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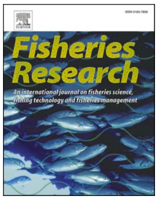

Short communication

Vertical habitat selection of sardine juveniles inferred from oxygen stable isotope of otolith

Tatsuya Sakamoto[a,b,*,1,2], Toyoho Ishimura[c,d,3], Tomohiko Matsuura[e], Motomitsu Takahashi[a,4]

[a] Fisheries Resource Research Institute, Japan Fisheries Research and Education Agency, Nagasaki, Japan
[b] The Hakubi Center for Advanced Research, Kyoto University, Kyoto, Japan
[c] Department of Chemistry and Material Engineering, National Institute of Technology, Ibaraki College, Ibaraki, Japan
[d] Graduate School of Human and Environmental Studies, Kyoto University, Kyoto, Japan
[e] Fisheries Technology Institute, Japan Fisheries Research and Education Agency, Ibaraki, Japan

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ABSTRACT

Marine organisms can change their habitat depth based on feeding strategies and physiological requirements. Here, we investigated habitat depth selections of juvenile sardines in the western and eastern North Pacific, Sea of Japan, and East China Sea from summer to autumn, which have been poorly documented. Habitat depth was estimated by comparing stable oxygen isotope values at the edges of otoliths formed several weeks before capture with *in situ* temperature and salinity observations near the sampling sites. The estimated depths at the three stations in the Sea of Japan for which acoustic data were available were consistent with the maximum acoustic scattering layer. Habitat depths in the eastern North Pacific, Sea of Japan, and the East China Sea varied considerably between regions in the upper 70 m. Still, they were mostly ± 10 m from the seasonal thermocline. Average temperatures at the thermocline in the regions were 16.8–24.5°C, which included temperatures significantly higher than the presumed optimal temperatures. However, the habitat depths in the subarctic North Pacific, where the mean temperature at the thermocline was 8.4°C, were consistently in the surface mixed layer above the thermocline. These results suggested that juvenile sardines tend to reside in the thermocline to feed efficiently on aggregated plankton, provided the temperature is physiologically tolerable. Our results may be useful for increasing sampling efficiency, validating assumptions in behavioural models, and providing insight into how atmospheric forcing affects sardine growth and survival.

1. Introduction

The biotic and physical environments in the ocean change significantly with depth, and marine organisms change their habitat depths depending on various factors, such as prey abundance, physiological requirements, and predator avoidance (e.g., Andrzejaczek et al., 2019). Therefore, knowledge of vertical habitat selection is essential for understanding species' feeding and life-history strategies and the interactions between prey and predator. The vertical structures of physical variables are particularly important when the ocean is stratified, owing to seasonal warming of the surface layer. In a stratified water column, the seasonal thermocline becomes a boundary that separates warmer, sunlit surface water from cooler, nutrient-rich deep water. A thin layer of significantly high phytoplankton density, referred to as the subsurface chlorophyll maximum, is often found around the thermocline (e.g., Carter et al., 1987; Sharples et al., 2001; Hickman et al., 2012; Barnett et al., 2019), and various zooplankton and fish species are known to aggregate around the thermocline (e.g., Harris, 1988; Perry and Neilson, 1988; Benoit-Bird, 2009; Sánchez-Velasco et al., 2013; Furukawa et al., 2014; Madigan et al., 2021). Thus, the thermocline may be an important

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* Corresponding author at: Fisheries Resource Research Institute, Japan Fisheries Research and Education Agency, Nagasaki, Japan.
E-mail address: sakamoto.tatsuya.3p@kyoto-u.ac.jp (T. Sakamoto).

[1] Present address: Yoshidanihonmatsucho, Kyoto Sakyo-ku, Kyoto, 606–8316 Japan

[2] https://orcid.org/0000-0003-0672-4168

[3] https://orcid.org/0000-0001-9708-3743

[4] https://orcid.org/0000-0002-7659-6686

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factor influencing the choice of pelagic fish habitat depth, albeit differently for each species (Gray and Kingsford, 2003; Alvarez et al., 2021).

