; Suyama et al. 2020) were used for analysis. The distribution pattern of age-1 Pacific saury also satisfied the conditions for testing the biological interaction illustrated in Fig. 1 (see Section 3.2). Hereafter, we refer to age-1 Pacific saury as 'Pacific saury'.

Spatial overlaps of Pacific saury and each potential competitor were quantified by 2 overlap indices. The first index used density data (biomass-weighted overlap index [*B*]; Carroll et al. 2019) and was calculated as follows:

$$B = \sum_i^n [D_{p,i} / \max(D_p) \times D_{c,i} / \max(D_c)] / \sum_i^n D_{p,i} / \max(D_p) \quad (1)$$

where $D_{p,i}$ is the density of Pacific saury at the i^{th} station and $D_{c,i}$ is the density of the potential competitor (i.e. Japanese sardine, chub mackerel, or Japanese anchovy) at the i^{th} station. B was calculated every year for each pair of Pacific saury and the potential competitor to provide insight into the magnitude of competitor biomass that overlaps with Pacific saury. The second index quantified overlap patterns using

Table 2. Annual surveys considered in this study. SST: sea surface temperature

Year	No. of stations	SST range (°C)	Latitude range	Longitude range
2003	125	7.4–21.1	37° 01'–45° 02' N	142° 59' E–166° 59' W
2004	138	7.3–20.0	36° 26'–44° 59' N	144° 56' E–164° 55' W
2005	135	7.9–22.0	33° 59'–46° 12' N	144° 55' E–164° 58' W
2006	145	8.5–19.6	34° 46'–44° 47' N	144° 31' E–164° 58' W
2007	124	8.7–21.4	34° 24'–45° 16' N	142° 58' E–164° 56' W
2008	142	8.8–19.4	36° 47'–47° 25' N	142° 59' E–164° 51' W
2009	144	7.2–22.3	34° 46'–47° 00' N	142° 58' E–164° 59' W
2010	124	7.2–23.3	36° 19'–46° 49' N	142° 58' E–164° 55' W
2011	92	7.9–19.0	36° 55'–47° 46' N	144° 58' E–176° 59' W
2012	127	7.9–18.5	37° 05'–48° 51' N	142° 56' E–164° 59' W
2013	116	7.2–19.6	36° 09'–48° 35' N	143° 09' E–164° 58' W
2014	122	8.2–21.8	37° 01'–46° 50' N	143° 58' E–164° 58' W
2015	111	7.3–20.4	36° 29'–47° 28' N	143° 59' E–164° 58' W
2016	115	7.4–23.2	37° 01'–46° 02' N	143° 58' E–164° 58' W
2017	129	7.4–23.0	36° 30'–46° 19' N	142° 58' E–164° 58' W
2018	104	6.3–20.4	37° 31'–46° 00' N	151° 01' E–164° 57' W
2019	106	6.3–19.6	36° 05'–46° 02' N	150° 31' E–164° 57' W

presence/absence data (Jaccard similarity index [*C*]; Keil et al. 2021) as follows:

$$C = a / (a + b + c) \quad (2)$$

where a represents the number of sympatric occurrences between Pacific saury and another species, and b and c are the numbers of the stations occupied by either Pacific saury or the other species, respectively. C was calculated every year for each pair of Pacific saury and the potential competitor and gave the proportion of sites occupied by both species among all occupied sites, ranging between 0 (no overlap) and 1 (perfect overlap). These 2 overlapping indices were compared to understand the spatial overlap among species.

As a proxy for the SST preference of Pacific saury, the Pacific saury log-density-weighted mean of SST (GT ; Bez & Rivoirard 2000) was estimated for each survey line in each year as follows:

$$GT_{(j,k)} = \left[\sum_i S_{i,j,k} \times D_{PS(i,j,k)} \right] / \sum_i D_{PS(i,j,k)} \quad (3)$$

where $S_{(i,j,k)}$ and $D_{PS(i,j,k)}$ are the SST and natural log-transformed density (after adding 1 as a constant) of Pacific saury at the i^{th} sampling station on the j^{th} survey line in year k , respectively. SST and density were not standardized; therefore, $GT_{(j,k)}$ indicates the center of distribution of Pacific saury with respect to SST along the j^{th} survey line in year k . By confirming that GT varies spatio-temporally depending on the densities of potential competitors, we inferred the apparent effect of biological interactions on the distribution of Pacific saury (Fig. 1). A linear

model (LM) analysis was employed to conduct such statistical comparisons of GT and show the biological interaction effect on the distribution of Pacific saury with regard to SST gradients while also considering intra-specific density-dependent effects. We developed the full model as follows:

$$\begin{aligned} GT_{(j,k)} = & \alpha + \beta_1 mD_{PS(j,k)} + \beta_2 mD_{JS(j,k)} + \\ & \beta_3 mD_{CM(j,k)} + \beta_4 mD_{JA(j,k)} + \beta_5 date_{(j,k)} + \\ & \beta_6 limit_j \times sstmin_{(j,k)} + year_k + \varepsilon \end{aligned} \quad (4)$$

where α is the intercept and β_{1-6} are parameters to be estimated. Parameter ε denotes an error term, where $\varepsilon \sim N(0, \sigma^2)$. The terms $mD_{PS(j,k)}$, $mD_{JS(j,k)}$, $mD_{CM(j,k)}$, and $mD_{JA(j,k)}$ are the natural log-transformed mean densities after adding one (as a constant) of Pacific saury, Japanese sardine, chub mackerel, and Japanese anchovy, respectively, on the j th survey line in year k ; $year_k$ is the year effect in year k included as a categorical variable; $date_{(j,k)}$ is the mean survey date for the j th survey line in year k , expressed as the number of days since 1 June. Since Pacific saury typically migrate northward to subarctic waters during the survey season, a larger number of days since 1 June is expected to result in a lower GT . The lowest SST of each survey line tended to be higher in the area west of $158^\circ E$ than the area east of $158^\circ E$ (see Section 3.3) because the northern limits of survey lines in the areas west and east of $158^\circ E$ were determined based on accessibility to the water and $SST \leq 9^\circ C$, respectively. Therefore, it is impossible to compare GT directly between areas west and east of $158^\circ E$. To incorporate the effect of the area restriction on GT , the interaction term $limit_j \times sstmin_{(j,k)}$ was included. $limit_j$ is a binary variable, where 1 and 0 indicate that the northern limits of j th survey lines were determined by the area restriction (the area west of $158^\circ E$) or by SST being $\leq 9^\circ C$ (the area east of $158^\circ E$), respectively. $sstmin_{(j,k)}$ is the difference between the lowest SST of the j th survey line in year k and the lowest SST of all data ($6.3^\circ C$); thus, it tends to be higher with the extent of area restriction. Because $sstmin_{(j,k)}$ works in interaction with $limit_j$, it has no effect in the area without the restriction (east of $158^\circ E$). In the area west of $158^\circ E$, where the northern part of the research area was restricted, $limit_j \times sstmin_{(j,k)}$ works as a proxy for the extent of the area restriction, which can affect GT . The Bayesian information criterion (BIC) was compared among models of all combinations of explanatory variables in the full model using the 'dredge' function from the R package 'MuMIn' (Bartoń 2020). The best model had the lowest BIC. In addition, we

used standard t -tests to check the significance of each coefficient in the models. To understand the spatio-temporal variation of the extent to which potential competitors affected the distribution of Pacific saury, the following analysis was conducted. The best model was used to predict GT for all observations (GT_{observed}). The same best model was also used to predict GT under the assumption that all competing species' densities were zero (GT_{zero}). The difference between these 2 predictions was calculated as follows:

$$\Delta GT = GT_{\text{observed}} - GT_{\text{zero}} \quad (5)$$

where ΔGT indicates how many degrees GT changed due to the presence of a potential competitor at a given survey line in a given year. Negative ΔGT means that the SST at the center of the Pacific saury distribution was lowered by the potential competitors, and vice versa. Spatio-temporal variation in ΔGT reflects the estimated extent over which potential competitors affect the distribution of Pacific saury. All statistical analyses were conducted using R version 4.1.2 (R Core Team 2021).

