



Contribution to the Theme Section 'Small pelagic fish: new research frontiers'

Interdecadal variabilities in growth and temperature trajectories of *Trachurus japonicus* juveniles: 1960s–1970s versus 2000s–2010s

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ABSTRACT: Changes in the distribution range and timing of life events in fish in response to warming oceans have been reported in several marine ecosystems. However, few studies have demonstrated the impact of increasing temperature on the individual growth and thermal trajectories of fish. We examined the growth and temperature trajectories of juvenile Japanese jack mackerel *Trachurus japonicus* in the western waters off Kyushu, Japan, based on growth increments and high-resolution isotopic analyses of archived otoliths between the 1960s–1970s and 2000s–2010s. *T. japonicus* juveniles in the 2000s–2010s hatched from February to April, whereas juvenile hatching in the 1960s–1970s ranged from March to May, corresponding to earlier spawning in recent decades. The otolith radius from the nucleus to specific dates represents the somatic growth trajectory of the fish: this distance was larger from April to August in the 2000s–2010s than that in the 1960s–1970s, indicating that earlier hatching in the 2000s–2010s resulted in a larger body size throughout life than in the 1960s–1970s. The trajectories of the oxygen stable isotope ratios in otoliths showed that the temperatures experienced by the fish from spring to summer were comparable between the study periods. Our results suggest that warming during late winter in recent decades has resulted in earlier spawning and occurrence of *T. japonicus* juveniles, resulting in the fish experiencing comparable thermal conditions between the 2 study periods. The phenological shift in spawning seemed to be recorded in individual growth and the temperature trajectories in the otoliths of *T. japonicus*.

KEY WORDS: Ocean warming · Phenology · Otolith · Juvenile fish · Growth · Temperature

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1. INTRODUCTION

The increase in seawater temperature during the twentieth century has had a critical impact on marine ecosystems, influencing the distribution range of various marine organisms, including fish, which have shifted poleward to cooler waters in warming oceans, and their life events, such as the onset of spawning, which occurs earlier, especially in the spring (Perry et al. 2005, Poloczanska et al. 2013, Rubenstein et al. 2019, Langan et al. 2021, Cooley et al. 2022). Asch (2015) examined the seasonal occurrence of fish lar-

vae from 1951 to 2008 in California Current ecosystems and demonstrated that the occurrence of offshore and pelagic fish species was hastened, while the occurrence of neritic and demersal species was delayed during the study period. The effects of increasing water temperature on the change in the distribution range and life event phenology of fish are species-specific; however, how individual fish respond to warming oceans remains unclear.

Archived otoliths (ear stones) are powerful for elucidating the effects of increasing temperature on individual fish lives. Microchemical analysis using stable

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oxygen isotopes in otoliths revealed the temperature trajectory experienced by fish (Campana 1999). The oxygen stable isotope ratio of the archived otoliths of Icelandic cod *Gadus morhua* indicates that the cod has experienced decadal changes in ambient water temperature over the last 100 yr (von Leesen et al. 2020). Based on the size at ages estimated from the annuli of archived otoliths, the growth of *G. morhua* has increased during warm periods over the last century (Denechaud et al. 2020). Although previous studies have demonstrated inter-annual to decadal variability in growth rates in response to temperature variations, daily to monthly growth traits and environmental trajectories are essential for examining life-event phenology.

The development of micromilling devices and high-sensitivity mass spectrometry has enabled the reconstruction of temperature trajectories experienced by fish on a daily to monthly basis (Ishimura et al. 2004, Sakai 2009). Fine-scale analyses of stable oxygen and carbon isotopes in otoliths have revealed temperature and metabolic trajectories during the early life stages of various fish species (Higuchi et al. 2019, Sakamoto et al. 2019, 2022). Recent studies on the otolith oxygen stable isotope ratio of Japanese jack mackerel *Trachurus japonicus* juveniles using high-resolution devices have elucidated the daily thermal conditions experienced during the early juvenile stage (Muto et al. 2022) and the temperature decline as the ontogenetic habitat layer shifts from the surface to the near-bottom layers (Enomoto et al. 2022). As otoliths of *T. japonicus* juveniles are large relative to their body size and have a wide (approximately 35 μm) daily growth increment (Xie et al. 2005, Muto et al. 2022), *T. japonicus* can be used as a model to examine the temperatures experienced during early life stages using the otolith oxygen stable isotope ratio.

T. japonicus is distributed in continental shelf waters along the subtropical Kuroshio and Tsushima Warm Currents and is an important fishery target, especially in western Japan (Yoda et al. 2022; see our Fig. 1). *T. japonicus* spawning subsequently occurs from the southern East China Sea (ECS) in the winter to the coastal waters off central Japan in early summer (Yasuda et al. 2022, Yoda et al. 2022; see our Fig. 1). The growth patterns of *T. japonicus* were studied based on otolith annuli and morphology in the ECS in the 1960s and 1970s (Hotta & Nakashima 1971, Nakashima 1982), and the otoliths used in previous studies have been archived at the Nagasaki Station of the Japan Fisheries and Education Agency since the 1950s. The daily growth trajectory and hatching period of *T. japonicus* larvae and juveniles have been reported based on daily otolith growth increment

analysis after the 2000s in the ECS (Takahashi et al. 2012, 2016, 2022a,b, Sassa et al. 2014, 2021). The warming trend in the ECS in recent decades is one of the most prominent among the world's oceans (Sasaki & Umeda 2021); thus, archived otoliths of *T. japonicus* from the 1960s–1970s and 2000s–2010s may provide a unique opportunity to examine the growth and temperature trajectories of individual fish in response to the warming ocean. Although the impact of increasing temperatures on the distribution ranges of zooplankton and fish species has been reported in the ECS (Xu et al. 2013, Hu et al. 2022), no study has addressed how individual fish respond to warming in the ECS. Using long-term archived otoliths, we examined the growth and temperature/metabolic trajectories of *T. japonicus* juveniles collected from the western waters off Kyushu Island in the northern ECS based on daily growth increments and high-resolution stable isotopic analyses.