Sardines (*Sardinops, Sardina* spp.) are planktivorous, small pelagic fish distributed worldwide in temperate oceans. They play an important role in energy transfer from low to high trophic levels in productive regions (Cury et al., 2000), alter the distribution of competing species (Fuji et al., 2023) and are important targets for pelagic fisheries. The vertical distribution of eggs and larvae has been well studied and is often concentrated in the upper 30 m (Checkley et al., 1997; Yatsu et al., 2005; Alexandra Curtis et al., 2007; Tanaka and Franks, 2008). The behaviour of adult schools has been observed acoustically, forming dense schools during the day and dispersing widely at night (Inagake and Hirano, 1983; Giannoulaki et al., 1999; Zwolinski et al., 2007; Kaltenberg and Benoit-Bird, 2009; Coetzee et al., 2010). In some regions, schools are attracted to thin plankton layers (Benoit-Bird, 2009) or thermoclines (Inagake and Hirano, 1983). However, vertical distribution during the juvenile stage has rarely been reported. Studies have shown that growth and survival processes during the juvenile stage can significantly affect the population growth of sardines (Takahashi et al., 2008; Sakamoto et al., 2022). In addition, the strength of stratification and thermocline depth have been linked to population fluctuations in small pelagic fish in coastal upwelling regions (Lasker, 1981; Pizarro and Montecinos, 2004; van der Lingen et al., 2006). Therefore, understanding the vertical distribution of juveniles can provide insights into sardine population dynamics and support simulation studies investigating dynamics, where behavioural models have had to rely on assumptions about habitat depths that have not been empirically verified (e.g., Okunishi et al., 2012; Rose et al., 2015; Sakamoto et al., 2019).

Acoustic surveys have been the primary and most efficient tool for studying the habitat depth of schools of pelagic fish species. However, a potential limitation is the difficulty in accurately identifying species based on echo traces, which often depends on expert knowledge (Fernandes, 2009) or extensive net sampling of acoustic targets. Otolith chemistry is a complementary approach that has several advantages. Otoliths are incrementally growing calcium carbonate in the inner ear, whose chemical composition often reflects the environment where it was formed (Campana, 1999). The stable oxygen isotope (δ^{18}O) of the otolith is mainly influenced by temperature and δ^{18}O of ambient water, which has been experimentally confirmed for sardines in the North Pacific (Dorval et al., 2011; Sakamoto et al., 2017). The δ^{18}O of seawater is significantly correlated with salinity in region-specific ways (LeGrande and Schmidt, 2006). Therefore, otolith δ^{18}O at a given depth can be predicted from the vertical profiles of temperature and salinity, which allows estimation of the habitat depth of a fish by comparing the predicted and observed δ^{18}O of the otolith (e.g., Lin et al., 2012; Shiao et al., 2017). The development of microvolume analysis (Ishimura et al., 2004, 2008) has enabled isotopic analysis on a 10-day scale for sardine juveniles (Sakamoto et al., 2019) and even on a daily scale for species with large otoliths (Muto et al., 2022). Therefore, the otolith isotope approach cannot resolve diel vertical migrations like acoustic surveys. Instead, it estimates averages over weeks that may robustly reflect species habitat selection.

In this study, we investigated the vertical distribution of sardine juveniles using the stable oxygen isotope ratios of otoliths. Recently, Aono et al. 2024 suggested the vertical distributions of juveniles were likely different between the northern and southern Sea of Japan. However, the mechanism for this variation has not yet been revealed. Therefore, we extended the sampling areas to the western and eastern North Pacific and marginal seas to reveal general strategies for habitat depth selection by juvenile sardines around the North Pacific (Fig. 1). Using microvolume analysis at the edges of otoliths (Sakamoto et al., 2017), the mean habitat depths of juvenile sardines for several 10 days before capture were estimated. The estimated depths were compared with the results of an acoustic survey conducted at a limited number of stations for validation.

2. Material and methods

2.1. Sample collection

Otolith δ^{18}O data for the Japanese sardine *Sardinops sagax melanostictus* in the Sea of Japan and the nearshore and offshore western North Pacific have already been published for some sites (Oda et al., 2016; Sakamoto et al., 2019; Aono et al., 2024). To increase the spatial coverage of the dataset, we used juvenile Japanese sardines around Toyama Bay and the Oki Islands in the Sea of Japan, juveniles of the Pacific sardine *Sardinops sagax sagax* off La Jolla captured in commercial fisheries from August to November from 2004 to 2019, and juveniles in the Kuroshio-Oyashio transition zone captured in midwater trawl surveys in May 2014 and 2016 (Fig. 1). Samples were frozen after landing or on board, stored at −20°C, and thawed in a laboratory for dissection. The weight and standard length were measured, and otoliths (sagittae) were collected. The otoliths were cleaned under a microscope with fresh water to remove the remaining tissues, air-dried, and stored at room temperature. The standard lengths ranged from 71 to 140 mm. As the standard length at 50 % maturity (L_{50}) has been reported as 14–15 cm in both Japanese and Pacific sardines (Yoneda et al., 2013; Dorval et al., 2015), we considered our specimens as juveniles. The results of otolith microstructure analysis (see below) showed that they were age-0.