3. RESULTS

3.1. Annual fluctuations in encounter probabilities and densities of target species

The encounter probability and median natural log-transformed densities of positive catch (hereafter, 'log-density') of the 4 small pelagic fishes varied substantially across years (Fig. 3). The encounter probability and median log-density of Japanese anchovy were relatively high from 2003–2012 but declined sharply after 2013. In contrast, the encounter probability and median log-density of chub mackerel were low until 2013, except for spikes in 2007. In 2013, some very high log-densities (>10) were observed, and median log-densities increased sharply thereafter. Chub mackerel encounter probability also increased gradually after 2012. The encounter probability of Japanese sardine was low (<0.15) before gradually increasing after 2012, except in 2010 and 2011. The median log-density of Japanese sardine gradually increased and was highest among the 4 species after 2013. Pacific saury showed no apparent annual trend in encounter probability, but a moderate decreasing trend was seen in the median log-density beginning in 2003, although it was relatively stable compared to the log-density of the other 3 species.

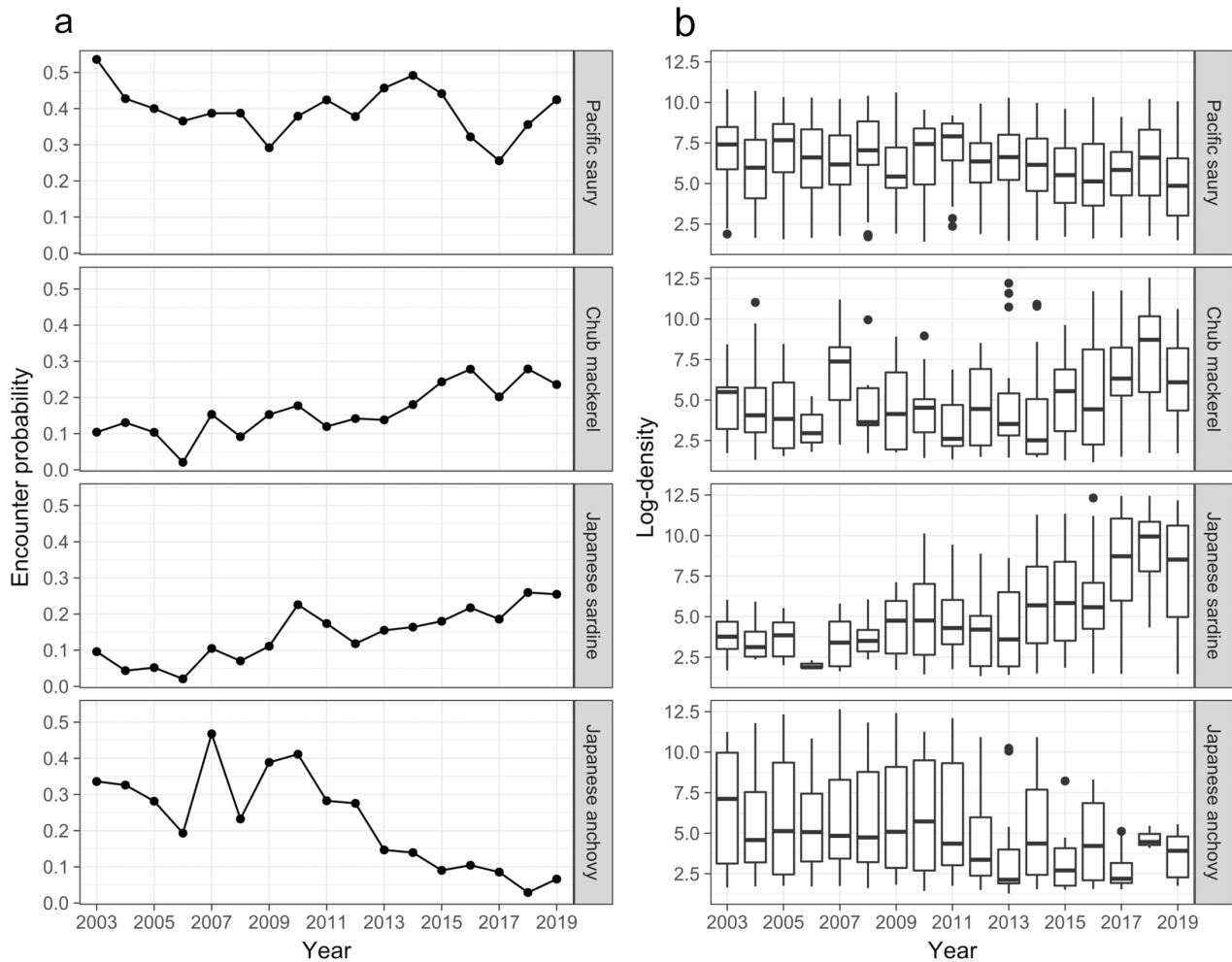


Fig. 3. (a) Encounter probabilities and (b) boxplots of the natural log-transformed density of positive catches of the 4 target species. **Bold** lines: medians; boxes: 25th and 75th percentiles; whiskers: 1.5× interquartile range; points: outliers

3.2. General distribution patterns of target species

The distributions of Pacific saury and potential competitors were adjacent to each other, with Pacific saury tending to inhabit areas to the northeast of the range of its potential competitors (Fig. 4). Distribution patterns for all years are shown in Fig. S3.

Pacific saury was broadly distributed in the area west of 165° W (Fig. 5). In contrast, other species were mainly distributed in the WA, and very few individuals of these species were found in the EA. Log-densities of Pacific saury exceeding 10 were observed in the area between 155° E and 180° longitude (Fig. 5). Log-densities of Japanese sardine exceeding 10 were observed in the area between 150° E and 180° longitude. Similarly high log-densities of chub mackerel were observed in the area between 145° and 170° E. Japanese anchovy had log-densities higher than 10 in the WA.