2. MATERIALS AND METHODS

2.1. Ambient thermal conditions

To monitor long-term changes in environmental conditions in the study area, sea surface temperature (SST) and salinity data sets at historical monitoring sites off western Kyushu (Fig. 1) were obtained from the Fishery Resource Conservation (FRESCO) System, a database operated by the Fisheries Agency of Japan. The SST and salinity data for each month were averaged and compared between the 1960s–1970s and 2000s–2010s using ANOVA with a Student's *t*-test or Wilcoxon test after testing the data for normality and homogeneity using the Shapiro-Wilk and Bartlett tests.

2.2. Selection of the archived otolith

Sagittae, a pair of saccular otoliths (hereafter referred to as otoliths) of *Trachurus japonicus* juveniles collected from the western waters off Kyushu Island were used to reconstruct growth and temperature trajectories (Fig. 1). To elucidate the growth response to increasing thermal conditions since the 1960s, 10 yr of study data from the 1960s–1970s and 2000s–2010s were selected (Table 1). As the structure of the daily growth increments of otoliths becomes obscure during winter due to suboptimal temperatures (Namiki et al. 2010), we selected only the young-of-the-year otoliths collected from August to October (Table 1). As

young-of-the-year otoliths were rarely archived from summer to fall in the 1960s–1970s, 5 otoliths of *T. japonicus* juveniles were randomly selected for growth analysis for each study year. In this study, the interannual variations in growth traits were not analyzed due to the small number of samples, and we focused on the differences in the biological traits between the 1960s–1970s and 2000s–2010s. The otoliths were embedded on a glass slide using Petroproxy 154 (Palouse Petro Products), ground in the sagittal plane using 2000 grit sandpaper and polished using 3 μm alumina powder.

2.3. Growth analysis

The body size of *T. japonicus* juveniles in the 1960s–1970s, often recorded as fork length (FL), was converted to standard length (SL) using the SL–FL relationship. This was estimated based on the individuals' measured SL and FL ($SL = 0.830 \times FL + 0.496$; $n = 125$, $R^2 = 0.977$, $p < 0.001$). Otolith measurements of *T. japonicus* juveniles were performed as previously described (Takahashi et al. 2012). The total number of otolith growth increments and width between the increments were measured along the transect line at the posterior portion of the rostrum at 100–500 \times magnification using an otolith measurement system (ARP/W+RI, RATOC System Engineering). Only 3 otoliths were measurable for 1964 and 1973 because the structures of the daily growth increments were less clear; therefore, the total numbers of otoliths analyzed for growth were 46 and 50 in the 1960s–1970s and 2000s–2010s, respectively (Table 1). The ages of juveniles were estimated by adding 2 to the total number of otolith increments because the first increment forms 2 d after hatching (Xie et al. 2005), and the hatching dates were estimated by subtracting the age from the collection date. Differences in the mean SL, age, and hatching date of *T. japonicus* juveniles between the study periods were tested using ANOVA with a Student's *t*-test or Wilcoxon test after testing for data normality and homogeneity using Shapiro-Wilk and Bartlett tests. The effect of cumulative mortality on

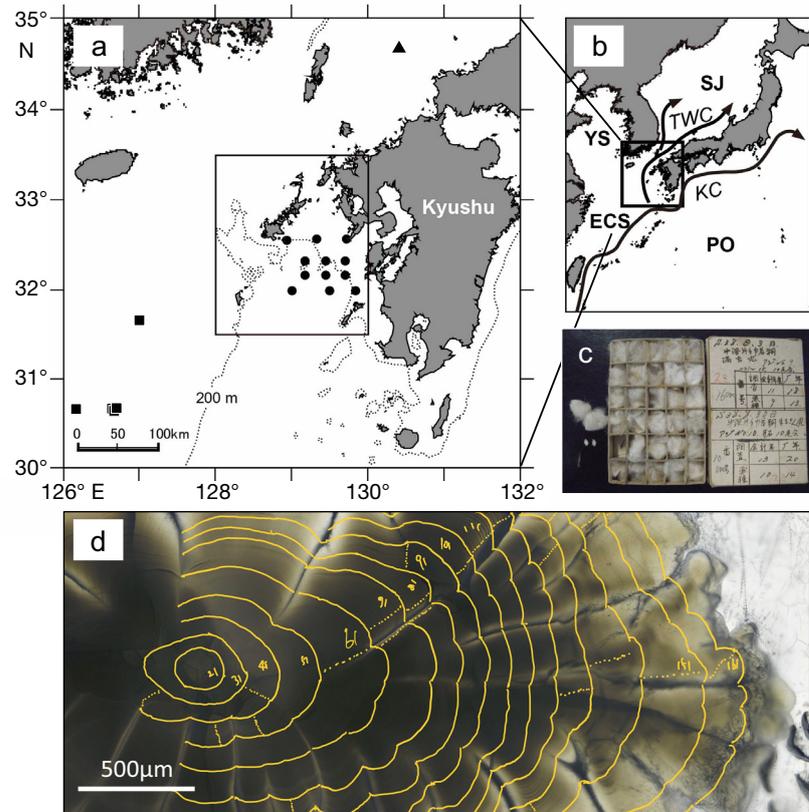


Fig. 1. (a) Catch area of *Trachurus japonicus* juveniles (rectangle) and historical monitoring sites for sea surface temperature (SST) and salinity (solid circles) off western Kyushu, Japan. Sampling locations of *T. japonicus* juveniles in the northern ECS in Enomoto et al. (2022) (solid squares) and the southwestern Sea of Japan in Muto et al. (2022) (solid triangle) for data presented in Fig. 7. (b) Current structures and names of seas around the study area; KC: Kuroshio Current; TWC: Tsushima Warm Current; PO: Pacific Ocean; ECS: East China Sea; YS: Yellow Sea; SJ: Sea of Japan. (c) Sagittae of *T. japonicus* juveniles collected in August 1963. (d) A sagitta of *T. japonicus* juvenile of 112 mm standard length at 173 days post-hatch (dph) collected in 2003, with lines showing every 10 growth increments from 21 dph for micromilling

the hatching date distribution was considered negligible because most juveniles were aged > 100 d post-hatching (dph, see Section 3.2) and the instantaneous mortality rate was very low (Campana & Jones 1992); thus, the observed hatching date was not adjusted.