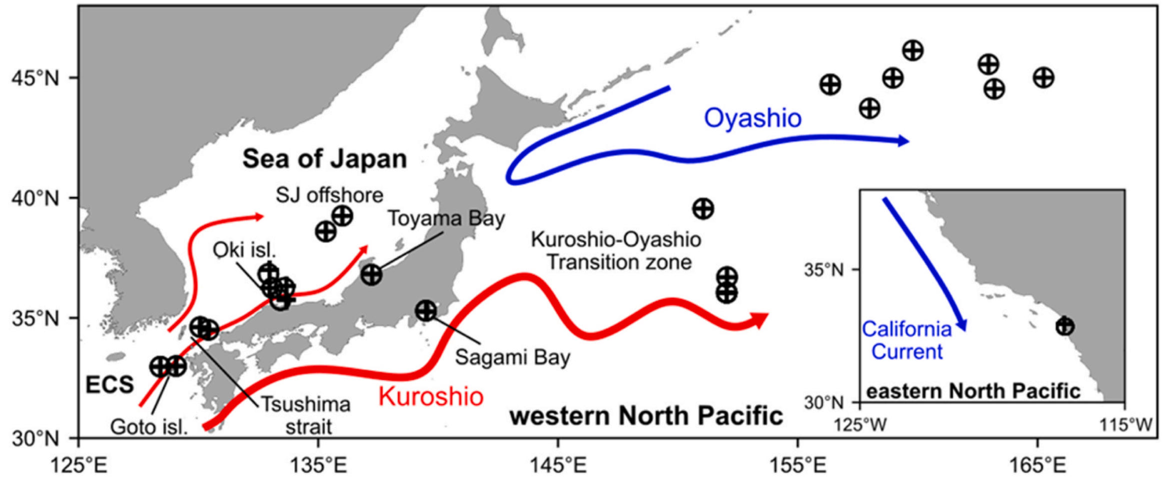

Fig. 1. Locations of fish sampling (o) and CTD observation (+). "ECS" stands for the East China Sea. The red and blue arrows indicate the schematics of warm and cool currents, respectively.

2.2. Otolith microstructure and isotope analyses

The otoliths were embedded in epoxy resin Petropoxy 154 (Burnham Petrographics LLC) or p-resin (Nichika, Inc.). The otoliths were ground along the sagittal plane to expose the core and smoothed using an alumina polishing suspension (BAIKOWSKI International Corporation). Daily increments were observed using an otolith measurement system (RATOC System Engineering Co., Ltd.), and otolith portions that had formed during 32 days or less before capture were milled using a GEOMILL 326 high-precision micro-milling system (Izumo-web). It was confirmed that the resins did not release gases when they reacted with phosphoric acid. Therefore, resin contamination during micro-milling does not significantly affect the subsequent isotope analysis. The stable oxygen isotope values of the otolith powder were measured using a continuous-flow isotope ratio mass spectrometry system (MICAL3c with IsoPrime 100). The otolith powder was reacted with phosphoric acid at 25°C, and the resulting CO_2 gas was introduced into the mass spectrometer via a vacuum purification line (Ishimura et al., 2004; 2008). The estimated weight of otolith powder was typically between 0.5 and 7.0 µg. The $\delta^{18}O$ values of otoliths were reported in δ-notation against the VPDB (Vienna Pee Dee Belemnite) reference standard and given as a ‰ value. The analytical precision was better than ± 0.10 ‰. To facilitate a comparison with the isotopic values reported in previous studies (e.g., Sakamoto et al., 2017; 2019; Aono et al., 2024), we used the acid fractionation factor of calcite.