The distributions of Pacific saury and the other 3 species were adjacent with respect to SST, with some overlap (Fig. 6). Pacific saury were mainly found in water colder than 15°C, while the other species were mainly distributed in water warmer than 15°C (Fig. 6). The highest encounter probability of Pacific saury was observed at 12°C (Fig. 6). Encounter probability decreased from 12–19°C, and no Pacific saury were observed in water warmer than 20°C. Median log-densities of Pacific saury higher than 5 were observed between 7 and 13°C. Chub mackerel encounter probability peaked at 20°C and showed a dome shape with a heavy tail on the colder side and a steep decline at warmer temperatures. Median log-density of chub mackerel showed no clear trend along SST. Encounter probability of Japanese sardine increased gradually to a peak at 17°C and decreased in warmer temperatures to zero above 22°C. There was no clear trend of log-density of

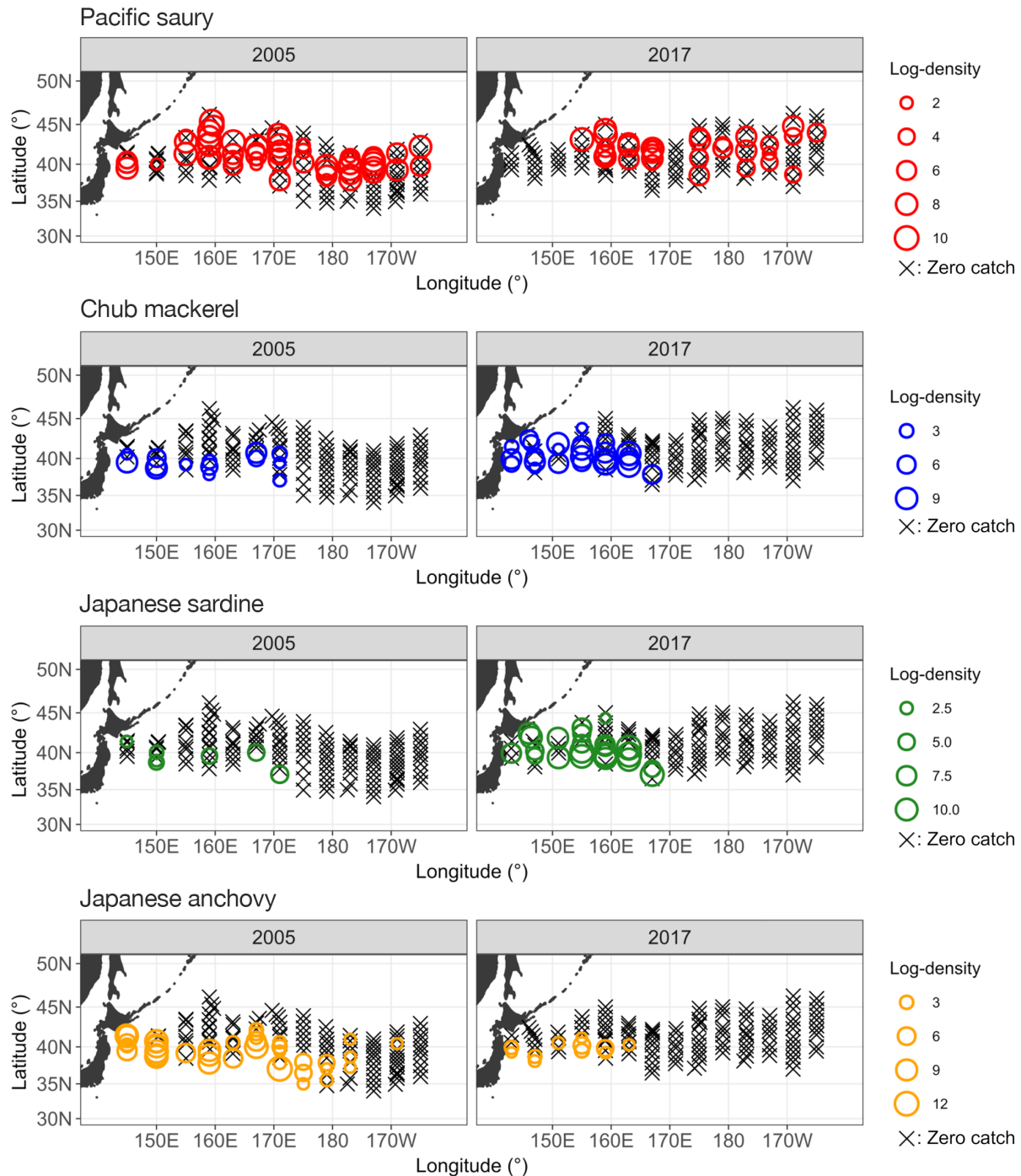


Fig. 4. Log-transformed densities of 4 target species illustrating the geographical distribution pattern in 2 years representative of the early (2005) and late (2017) period

Japanese sardine along SST. Japanese anchovy showed a monotonic increase in encounter probability from cold to warm water, while log-density peaked at 17°C and decreased sharply thereafter.

The overlap indices C and B were generally low regardless of species or year (<0.25 in C ; <0.1 in B),

indicating a separation in the main distributions of Pacific saury and its potential competitors with only a slight overlap (Fig. 7). However, C differed among species and years. Japanese anchovy showed higher C when its encounter probability and log-density (2003–2010) were higher compared with the other