The relationship between the SL and otolith radius from the nucleus to the outermost increment in *T. japonicus* is represented by a linear equation (Xie & Watanabe 2005, Kanaji et al. 2009, Takahashi et al. 2022b). In this study, the radius from the nucleus to the daily growth increments and the width between increments in otoliths were used as indices of body size and growth rate at age, respectively. To examine ontogenetic changes in somatic growth, differences in the otolith radius at ages with 10 d intervals from 10 to 120 dph and the mean increment widths at 10 d intervals between the study periods were tested using

Table 1. Archived otolith of *Trachurus japonicus* juveniles for growth and stable isotope analyses of the 1960s–1970s and the 2000s–2010s

Period	Year	Date	No. of otoliths analyzed	
			Growth	Stable isotope
1960s–	1963	13 Sep	5	3
1970s	1964	1 Sep	3	0
	1967	17 Aug	5	3
	1969	2 Sep	5	3
	1970	3 Sep	5	3
	1972	16 and 26 Sep	5	0
	1973	26 Sep	3	0
	1975	13 Aug	5	3
	1976	17 Sep	5	0
	1979	12 Oct	5	0
	Subtotal		46	15
2000s–	2003	6 Aug	5	3
2010s	2004	6 Aug	5	3
	2006	21 Aug	5	3
	2008	10 Aug	5	0
	2009	25 Aug	5	3
	2011	6 Sep	5	3
	2012	5 Sep	5	3
	2014	12 Sep	5	0
	2015	12 Sep	5	3
	2016	17 Sep	5	0
	Subtotal		50	21

repeated-measures MANOVA with a post hoc *F*-test (Chambers & Miller 1995) because most juveniles had an age of > 120 dph (see Section 3.2). To elucidate seasonal changes in somatic growth, differences in the otolith radius at dates on days-of-the-year 100 to 250 were compared between the study periods using ANOVA with a Student's *t*-test or Wilcoxon test after testing for data normality and homogeneity using Shapiro-Wilk and Bartlett tests. As deviations in the mean otolith radius and mean increment width increased with age, the otolith radius and increment width were naturally log transformed in the statistical tests.

2.4. Otolith isotope analysis

Three otoliths were randomly selected for otolith isotope analysis from the 5 analyzed for growth during 5 study years in the 1960s–1970s and 7 study years in the 2000s–2010s (Table 1). The otolith was incrementally micromilled from the outer margin to the nucleus using a high-precision micromilling system (Geomill326, Izumo Web, Izumo; Sakai 2009). The milling depth was set to 100 μm for all segments. The temporal resolution of the milled otolith was constant at 10 d in the marginal area, and the resolution around

the nucleus was approximately 30 d. A total of 11–17 segment samples were obtained from each otolith (Fig. 1). The mid-date and mid-age were estimated based on the ranges in the date and age of each segment and were rounded down to compare seasonal and ontogenetic changes in oxygen and carbon stable isotope ratios with those of growth trajectories.

To estimate the temperature and metabolic trajectories experienced during the larval and juvenile stages, the oxygen ($\delta^{18}\text{O}_{\text{oto}}$) and carbon ($\delta^{13}\text{C}_{\text{oto}}$) stable isotopes of *T. japonicus* otoliths were analyzed using an isotope ratio mass spectrometer (Delta V Plus; ThermoFisher Scientific). The otolith powder samples were transferred into a 4.5 ml glass vial filled with pure helium and reacted with phosphoric acid at 72°C. The $\delta^{18}\text{O}_{\text{oto}}$ and $\delta^{13}\text{C}_{\text{oto}}$ values are reported in delta (δ) notation relative to the Vienna Pee Dee Belemnite (VPDB), based on NBS-19 value of -2.20‰ for $\delta^{18}\text{O}$ and $+1.95\text{‰}$ for $\delta^{13}\text{C}$. No correction was applied for the acid fractionation factor between calcite and aragonite (phosphoric acid–calcium carbonate reaction temperature of 72°C; Kim et al. 2007). Detailed analytical conditions have been reported previously (Shirai et al. 2018, Enomoto et al. 2022).

2.5. Temperature and metabolic trajectories in relation to growth

To examine the seasonal and ontogenetic changes in the temperature and metabolic trajectory between the 2 study periods, differences in the $\delta^{18}\text{O}_{\text{oto}}$ and $\delta^{13}\text{C}_{\text{oto}}$ values on days of the year and at ages with 10 d intervals from 10 to 120 dph between the study periods were tested using ANOVA with Student's *t*-test or Wilcoxon test after testing for data normality and homogeneity using Shapiro-Wilk and Bartlett tests. As no species-specific $\delta^{18}\text{O}_{\text{oto}}$ –temperature relationship was available for *T. japonicus*, we used $\delta^{18}\text{O}_{\text{oto}}$ values without conversion from $\delta^{18}\text{O}_{\text{oto}}$ to temperature. The $\delta^{18}\text{O}_{\text{oto}}$ value is affected by both the ambient temperature and seawater $\delta^{18}\text{O}$, the latter of which is associated with salinity, while $\delta^{18}\text{O}_{\text{oto}}$ is negatively correlated with temperature in various fish species (Høie et al. 2004, Geffen 2012, Kitagawa et al. 2013, Sakamoto et al. 2017). As the variability in sea surface salinity in the study area was low between the study periods except for the rainy season in June and July (see Section 3.1), we assumed that the effects of the variability in seawater $\delta^{18}\text{O}$ would be negligible.

The otolith oxygen stable isotope ratios of *T. japonicus* juveniles caught in the 2000s–2010s have been reported in waters adjacent to the study area: the

northern ECS, southwest of the study area (Fig. 1a) (Enomoto et al. 2022, $n = 21$), and the southwestern Sea of Japan, northeast of the study area (Muto et al. 2022, $n = 3$). To compare the temperature trajectories with those in the adjacent waters, the mid-age standardization method in this study was applied to the $\delta^{18}\text{O}_{\text{oto}}$ data sets from previous studies, and the effect of reaction temperature was corrected to 25°C , which resulted in approximately -0.09‰ from the $\delta^{18}\text{O}$ values in Enomoto et al. (2022) and this study. The number of $\delta^{18}\text{O}_{\text{oto}}$ values per individual otolith was 6–19 in the northern ECS, which corresponded to weekly and monthly scales, and 18–47, which corresponded to daily and weekly scales, in the southwestern Sea of Japan. As there was a large difference in temporal resolution among the data sets, no statistical test was conducted.