The data published in the previous studies (Oda et al., 2016; Sakamoto et al., 2019; Aono et al., 2024) were mostly obtained using the same otolith processing procedures and isotopic analysis system as in this study, except for the data in Oda et al. 2016, where the daily increments of otolith were not observed, and the areas 50–250 µm from the edge were extracted. Based on the analysis of daily increments for age-0 sardines captured in the subarctic Pacific in September 2010 (Sakamoto et al., 2022) and in Sagami Bay in November 2020 (unpublished), daily otolith growth rates were assumed to be 1.8 µm/day for juveniles in the subarctic Pacific in September 2010 and 5 µm/day in Sagami Bay in August 2008. The duration of formation for each extracted area in Oda et al. 2016 was estimated based on this assumption, and published data with a duration of < 30 days were included in our analysis. As a result, our dataset included the otolith $\delta^{18}O$ from 62 individuals, for the otolith portion that was formed during 8–32 days before capture, on average 19 ± 6 (1 SD) days. The complete dataset is presented in Appendix.

2.3. Estimation of the thermocline and sardine distribution depths

Conductivity-temperature-depth (CTD) profiles observed at the station closest in space and time to the sardine sampling sites were collected. For samples collected during cruise surveys conducted by the Japan Fisheries Research and Education Agency (Sakamoto et al., 2019; Aono et al., 2024), CTD profiles observed immediately before midwater trawl sampling were available. For samples from coastal fisheries around Japan, data from monthly observation cruises conducted by the Tottori Prefectural Fisheries Research Centre around the Oki Islands, Toyama Prefectural Agriculture, Forestry, and Fisheries Research Centre in Toyama Bay, and the Kanagawa Prefectural Fisheries Technology Centre in Sagami Bay in the Pacific coastal area were provided by the institutes. For the Pacific sardine samples collected in the eastern North Pacific Ocean, CTD data from CalCOFI cruises 0411 and 0610 at station 93.26.7 were downloaded from the CalCOFI Data Portal website (https://calcofi.org/data/). As a result, CTD data measured within 25 days, mostly within two weeks, before fish sampling and within ± 0.25° from the fish sampling point were used (Appendix).

The thermocline depth was defined as the depth at the first significant peak in the vertical temperature profile's decline rate. The depth was determined using the *signal.find_peaks* function in the Scipy 1.6.2 library (Virtanen et al., 2020) based on Python 3.8.8 on the 5 m rolling mean temperature, with the threshold for the minimum peak height set at 0.20°C/m. When no peak was detected due to relatively weak stratification, which was the case in May 2014 and 2016, the threshold for the minimum peak height was adjusted to 0.15°C/m, and the peak was searched for again. From the temperature and salinity profiles, the profile of predicted otolith $\delta^{18}O$ was calculated based on the empirical relationships. These include:

$$\text{Otolith } \delta^{18}O_{VPDB} = \text{Seawater } \delta^{18}O_{VSMOW} - 0.18 * \text{Temperature } (^\circ C) + 2.69 \quad (1)$$

(Sakamoto et al., 2017)
and

$$\text{Seawater } \delta^{18}O_{VSMOW} = a * \text{Salinity} + bw \quad (2)$$

here a = 0.272 and b = −9.19 for the East China Sea and the Sea of Japan, a = 0.279 and b = −9.64 for the California Current region (Sakamoto et al., 2022) and a = 0.595 and b = −20.36 for the nearshore and offshore western North Pacific. The parameters for the East China Sea and Sea of Japan were determined by linear regression analysis of 1642 data points with salinity > 30 sampled from the area between 2015 and 2020 extracted from Kodama et al. (2024), those for the western North Pacific were determined from 87 data points from the Kuroshio-Oyashio system from 2012 to 2015, taken from Sakamoto et al. (2018). The median of the depth range where the difference between the predicted and analysed otolith $\delta^{18}O$ was less than 0.25 ‰ was considered the distribution depth of the sardine (Fig. 2). Here, 0.25 ‰ represents the total error propagated independently from Eq. (1) representing biological and analytical error (root mean square error = 0.18 ‰, Sakamoto et al., 2017) and from Eq. (2) representing the error in the conversion (largest root mean square error among three equations = 0.18 ‰), calculated as the root sum square of the two. The depth estimated using this method was generally equal to the depth with the least difference. However, if the smallest difference was found within the surface mixing layer where the predicted otolith $\delta^{18}O$ is almost uniform, the output depth would be approximately the median of the surface mixing layer.