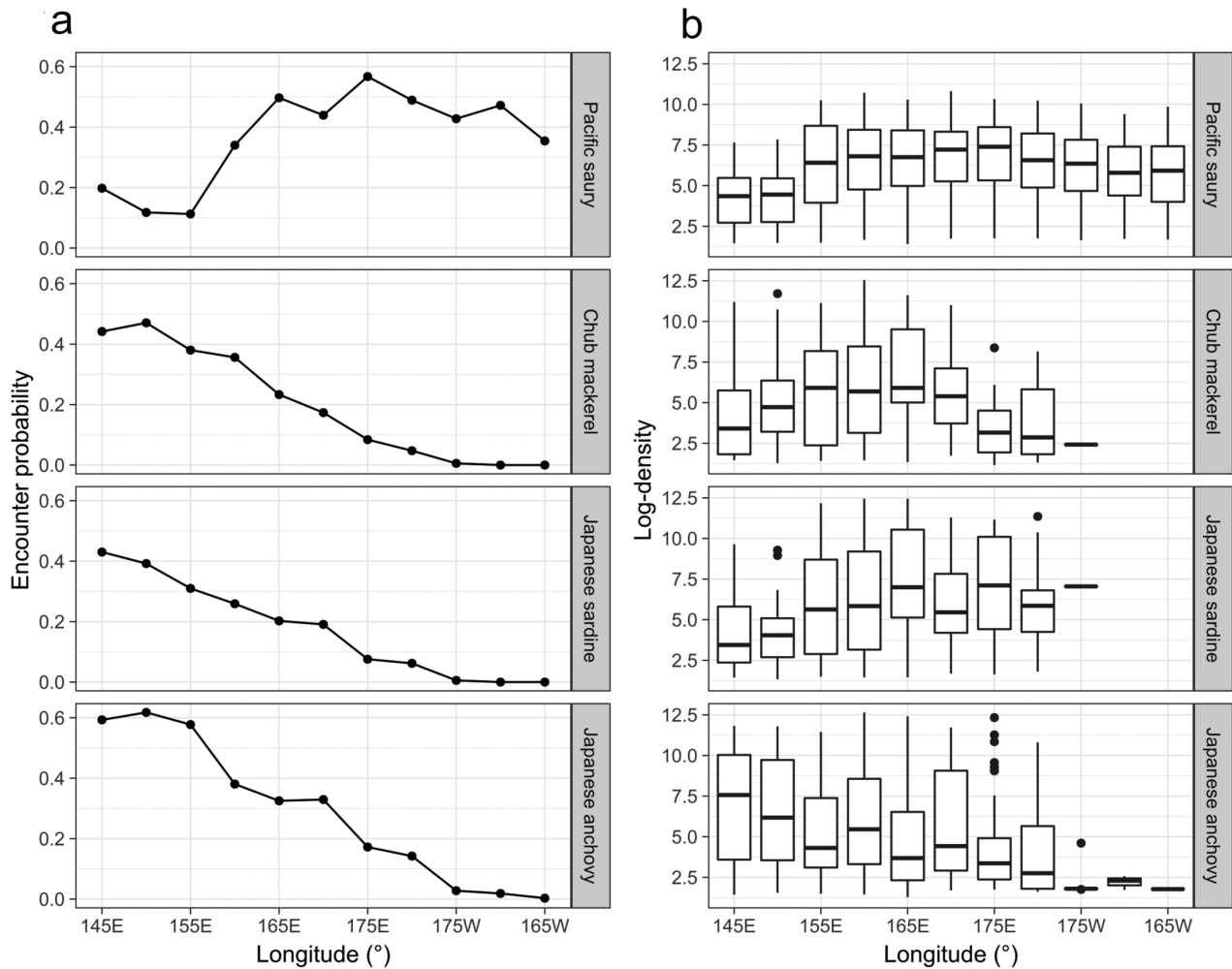


Fig. 5. Longitudinal changes in (a) encounter probabilities and (b) natural log-transformed positive catch rates of the 4 target species. Boxplot parameters as in Fig. 3. Horizontal axis labels denote the upper limit of the longitude in each bin

species and years. Meanwhile, C of Japanese sardine and chub mackerel was generally lower than 0.1 regardless of year. Conversely, B generally showed very low values (<0.1) regardless of species and year (Fig. 7).

3.3. Annual change of distribution patterns of target species along SST

Most Pacific saury were observed between 7 and 15°C, although log-densities higher than 5 were sometimes observed between 15 and 20°C before 2012 (Fig. 8). After 2012, Pacific saury in the WA sometimes occurred in waters with SSTs colder than 7.5°C—especially in 2018 and 2019—although no Pacific saury were observed under this SST condition before 2012. Conversely, no Pacific saury with log-

density > 5 were found in water warmer than 15°C after 2015. In the EA, no clear annual trend was found between year and distribution pattern of Pacific saury along SST.

Prior to 2012, most Japanese sardine and chub mackerel occurred in waters warmer than 15°C SST in the WA (Fig. 8). However, after 2012, these fish started to inhabit waters colder than 15°C, with log-densities higher than 7.5. The edge of the species' distributions was around 10°C SST. Japanese anchovy had higher log-densities (>10) mainly in waters with SSTs warmer than 15°C before 2011.

As expected, sst_{min} showed higher values in the area west of 158°E because of the limitation at the northern part of the study area (Fig. 9a). GT also tended to show higher values in the western area of 158°E (Fig. 9b). After 2012, GT in the WA, especially between 160 and 175°E, decreased

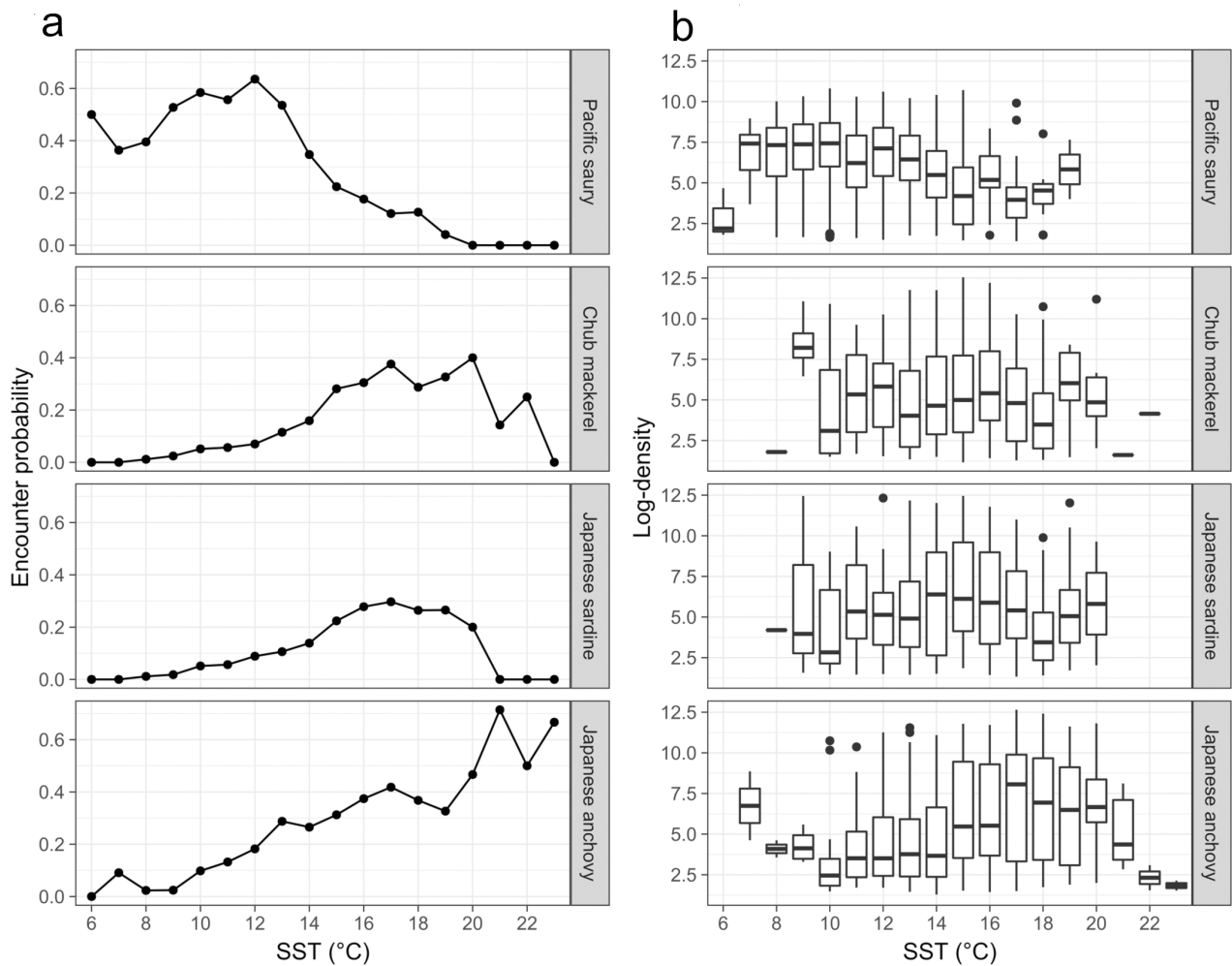


Fig. 6. (a) Encounter probabilities and (b) natural log-transformed positive catch rates of the 4 target species along a sea surface temperature (SST) gradient. Boxplot parameters as in Fig. 3. Horizontal axis labels denote the upper limits of SST in each bin

compared with previous years and frequently showed values lower than 10°C. Such a tendency was not observed in the EA.