The $\delta^{13}\text{C}_{\text{oto}}$ value depends on the relative contribution of dissolved inorganic carbon (DIC) in ambient water and metabolic carbon derived from the metabolism of nutrients through the bloodstream and endolymph fluid (Solomon et al. 2006); therefore, the $\delta^{13}\text{C}_{\text{oto}}$ value is a negative function of the field metabolic rate of fish (Chung et al. 2019). The decrease in the $\delta^{13}\text{C}$ of DIC in seawater due to the burning of ^{12}C -enriched fossil fuels since the mid-twentieth century (Keeling et al. 1979, Quay et al. 1992) is named the Suess effect. Since the $\delta^{13}\text{C}$ of DIC in seawater has declined constantly at $0.023\text{--}0.024\text{‰ yr}^{-1}$ since 1960 in the western North Pacific (Asami et al. 2021), we assumed that the $\delta^{13}\text{C}_{\text{oto}}$ would have declined by $0.92\text{--}0.96\text{‰}$ during the 40 yr studied here. To compare the field metabolic rate between the study periods, 0.94‰ was added to the $\delta^{13}\text{C}_{\text{oto}}$ values at 10 d intervals for each individual during the 2000s–2010s.

To further examine the life stages in which temperature and metabolic indices were strongly related to somatic growth, the relationships between $\delta^{18}\text{O}_{\text{oto}}/\delta^{13}\text{C}_{\text{oto}}$ and mean otolith increment width were examined at 10 d intervals from 10 to 120 dph using linear regression analysis in each study period. All statistical analyses in this study were conducted using JMP version 14.0 (SAS Institute).

3. RESULTS

3.1. Thermal and salinity conditions in the study area

Mean SST in the study area during the 2000s–2010s increased from $16.9 \pm 1.2^\circ\text{C}$ in February to $29.1 \pm 0.9^\circ\text{C}$ in August, and then declined to $27.5 \pm 1.0^\circ\text{C}$ in

September; meanwhile, in the 1960s–1970s, it increased from $15.2 \pm 1.9^\circ\text{C}$ in February to $27.3 \pm 1.3^\circ\text{C}$ in September (Fig. 2a). The SST in the 2000s–2010s was significantly higher from February to May and August (Table S1 in the Supplement at www.int-res.com/articles/suppl/m741p301_supp.pdf). Mean sea surface salinity was constant at approximately 34.5 from February to May and then sharply dropped to 33.0 from July to September; a significant difference was found between the study periods during February to July without including March (Fig. 2b, Table S1).

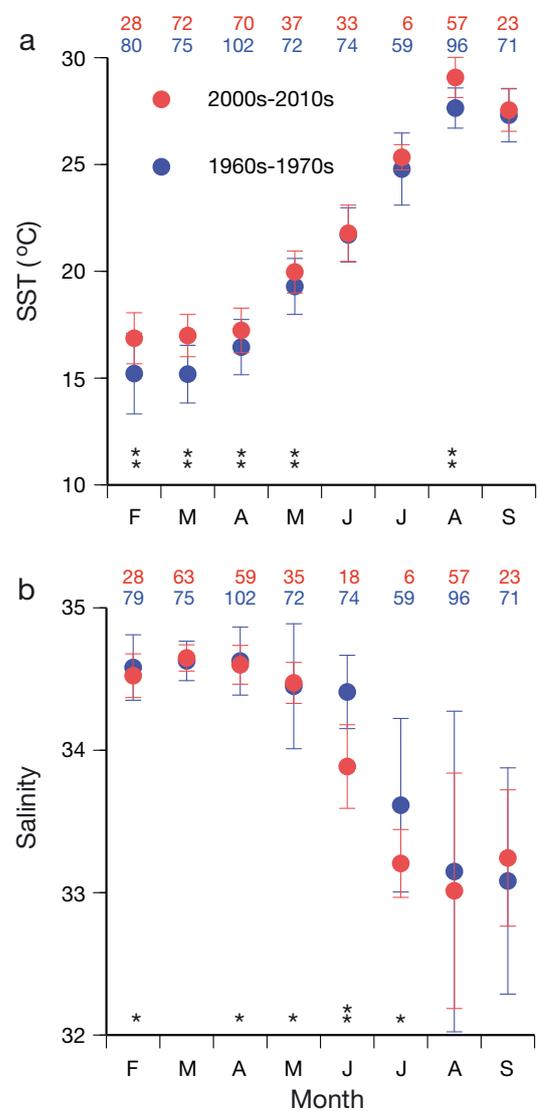


Fig. 2. Monthly mean (\pm SD) (a) sea surface temperature (SST) and (b) salinity in the historical monitoring sites during the 1960s–1970s (blue) and 2000s–2010s (red). Numbers above the panels: sample sizes in the 1960s–1970s (blue) and the 2000s–2010s (red). Asterisks indicate significant differences between the 2 study periods (* $p < 0.05$; ** $p < 0.01$)

3.2. Body size, age, and hatch dates

The mean SL of the *Trachurus japonicus* juveniles used in each study year ranged from 92 to 128 mm, and the mean SL during the 2000s–2010s was significantly higher than that during the 1960s–1970s (Fig. 3a; $\chi^2_1 = 20.5$, $p < 0.001$). The mean age of juveniles in each study year ranged from 135 to 183 dph, and the mean age during the 2000s–2010s was significantly higher than that during the 1960s–1970s (Fig. 3b; $F_{1,94} = 4.9$, $p = 0.029$). Although the hatching date distribution of *T. japonicus* juveniles was concentrated in late March and early April during both study periods, most of the juveniles hatched in April and May in the 1960s–1970s, whereas in the 2000s–2010s, most hatched in February and March (Fig. 3c). The mean hatch date in the 2000s–2010s was day-of-the-year 79, and it was approximately 3 wk earlier than that in the 1960s–1970s (day-of-the-year 100; $F_{1,94} = 1635.7$, $p < 0.001$).