Seasonal temperature variations are an important source of uncertainty here. The $\delta^{18}O$ values at the edge of the otolith reflect the mean temperature and salinity in the 8–32 days before capture. Because sea temperatures in the upper 50 m of the mid-latitudes of the North Pacific can change by up to 3°C within a month (Hosoda et al., 2015), we hypothesised that the mean vertical temperature profile in a month

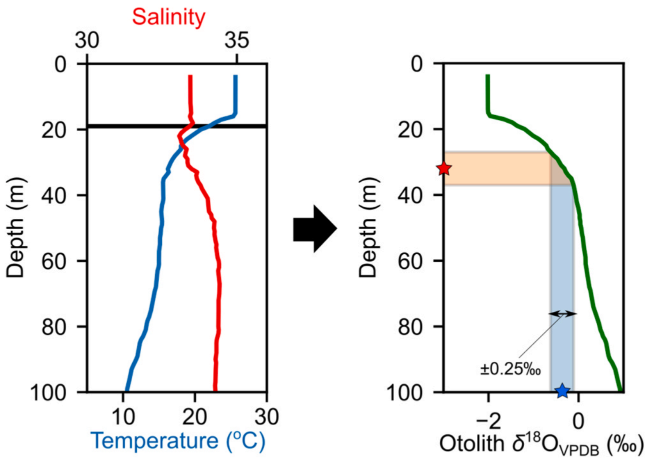

Fig. 2. Schematic of the estimation of habitat depth (red star) from CTD profiles (left panel) and otolith $\delta^{18}O$ (blue star). Green line (right panel) is the profile of predicted otolith $\delta^{18}O$ based on temperature and salinity profiles. Black line (left panel) is the thermocline depth. The red shade (right panel) shows the prediction window from the error of ± 0.25 ‰ in otolith $\delta^{18}O$.

before capture may differ by up to 1.5°C from the profile at capture. We therefore tested the sensitivity of habitat depth estimates to seasonal temperature variation by shifting the overall temperature profiles by ± 1.5°C and recalculating depth. Sensitivity to changes in the shapes of the temperature profiles was also assessed. For the 6 individuals caught near the Oki Islands on 1st September 2015 or 3rd September 2019, CTD observations were available near the sampling site on the following day (2nd September 2015 and 4th September 2019) and also about a month earlier (29th July 2019 and 26th July 2019). We therefore averaged the temperature and salinity profiles in July and September of each year and recalculated the depth of sardine habitat to quantify the impact.

2.4. Acoustic survey data for validation

To validate the predicted habitat depths, they were compared with acoustic data collected using a hull-mounted scientific echosounder (Simrad EK60) operating at 38 kHz at three stations in the Sea of Japan. The echosounder was calibrated using tungsten carbide with 6 % cobalt spheres during the survey, according to the calibration protocols of the ICES report (Demer et al., 2015). The mean volume backscattering strength during trawling, used as a proxy for fish biomass in each layer, was calculated for each 10-metre bin using acoustic data processing software (Echoview 12.1.27). It should be noted that the backscattering may belong to species other than sardine. The numerical proportion of sardine in the fish and squid caught by the trawl net were 15, 11 and 0.5 % at the Sea of Japan offshore, Tsushima Strait and Goto Islands stations, respectively. The dominant species in the catch were Japanese flying squid *Todarodes pacificus* (53 %), Japanese horse mackerel *Trachurus japonicus* (61 %) and round herring *Etrumeus micropus* (94 %), respectively. Meanwhile, mixed species assemblages with similar body sizes are a common form of small pelagic fish distribution in field (e.g., Louw et al., 2014). We therefore assumed that the sardines were mixed in or near the shoal of dominant species, and hypothesised that they were likely distributed at or near the layer where greater backscattering intensity was detected.