In the LM analysis, the explanatory variables mD_{PS} , mD_{JS} , and the interaction between *limit* and *sstmin* were included in the best model selected by BIC (Table 3). The coefficient of determination (adjusted- R^2 value) of the best model was 0.40. In the best model, all selected coefficients were significantly different from 0 (t -test, $p < 0.05$) and mD_{JS} and mD_{PS} had negative effects on GT , implying a northward shift towards colder waters when densities of either species were higher. The estimated coefficient for the *limit* \times *sstmin* interaction was positive in the area with the restriction (west of 158° E). The coefficient for mD_{JS} was negative and significant in all top 5 models. The mD_{JA} term was included in the sec-

ond- and fourth-best models, although the coefficient was not significantly different from 0 in the second-best model ($p > 0.05$). The mD_{CM} term was included in the third- and fourth-best models with a non-significant negative coefficient ($p > 0.05$). The term *date* was only included in the fifth-best model but had a non-significant coefficient ($p > 0.05$). The difference in temperature-weighted density, ΔGT , showed larger negative values (ranging from -1.5 to -2.0°C) in the area between 155° E to 180° longitude after 2013 (Fig. 10). In particular, the largest negative values of ΔGT were observed between 155° and 165° E (dropped more than 1.75°C; Fig. 10), where Japanese sardine were most abundant (Fig. 5). Conversely, ΔGT was mostly 0, regardless of year, in the EA, where almost no Japanese sardine were observed (Fig. 10).

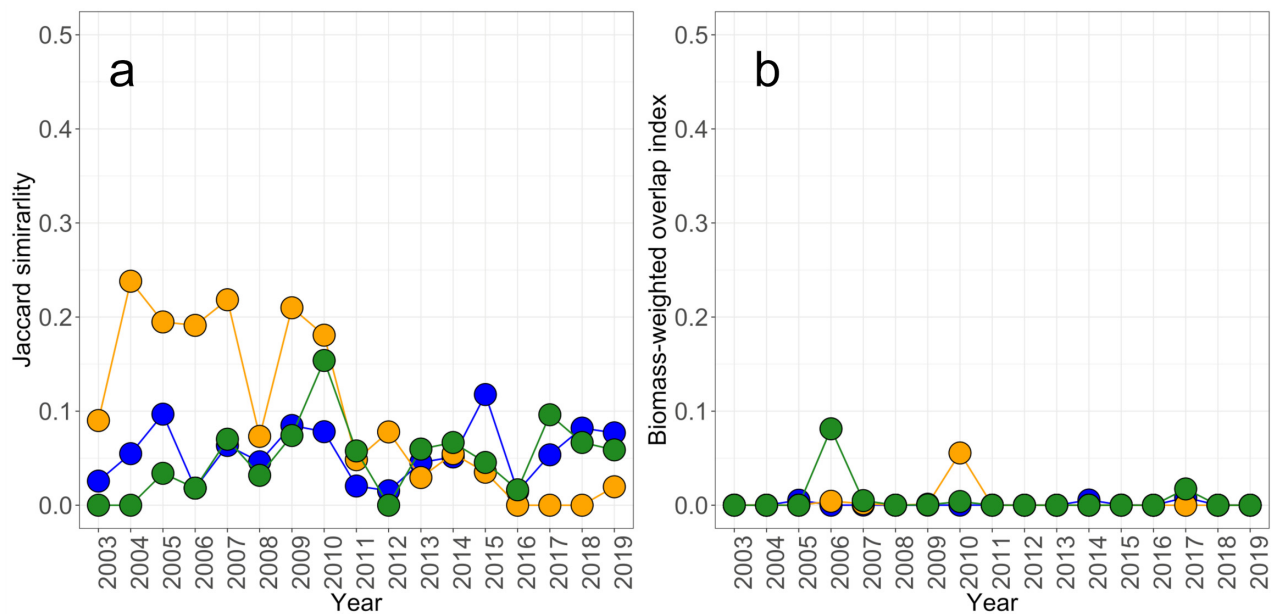


Fig. 7. Annual (a) Jaccard similarity and (b) biomass-weighted overlap index between Pacific saury and each potential competitor. Blue, green, and yellow plots indicate the index between Pacific saury and chub mackerel, Japanese sardine, and Japanese anchovy, respectively

Table 3. Coefficients of models selected based on the Bayesian information criterion (BIC). The best model is represented in **bold**. See Section 2.2 for explanation of variables. lim(+): west of 158°E; lim(-): east of 158°E. ***p < 0.001; **p < 0.01; *p < 0.05

				Variables					
mD_{PS}	mD_{JS}	mD_{CM}	mD_{JA}	date	lim(+) × sst_{min}	lim(-) × sst_{min}	Intercept	Delta BIC	Adj. R ²
-0.24***	-0.18***				0.44***	-	14.00***	0	0.40
-0.27***	-0.19***		0.06		0.39***	-	14.04***	1.76	0.40
-0.24***	-0.13**	-0.07			0.48***	-	13.98***	3.14	0.40
-0.26***	-0.14**	-0.09	0.07*		0.42***	-	14.02***	3.74	0.41
-0.24***	-0.18***			-0.01	0.44***	-	14.14***	4.98	0.39

4. DISCUSSION

Extensive long-term quantitative survey data suggest that biological interactions can be one of the factors influencing the large-scale distribution of small pelagic fishes in the open ocean. Pacific saury was observed in both WA and EA, but its potential competitors were observed only in WA (Fig. 5). In addition, each pair of Pacific saury and a potential competitor showed a parapatric distribution, and the habitat SSTs for Pacific saury and the potential competitors were partially overlapping (Fig. 6). The characteristics of these distributions allowed us to compare the distribution pattern of Pacific saury with various densities of the potential competitors (Fig. 1). Such comparison can separate the effects of biological interactions and abiotic factors on the dis-

tribution of Pacific saury under the assumption that other unknown factors important for the distribution of Pacific saury were not substantially different among periods and areas (Anderson et al. 2002). The distribution of Japanese sardine expanded to colder waters with increasing density, as suggested by Barange et al. (2009) (Figs. 3 & 8). The center of Pacific saury distribution shifted to colder regions only in the area and period where Japanese sardine occurred at higher densities, i.e. in the WA during 2013–2019 (Figs. 8 & 9b). The best LM model based on BIC included both the density of Japanese sardine and Pacific saury as explanatory variables, suggesting that intra- and inter-species interactions potentially alter the distribution of Pacific saury. This finding is expected based on results from field and lab studies on other species (Elliott 1975, Swain