3.3. Seasonal changes in somatic growth, $\delta^{18}\text{O}_{\text{oto}}$ and $\delta^{13}\text{C}_{\text{oto}}$

The mean otolith radius showed a sigmoidal increase from March to September in the 2 study periods (Fig. 4a). The mean otolith radius on day-of-the-year 100 in the 1960s–1970s, corresponding to the mean hatch date, was significantly smaller than that in the 2000s–2010s, and a significant difference was observed up to day-of-the-year 250 in early September (Table S2). The mean $\delta^{13}\text{C}_{\text{oto}}$ gradually increased from April to August, and the mean values in the 2000s–2010s were significantly higher than those in the 1960s–1970s throughout all seasons, except for those at 230 and 240 dph (Fig. 4b, Table S2). The mean $\delta^{18}\text{O}_{\text{oto}}$ increased in April and decreased from May to August (Fig. 4c). Although there were significant differences at the edges of the seasonal trend in $\delta^{18}\text{O}_{\text{oto}}$ with a small amount of data (Table S2), no significant differences were found between late April and mid-August.

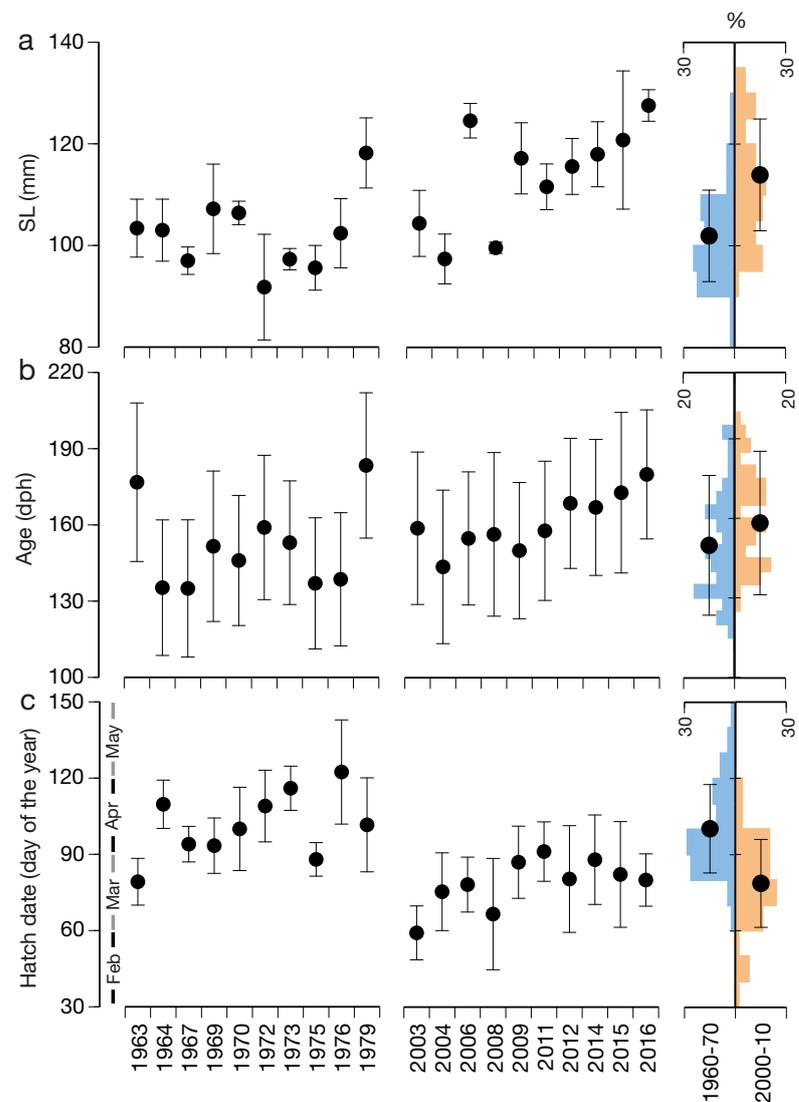


Fig. 3. Mean (\pm SD) (a) standard length (SL), (b) age, and (c) hatch date of *Trachurus japonicus* juveniles in the survey years during 1963–1979 and 2003–2016. Right side panels show the mean SL, age, and hatch date with frequency distribution of individual data sets in the 1960s–1970s (light blue) and 2000s–2010s (orange)

3.4. Ontogenetic changes in growth, $\delta^{18}\text{O}_{\text{otor}}$ and $\delta^{13}\text{C}_{\text{oto}}$

The mean otolith radius at different ages increased from approximately 30 μm at 10 dph to 2000 μm at 120 dph during both study periods, and the otolith growth trajectories were significantly different between the study periods (Fig. 5a; $F_{11,83} = 0.256$, $p = 0.046$). The mean otolith radius during 50–70 dph in the 1960s–1970s was significantly higher than that in the 2000s–2010s (Table S3). The mean otolith increment width increased sharply from approximately 4 μm at 10 dph to 25–30 μm at 40 and 50 dph and then