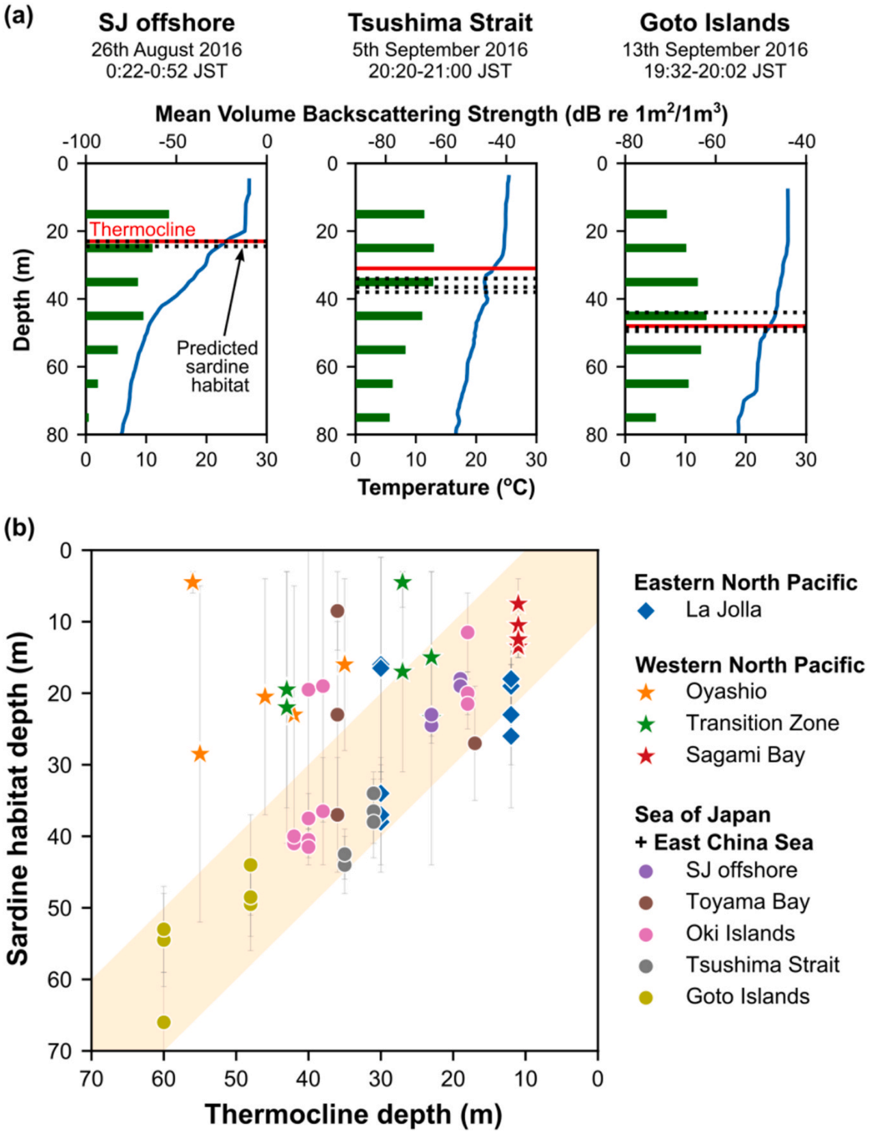

Fig. 3. Thermocline (red line), predicted habitat depth of sardine (dashed line) and the result of acoustic survey (green bars) at 3 stations in the Sea of Japan and East China Sea in 2016 (a). Relationship between sardine habitat depth and thermocline depth for each individual in each region (b). The error bars indicate prediction windows considering the ± 0.25 ‰ error in otolith δ^{18}O. The shade indicates the area where the difference between sardine habitat and thermocline depths is less than 10 m.

3. Results

Fifty-eight of 62 individuals analysed (25 sites) were successfully found to have depths in the water column where the predicted otolith δ^{18}O was similar to the analysed otolith δ^{18}O (< 0.25 ‰ difference). We failed to determine the depths of the three juveniles in the Oyashio region and one in the Kuroshio-Oyashio Transition Zone as there is no depth that predicted otolith δ^{18}O values that were close enough to the observed values. In the sensitivity analysis to the seasonal temperature variations, when temperature profiles were positively or negatively shifted by 1.5°C, predicted depths decreased by 9.0 m and increased by 8.6 m, respectively, on average. In addition, when the temperature and salinity profiles were averaged with the observation a month before for the 6 individuals caught in September 2015 and 2019 near Oki Islands, predicted depths decreased by 13.0 m on average. At the three stations in the Sea of Japan and the East China Sea in 2016 for which we had acoustic data, the layer with the highest scattering intensity in the upper 100 m varied from 10−20 m to 40−50 m, which corresponded or was adjacent to the predicted habitat layer based on otolith δ^{18}O (Fig. 3a). The estimated habitat depths for most individuals in the eastern North Pacific, Sea of Japan, and the East China Sea were within 10 m of the depth of the first peak of the vertical temperature change, which was defined as the thermocline depth (Fig. 3b). The habitats of most fish from the Kuroshio-Oyashio transition zone and the Oyashio region in the western North Pacific were in the surface mixed layer above the thermocline (Fig. 3b).