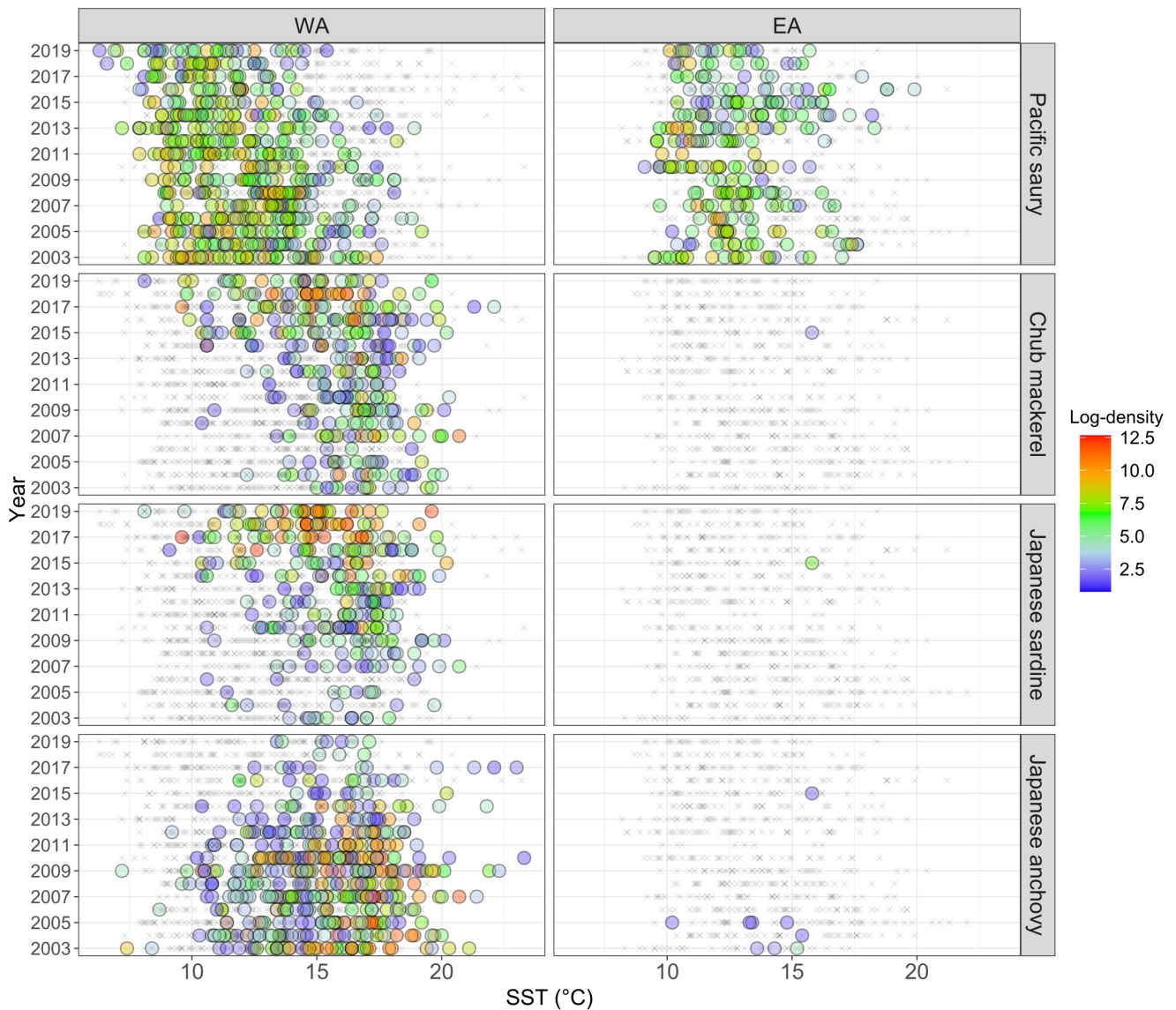


Fig. 8. Annual distribution pattern of 4 target species along sea surface temperature (SST) gradients in areas to the west (WA) and east (EA) of 180° longitude. Natural log-densities are indicated by the colors of circles. Zero catches are shown by the grey crosses

& Kramer 1995). The inter-species effects of Japanese sardine have also been indicated or hypothesized in previous studies (e.g. Tadokoro et al. 2005, Ito et al. 2007, Nakayama et al. 2018, Kamimura et al. 2021).

Pacific saury and Japanese sardine showed a parapatric distribution (Fig. 4) that was maintained even when Japanese sardine expanded its distribution into cold waters with increasing abundance (Fig. 7). This resulted in a shift of the center of distribution of Pacific saury to colder waters (Figs. 8 & 9). To clarify the mechanism by which Japanese sardine influences the distribution of Pacific saury, it is important

to consider the reason why Pacific saury and Japanese sardine maintain a parapatric distribution. Most explanations of parapatric distributions assume negative interactions as the cause of interspecific exclusion along geographical gradients; the species with the highest persistence potential displaces the other (Bull & Possingham 1995). Bull (1991) summarized the mechanisms resulting in parapatric distributions of organisms as follows: (1) differences in the preferred environments of different species, (2) competition, and (3) other interactions among organisms (e.g. predation). The results of this study do not suggest that the parapatric distribution was formed solely