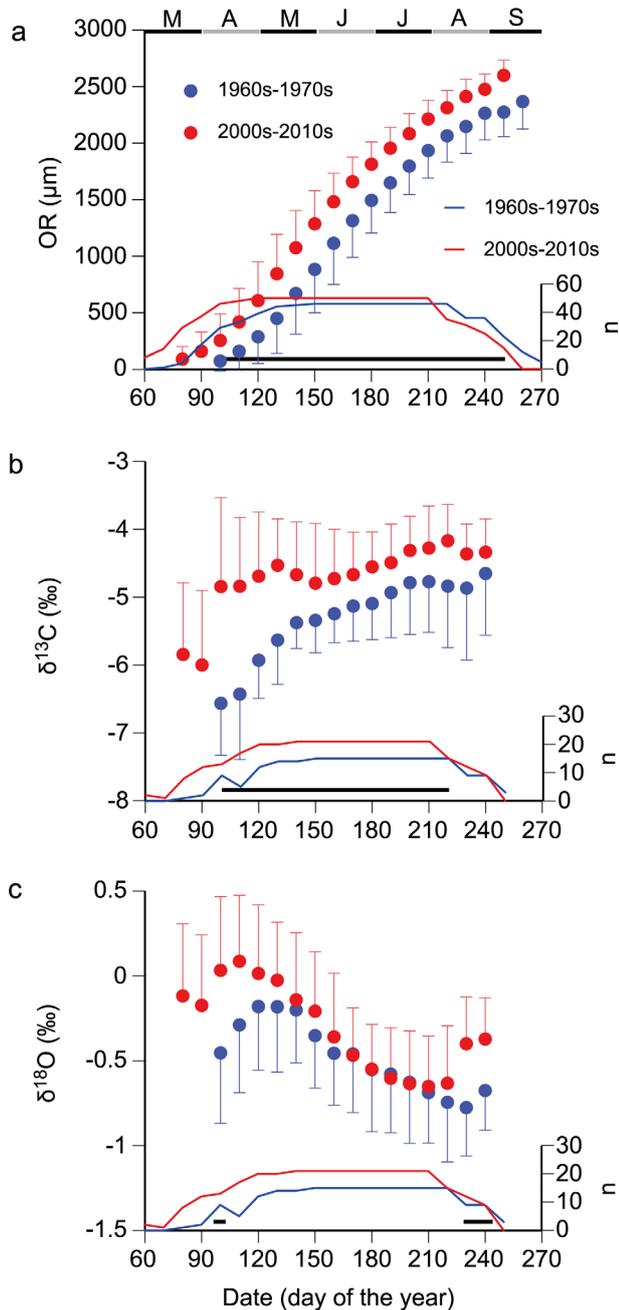


Fig. 4. Mean (\pm SD) *Trachurus japonicus* (a) otolith radius (OR), (b) carbon, and (c) oxygen isotope ratios at dates with 10 d intervals in days of the year in the 1960s–1970s (blue circles) and 2000s–2010s (red circles), with sample sizes shown with thin lines. Note that 0.94‰ was added to the $\delta^{13}\text{C}_{\text{oto}}$ values of each individual in the 2000s–2010s. To avoid confusion, the minus SD bars are only shown for the 1960s–1970s and plus SD bars are only shown for the 2000s–2010s. Thick horizontal lines: dates with significant ($p < 0.05$) differences between the 2 study periods

gradually decreased to 13 μm at 120 dph, and it was significantly different between the study periods (Fig. 5b; $F_{11,83} = 0.29$, $p = 0.025$). The mean increment

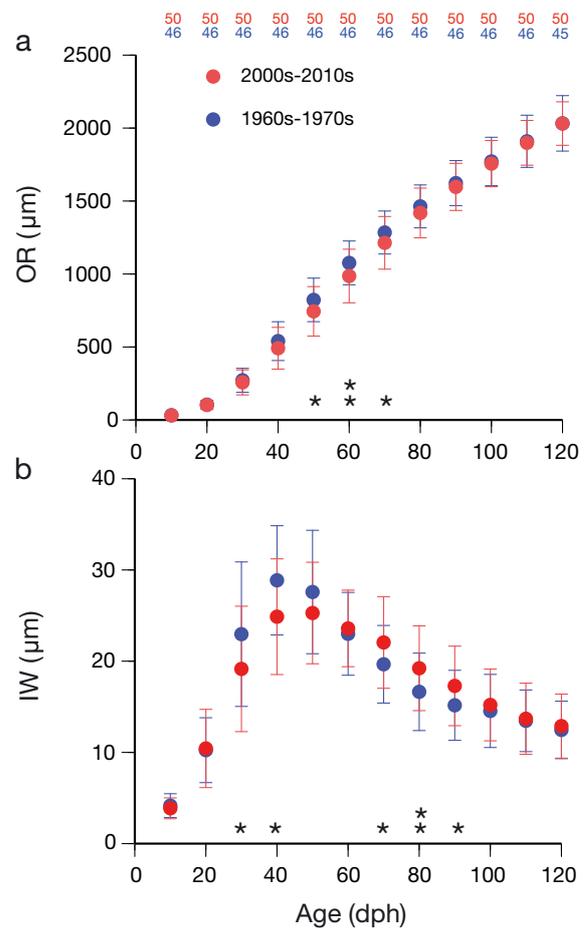


Fig. 5. Mean (\pm SD) (a) otolith radius (OR) and (b) increment width (IW) of otoliths of *Trachurus japonicus* juveniles at ages from 10 to 120 days post-hatch (dph) with 10 d intervals in the 1960s–1970s (blue) and 2000s–2010s (red). Numbers above the panels: sample sizes in the 1960s–1970s (blue) and 2000s–2010s (red). Asterisks indicate significant differences between the 2 study periods (* $p < 0.05$; ** $p < 0.01$)

widths at 30 and 40 dph in the 1960s–1970s were significantly higher than those in the 2000s–2010s, whereas the mean increment widths during 70–90 dph were smaller (Table S3).

The mean $\delta^{13}\text{C}_{\text{oto}}$ increased sharply from 10 to 40 dph and asymptotically after 50 dph (Fig. 6a). The mean $\delta^{13}\text{C}_{\text{oto}}$ values at 10–60 dph in the 2000s–2010s were significantly higher than those during the 1960s–1970s, except at 20 dph (Table S4). The mean $\delta^{18}\text{O}_{\text{oto}}$ increased from 10 to 40 dph and then gradually decreased, corresponding to the period with an asymptotic increase in $\delta^{13}\text{C}_{\text{oto}}$ (Fig. 6b). The mean values at 10–50 dph in the 2000s–2010s were significantly higher than those in the 1960s–1970s, except for those at 20 dph, which showed a large variation due to the small number of samples (Table S4). The $\delta^{18}\text{O}_{\text{oto}}$ trajectory in the northern ECS was compa-