The mean water temperature at thermocline depth in each region was 22.4−24.5°C in the Sea of Japan, East China Sea and Sagami Bay, 16.8°C in the eastern North Pacific, 16.9°C in the Kuroshio-Oyashio transition zone and 8.4°C in the Oyashio region (Fig. 4). The mean temperature at the habitat depth was 12.0−24.5°C in the western North Pacific, Sea of Japan and East China Sea (Japanese sardine) and 15.3°C in the eastern North Pacific (Pacific sardine) (Fig. 4).

4. Discussion

In this study, we investigated the vertical habitat selection of sardine juveniles in the western and eastern North Pacific, the Sea of Japan and the East China Sea based on otolith δ^{18}O. Note that the estimated depths are averages over several weeks and are likely biased towards those during the day because fish otolith growth is faster and slower at night (Wright et al., 1992; Tohse and Mugiya, 2008). Our results showed that habitat depth varied significantly in the upper 70 m between the regions (Figs. 3 and 4). The different habitat depths closely followed the variations in the depth of the seasonal thermocline in the eastern North Pacific, Sea of Japan, and East China Sea (Figs. 3b and 4), suggesting that juveniles change their vertical habitats depending on environmental conditions.

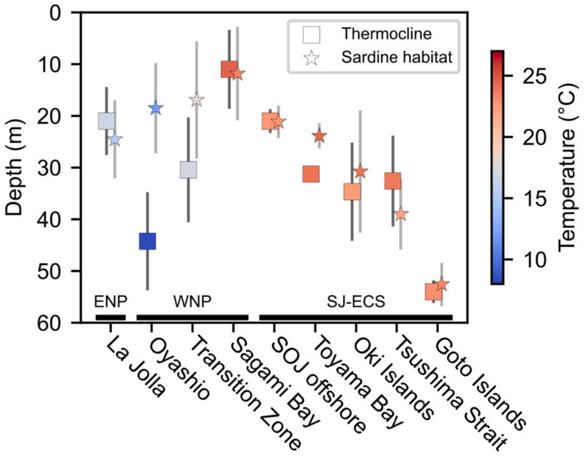

Fig. 4. Mean sardine habitat depth (star) and thermocline depth (square) in each region. Colors represent the temperature at the depths. Error bars show ±1 SD intervals. “ENP” stands for the Eastern North Pacific, “WNP” for the Western North Pacific and “SJ-ECS” for the Sea of Japan-East China Sea system.

It is more likely that habitat depth was selected primarily based on food availability rather than physiological controls. The metabolically optimal temperatures of juveniles of Japanese sardines in the western North Pacific and Pacific sardines in the eastern North Pacific are 15–18°C (Sakamoto et al., 2022). If the primary condition for habitat selection was to remain near the optimal temperature and maximise the individual’s aerobic scope, habitat depths in the Sea of Japan and East China Sea would have been significantly deeper than our estimates; for example, up to 80–100 m in the Tsushima Strait and Goto Islands (Fig. 3a). Studies on zooplankton have shown that although their diel vertical behaviours are significantly different among species, various species often aggregate in the thermocline (e.g., Harris, 1988). A tendency to distribute around the seasonal thermocline has also been observed in juveniles of other species (e.g., haddock in the North Atlantic, Perry and Neilson, 1988). Therefore, distribution around the thermocline may provide strong advantages for energy acquisition, especially for sardines, which can efficiently collect prey particles by filtration (van der Lingen et al., 2006). The observation that sardine and anchovy schools off the California coast are attracted to thin layers of aggregated zooplankton supports this hypothesis (Benoit-Bird, 2009). Nevertheless, habitat selection is not temperature-free because juveniles have been found above the thermocline in the subarctic Oyashio region of the North Pacific Ocean (Figs. 3 and 4). Temperatures at the thermocline in the area, which averaged 8.4°C, were too low near the presumed lethal temperature (about 7°C, Nakai, 1962), which may have caused the sardine to avoid the layer. These results suggest that sardine juveniles select habitat depths to maximise food availability as long as they are thermally tolerant.