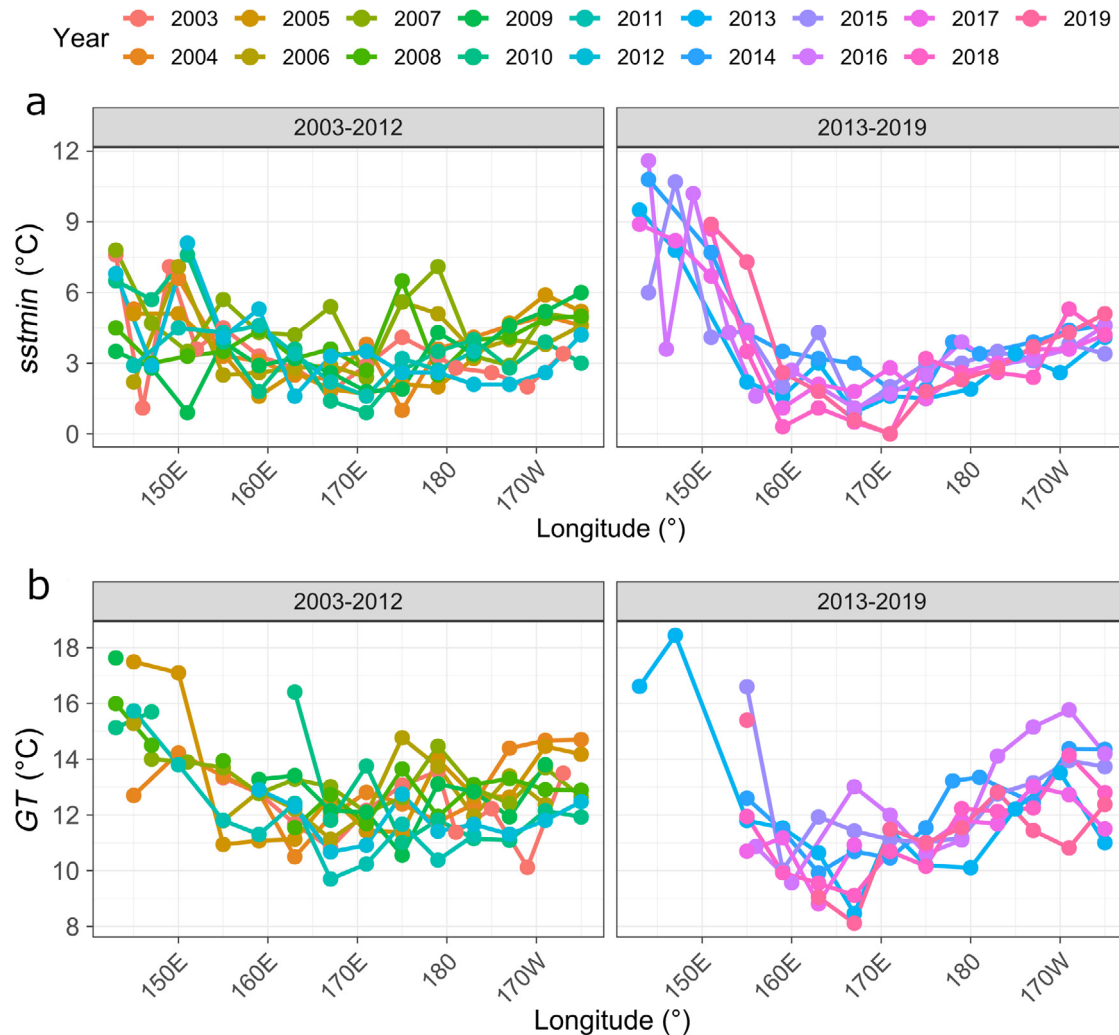


Fig. 9. Spatio-temporal variation in (a) minimum sea surface temperature (SST) of each survey line (*sstmin*), indicated as the difference from the minimum SST among all data (6.3°C) and (b) log-density-weighted mean of SST of Pacific saury (*GT*) during 2003–2012 and 2013–2019

by differences in the environmental preferences of Pacific saury and Japanese sardine because, although there was sufficient overlap in SST preferences between Pacific saury and its potential competitors (Fig. 6), the actual distributions overlapped only slightly (Fig. 7). Therefore, some biological interactions must be involved in maintaining the distributional patterns.

Competition may explain the mechanism by which Pacific saury and Japanese sardine maintained their parapatric distribution. Pacific saury and Japanese sardine may compete for their common prey items such as *Neocalanus* copepods (Tadokoro et al. 2005, Ito et al. 2007). The distribution centers of the 2 species were clearly separated (Figs. 4 & 7), suggesting that most individuals were not exposed to direct interspecific competition. However, in the case of

migratory species such as Pacific saury and Japanese sardine, frequent invasions of each other's territories would occur at the boundaries of their parapatric distributions, where direct competition could occur, at least in the short term (Bull 1991, Bull & Possingham 1995). Such direct competition might cause competitive exclusion, contributing to the formation and maintenance of clear boundaries for their parapatric distributions regardless of the expansion of Japanese sardine into colder waters after 2012.

In addition to the highest mean log-densities of Japanese sardine among 3 potential competitors after 2013 (Fig. 3), its unique feeding strategy (filter-feeding) may influence the distribution and/or growth of other species such as Pacific saury through their higher feeding pressure. Japanese sardines are primarily non-selective filter feeders, whereas

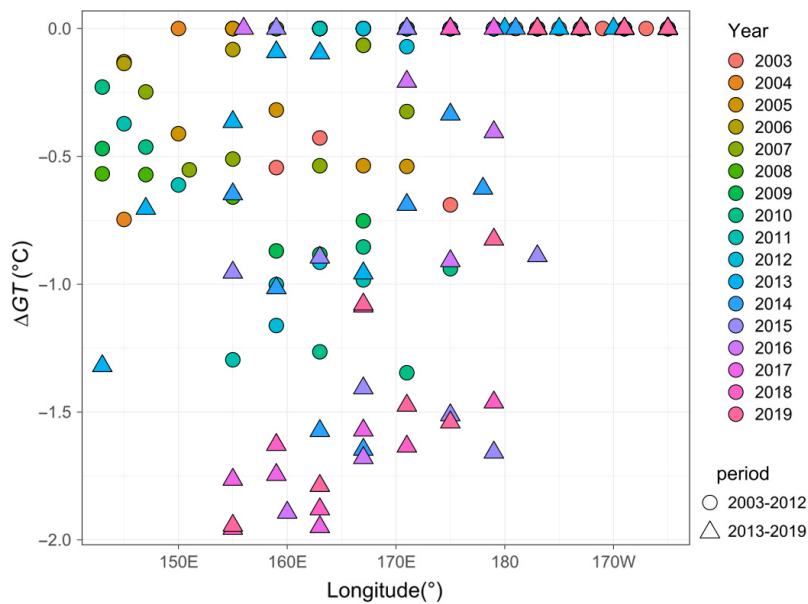


Fig. 10. Spatio-temporal variation in the difference between predicted values of the log-density-weighted mean of sea surface temperature of Pacific saury (GT) under conditions of zero log-density of Japanese sardine and values predicted by the best model using observed log-density of Japanese sardine (ΔGT). Each individual point is the ΔGT calculated for a given survey line in a given year

Japanese anchovy, chub mackerel, and Pacific saury are particulate feeders (Table 1). Filter feeders form dense schools that effectively capture not only small plankton but also large evasive zooplankton (Lazzaro 1987). The sardine *Sardinops sagax* can feed non-selectively by filtering, and its consumption efficiency increases with the size of the ambient prey (van der Lingen 1994). Moreover, compared with the consumption efficiency of anchovy *Engraulis capensis*, for sardine, the larger the prey, the greater the clearance efficiency per fish (van der Lingen 1994). This feeding strategy and the high sardine density may reduce the density of prey items such as *Neocalanus* copepods, as suggested by previous studies (Tadokoro et al. 2005, Ito et al. 2007), and can affect other species that share these prey items (Ito et al. 2007, Kamimura et al. 2021). Pacific saury is a particulate feeder like the anchovy *E. capensis*, and its main prey items are larger zooplankton such as *Neocalanus* copepods and krill (Miyamoto et al. 2020). Thus, if Japanese sardine and Pacific saury co-occur in an area, Japanese sardine may be more efficient in terms of feeding strategy. In that case, Pacific saury may have avoided coexisting with and being exposed to competition from Japanese sardine and shifted its main distribution to lower SST areas where Japanese sardine does not occur, to optimize its growth and survival.

The effects of chub mackerel on Pacific saury distribution were weaker than those of Japanese sardine. Negative coefficients of chub mackerel were selected in the third- and fourth-best models but were not significant (Table 3). The density of chub mackerel tended to be lower than that of Japanese sardine (Fig. 3), suggesting that chub mackerel may be less competitive with Pacific saury than Japanese sardine. Previous studies have suggested that Japanese sardine is a superior competitor and can potentially affect other species' ecology (Nakayama et al. 2018, Kamimura et al. 2021), supporting our results.