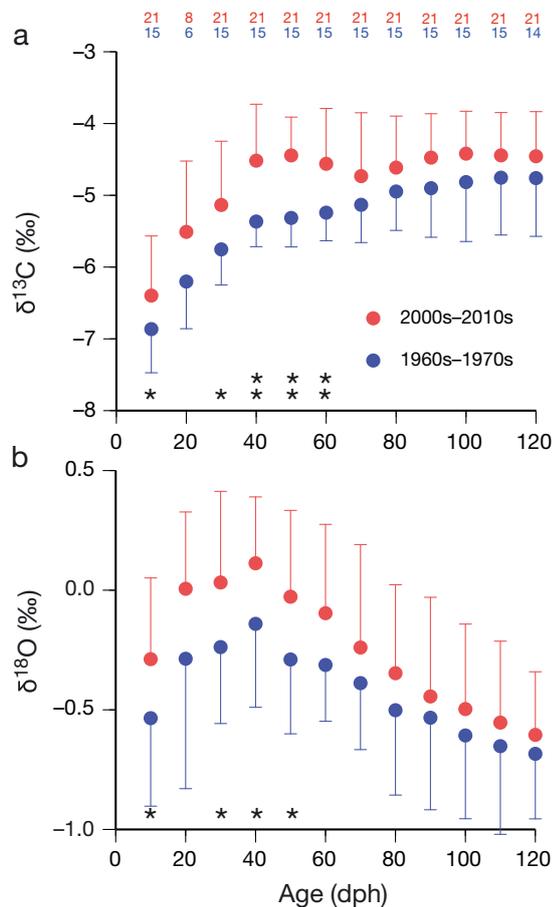


Fig. 6. Mean (\pm SD) (a) carbon and (b) oxygen isotope ratio of otoliths of *Trachurus japonicus* juveniles at ages from 10 to 120 days post-hatch (dph) with 10 d intervals in the 1960s–1970s (blue) and 2000s–2010s (red). Note that 0.94‰ was added to the $\delta^{13}\text{C}_{\text{oto}}$ values of each individual in the 2000s–2010s. To avoid confusion, the minus SD bars are only shown for the 1960s–1970s and plus bars are only shown for the 2000s–2010s. Numbers above the panels: sample sizes in the 1960s–1970s (blue) and the 2000s–2010s (red). Asterisks indicate significant differences between the 2 study periods (* $p < 0.05$; ** $p < 0.01$)

rable to that in the 2000s–2010s up to 60 dph, while it diverged after 60 dph (Fig. 7). The $\delta^{18}\text{O}_{\text{oto}}$ trajectory in the southwestern Sea of Japan was comparable to that in the 1960s–1970s and lower than that in the 2000s–2010s (Fig. 7).

The otolith increment width was negatively correlated with $\delta^{18}\text{O}_{\text{oto}}$ at 20 and 30 dph in the 1960s–1970s and at 30, 40, and 50 dph in the 2000s–2010s (Fig. 8a, Table 2), whereas no significant relationship was found after 60 dph in both study periods. The significant relationship between $\delta^{18}\text{O}_{\text{oto}}$ and increment width corresponded to the increasing period of the increment width in each study period. Although there was no significant relationship between $\delta^{13}\text{C}_{\text{oto}}$ and

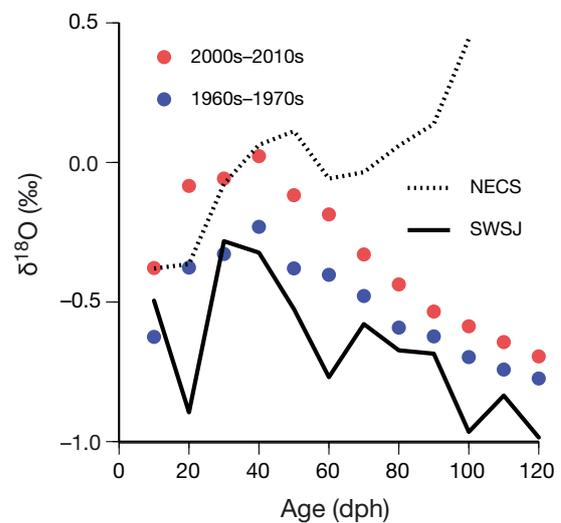


Fig. 7. Mean oxygen isotope ratios after correcting the effect of reaction temperature to 25°C of otolith of *Trachurus japonicus* juveniles at ages from 10 to 120 days post-hatch (dph) with 10 d intervals in the 1960s–1970s (blue circles) and 2000s–2010s (red circles). Thick solid and dashed lines: mean oxygen isotope ratios of otolith of *T. japonicus* juveniles reported in the southwestern Sea of Japan (SWSJ) and the northern ECS (NECS), respectively

the otolith increment width up to 100 dph, a significant relationship was found at 110 and 120 dph during the 2000s and the 2010s (Fig. 8b, Table 2).

4. DISCUSSION

4.1. Earlier hatching with earlier spawning

The hatching dates of *Trachurus japonicus* juveniles in this study mainly occurred in February and March during the 2000s–2010s, which is consistent with the reproductive indices and hatch date distribution of larvae and juveniles in the ECS. The gonad somatic index of adult female *T. japonicus* increased to >2 , which is indicative of possible spawning, from February to May, and peaked in March in the northern ECS during 1996–2004 (Mizuta et al. 2001, Yoda et al. 2004, 2014). Small (<3 mm body length) *T. japonicus* larvae are distributed at a higher density in the southern ECS in February and March (Sassa et al. 2006, 2008), and the hatching dates of *T. japonicus* juveniles based on the otolith daily increment analysis ranged from February to April, mainly in March, in the ECS (Takahashi et al. 2012). Based on the growth trajectory and hatch date distribution, *T. japonicus* juveniles that hatched mainly in March and were caught in the western waters off Kyushu from August to September were transported from the ECS, and not from the