This information may be useful in modelling studies to predict the distribution of sardines. Our results show that the assumptions of vertical movements applied in individual-based models in some previous numerical simulation studies, such as to "select the cell in the water column at their current location with the highest prey related to their consumption" for juvenile and adult sardines in the California Current System (Rose et al., 2015) or to" vertically migrate mainly within the surface mixed layer" for juveniles in the western North Pacific (Sakamoto et al., 2019), were fairly reasonable. For species distribution modelling of juvenile sardines based on habitat suitability (e.g., Zwolinski et al., 2011), it may be reasonable in stratified seasons to use variables such as temperature and chlorophyll concentration at the first thermocline rather than at the surface. However, this would also introduce uncertainties in the explanatory variables because large-scale variations can only be measured at the surface by satellites; hence, the best choice would be case-dependent. Similarly, when estimating individual migration histories based on a comparison between the chronology of temperature proxies and the distribution of seawater temperature (e.g., Darnaude and Hunter, 2018; Sakamoto et al., 2019; Hanson et al., 2022; Aono et al., 2024), using seawater temperature at the thermocline may improve the accuracy of prediction for sardine juveniles.

Vertical distribution may also influence how environmental variability affects fish growth and survival. The early growth rates and recruitment of sardine populations in the western and eastern North Pacific respond differently to temperature variations, with cooler and warmer temperatures tending to promote juvenile growth and recruitment, respectively (Sakamoto et al., 2022). For juveniles residing above the thermocline (e.g., in the western North Pacific), prey availability likely depends on the nutrient supply to the surface mixed layer. Thus, cooler surface temperatures with deeper mixing may increase prey abundance and faster sardine growth. In contrast, warmer surface temperatures could benefit juveniles residing around the thermocline (e.g., eastern North Pacific, Sea of Japan). In addition to shifting the zooplankton community structure towards smaller sizes, which is hypothesised to stimulate low-cost filter feeding (van der Lingen et al., 2006), greater stratification may lead to a greater accumulation of particles in the thermocline (Harder, 1968; Checkley et al., 2008), which may increase feeding efficiency. Therefore, vertical habitat selection may alter the mechanisms between physical forcing, fish growth, and survival. In addition to data on sardine habitat depth, comparisons between local zooplankton distribution and sardine growth in areas with different thermocline depths could deepen our understanding of this mechanism.

The major limitation of the otolith δ^{18}O-based method is that it is difficult to test diurnal vertical migrations, which may have important ecological functions such as predator avoidance. Because the estimated depths at the three stations in 2016 averaged over several weeks, which may have been biased towards those during the day, matched well with the highest scattering intensity during the night (Fig. 3a), it is possible that juvenile sardines do not make significant diurnal vertical migrations. However, further testing with different approaches is needed. In addition, although the sensitivity analysis showed that our estimates were relatively robust to uncertainty due to seasonal temperature variations, the effect of fish migration was not considered. Significant fish migrations may cause discrepancies between environments in the collection sites and the areas where the otolith growth occurred, and bias the estimation of habitat depth. Recent stable carbon and nitrogen isotope analysis of Japanese sardine have shown that juveniles in the Sea of Japan, East China Sea and the Pacific coastal area show slow or limited migrations while those in the Pacific offshore systematically migrate northwards (Sakamoto et al., 2023). This region-specific migratory behaviour may explain why we could not find habitat depths for the four individuals in the Oyashio region and the Kuroshio-Oyashio transition zone. Combining multiple approaches, such as multi-layer net sampling and acoustic surveys with the analysis described here is important to fully understand the strategies involved in vertical habitat selection and the effects on fish survival.

Disclosure

During the preparation of this work the authors used a software, InstaText, and a service, Editage, for language editing. After using these, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

CRediT authorship contribution statement

Tatsuya Sakamoto: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Toyoho Ishimura:** Writing – review & editing, Funding acquisition, Data curation. **Tomohiko Matsuura:** Writing – review & editing, Visualization, Formal analysis, Data curation. **Motomitsu Takahashi:** Writing – review & editing, Resources, Funding acquisition.

Declaration of Competing Interest

The authors declare no conflict of interest.

Data availability

We have shared the data as an Appendix.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107106.

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