Japanese anchovy also seems to have a weaker effect on the distribution of Pacific saury than Japanese sardine. The overlap in terms of biomass (i.e. B) of Japanese anchovy with Pacific saury was low throughout the time series, suggesting that these species also maintained a parapatric distribution.

On the other hand, Japanese anchovy showed a higher C index than Japanese sardine and chub mackerel during periods of their high abundance, indicating a slightly wider overlap in distribution with Pacific saury in terms of presence/absence (Fig. 7). Therefore, at a low density, Japanese anchovy can co-exist with Pacific saury, while chub mackerel and Japanese sardine can not. In addition, only the fourth-best LM includes a significant coefficient for mean density of Japanese anchovy, although the coefficient was positive (Table 3). These results suggest that Japanese anchovy has little effect on the distribution of Pacific saury with respect to SST. The smaller amount of feeding per individual in Japanese anchovy implied by its smaller body size (Fig. S2, Table 1) and the lower clearance rate per individual in particulate-feeding than in filter-feeding (van der Lingen 1994) might be possible reasons for their smaller effects on biological interactions because these characteristics would lead to lower feeding pressure per individual.

The intra-specific density-dependent effect on GT of Pacific saury was significant in all models in the LM analysis (Table 3). Atlantic cod *Gadus morhua* also showed a similar effect whereby higher densities led to a shift in their distribution to lower ambient temperatures (Swain & Kramer 1995). The mechanism was explained as follows: higher density leads to lower prey availability for each individual, result-

ing in a shift in distribution to lower temperatures to save energy by lowering their metabolism (Swain & Kramer 1995). The higher *GT* of Pacific saury in the EA in 2016 (Fig. 9) may partially stem from the decrease of Pacific saury density after 2012 (Hashimoto et al. 2020). Although the abundance of Pacific saury in the WA has also been declining in recent years (Hashimoto et al. 2020), the best model in this study suggested that the negative effect of Japanese sardine overwhelmed the positive effect of the decrease in Pacific saury abundance, resulting in a decrease in *GT* in the WA in recent years (Fig. 10).

The shift in range and center of distribution to colder water may have a negative impact on Pacific saury growth. Pacific saury were most frequently observed in waters around 12°C (Fig. 6). Prior to 2012, when there were few Japanese sardines, most *GT* values were between 10 and 14°C, except west of 158°E, where the survey area was restricted (Fig. 9b). Given sufficient prey, 12°C may be a suitable SST for Pacific saury. In rearing experiments, the swimming velocity of Pacific saury was highest at a water temperature of 12°C (Morioka et al. 2009). Swimming speed is a proxy for behavioral activity, especially in planktivorous fishes like Pacific saury (Plaut 2001). The high activity observed at 12°C may support the idea that this water temperature is suitable for activities such as feeding and predator avoidance in Pacific saury (Plaut 2001). However, since 2013, when the number of Japanese sardine increased, *GT* frequently dropped below 10°C in the region between 159° and 170°E, reaching a minimum of 8.1°C (Fig. 9b). These results suggest that the SST of the center of the Pacific saury distribution may have dropped more than 1.5°C in areas where Japanese sardine has been abundant (Fig. 10). Schools of Pacific saury were sometimes observed in waters where SSTs were below 7.5°C (Fig. 8). Although the density of their main prey, *Neocalanus* copepods, is generally higher in colder subarctic waters (Miyamoto et al. 2020), extremely low water temperatures may have a negative impact on the growth of Pacific saury. Under rearing conditions, the swimming velocity of Pacific saury decreased in waters between 12 and 5°C, and the number of deaths suddenly increased below 7°C (Morioka et al. 2009). This implies that colder conditions could be lethal for Pacific saury even when sufficient prey is available. The area where Japanese sardine possibly altered Pacific saury distribution (155°E to 180° longitude; Fig. 10) was the main distribution area of age-1 Pacific saury (Hashimoto et al. 2020), suggesting a possible population-level negative effect of Japanese

sardine on Pacific saury. In the future, it may be possible to verify this hypothesis by clarifying the spatio-temporal changes in the growth and body condition of Pacific saury.

The analyses in this study do not conclusively demonstrate that a biological interaction can alter the distribution of Pacific saury. Biological interactions were not directly observed in the field through competitor-removal experiments, observations of attacking behavior, or other means. Therefore, the possibility that other factors (e.g. unknown competitors, parasites, predators, environmental variables) may have altered the distribution of the target species can not be eliminated. Nevertheless, many researchers have established that our approach, based on Anderson et al. (2002), is useful for providing evidence that biological interactions affect distributions under conditions where it is difficult to directly observe actual competitive processes (Elith & Leathwick 2009, Robinson et al. 2011, Wiens 2011).

Prey distribution was not addressed in this study, but will have a significant impact on the distribution of small pelagic fishes in particular. The feeding environment in the western part of the study area is strongly influenced by the mixing of Kuroshio and Oyashio waters (Miyamoto et al. 2022). In particular, the Isoguchi Jet (Isoguchi et al. 2006), which is a quasi-stationary jet that separates from Kuroshio currents and extends northward, has a strong influence on the feeding environment for pelagic fishes in this area (Miyamoto et al. 2022). Various environmental factors that were suggested to be important for the distribution of Pacific saury, such as SSS, SSH, SSTG, and chl *a*, should be related to currents in this area (Chang et al. 2019, Hua et al. 2020, Liu et al. 2022, Xing et al. 2022). Long-term interannual variations in the current speed of the Isoguchi Jet (e.g. Nakano et al. 2018) may significantly change the feeding environment of Pacific saury—especially in the west, where the influence of these currents is particularly significant—and may alter their distribution only in the western area. Conversely, it should be noted that currents are also closely related to the distribution and density of potential competitors such as Japanese sardine in the study region. The Isoguchi Jet also plays a very important role in dispersal and recruitment by efficiently transporting Japanese sardine to more prey-rich subarctic water (Yatsu 2019, Miyamoto et al. 2022). Examining the spatio-temporal variation in the distribution of *Neocalanus* copepods, the main prey item of Pacific saury during early summer in the western and central North Pacific (Miyamoto et al. 2020), and the correspondence

between their distribution and that of Pacific saury would be useful to validate the results of this study, as would direct observations of the interactions between Pacific saury and Japanese sardine in captive experiments. In the future, a zooplankton data set with broad spatio-temporal coverage should be constructed.

This study suggests the possibility that an expansion in the distribution of potential competitors (especially Japanese sardine) can alter the distribution of Pacific saury with regard to SST. In addition, we observed that both inter- and intra-specific interactions can alter the distribution pattern of Pacific saury. To date, the effect of biological interactions on species distributions over large areas has been ignored in most studies, especially in the pelagic region (Robinson et al. 2011). However, the results of this study demonstrate the uncertainty involved in predicting the distribution of organisms based on environmental factors alone.

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