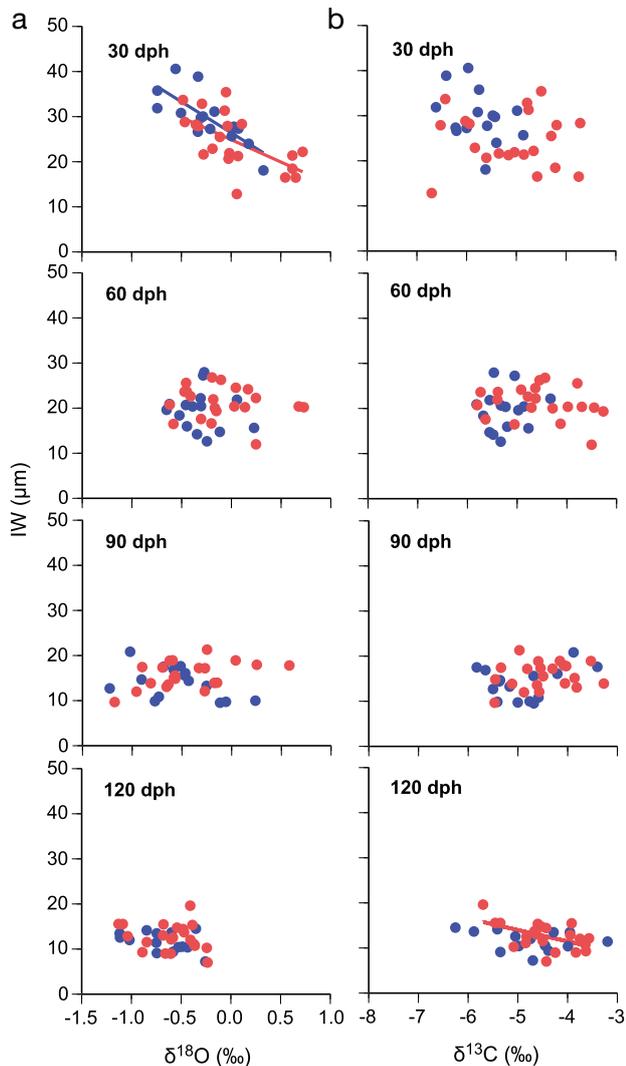


Fig. 8. Relationships between *Trachurus japonicus* otolith increment width (IW) and (a) oxygen and (b) carbon isotope ratios at 30, 60, 90, and 120 days post-hatch (dph) in the 1960s–1970s (blue) and 2000s–2010s (red). Solid lines indicate significant regression lines between increment widths and stable isotope ratios

coastal waters off Kyushu (Takahashi et al. unpubl. data). As the eggs and larvae of *T. japonicus* are transported northward from their spawning grounds by the Kuroshio Current and the Tsushima Warm Current in the ECS (Kozasa 1971, Kasai et al. 2008, Igeta et al. 2023), our results suggest it is highly probable that the juveniles that hatched mainly in February and March were transported from spawning grounds in the ECS into the western waters off Kyushu in recent decades.

The hatching dates of *T. japonicus* juveniles during the 1960s–1970s were mainly in April and May, which is consistent with the reproductive indices and larval occurrence in the northern ECS during the mid-

Table 2. Pearson's correlation coefficients for relationships between *Trachurus japonicus* otolith increment widths and δ¹⁸O and δ¹³C at ages with 10 d intervals. Asterisks indicate significant correlation (*p < 0.05; **p < 0.01). dph: days post-hatch

Age (dph)	δ ¹⁸ O		δ ¹³ C	
	1960–1970	2000–2010	1960–1970	2000–2010
10	–0.299	0.033	0.232	0.213
20	–0.838*	–0.449	–0.124	0.066
30	–0.769**	–0.616**	–0.340	–0.028
40	0.091	–0.557**	–0.083	–0.092
50	–0.022	–0.482*	0.123	–0.253
60	–0.129	–0.145	0.109	–0.232
70	–0.372	0.105	–0.044	0.063
80	–0.428	0.185	0.053	0.247
90	–0.457	0.462	0.277	0.172
100	–0.330	0.494	0.233	0.034
110	–0.476	0.407	0.058	–0.471*
120	–0.440	–0.212	–0.309	–0.535*

twentieth century. The gonad weight of large female *T. japonicus* (> 30 cm in total length) was > 10 g from February to May and peaked in April in the northern ECS, although it was highest in February and March in the southern and central ECS during 1955–1969 (Hotta & Nakashima 1971). The mean abundance and occurrence of *T. japonicus* larvae were also highest in April and May in the western waters off Kyushu in the 1950s and the 1960s (Fukataki 1960, Kozasa 1971). Our results suggest that juveniles that hatched in April and May in the northern ECS were more likely to be transported into the study area in the 1960s–1970s. In recent decades, *T. japonicus* juveniles that hatched in April have been distributed in the southwestern Sea of Japan, downstream along the Tsushima Warm Current in the study area, and they have been transported from the northwestern waters off Kyushu (Takahashi et al. 2022a). Thus, the expansion of the potential spawning area in March from the southern and central ECS in the 1960s–1970s to the entire ECS, including the northern ECS, may have resulted in the earlier hatching period in recent decades. Pooling the data by decade allowed detection in trends that may have been missed at the annual scale due to small sample sizes.

Spawning phenology for fish is associated with warming temperatures due to climate change for species with temperature-dependent gonadal development (Wedekind & Küng 2010, McQueen & Marshall 2017, Richardson et al. 2020). Although fishing also alters the reproductive and growth traits of fish through size-selective exploitation, the effects on short-lived fish species seem to more be unclear com-

pared with those on long-lived species (Heino et al. 2015). In this study, warming in late winter may have caused the earlier adult spawning and hatching of *T. japonicus* juveniles in the northern ECS in recent decades. The optimal spawning temperature for *T. japonicus* was found to be 17–18°C in rearing experiments (Ochiai et al. 1983). The mean SST in March in the study area was approximately 15°C during the 1960s–1970s, while it increased to 17°C during the 2000s–2010s. Previous studies on the optimal spawning temperature have reported that the temperature in March in the northern ECS was too low to spawn in the 1960s and the 1970s. Indeed, the mean SST in April in the 1960s–1970s increased to 16.5°C, becoming close to the minimum spawning temperature. Differences in the reproductive indices and larval occurrence between the 1960s and the 1970s and the 2000s and the 2010s were consistent with the differences in the hatching dates of *T. japonicus* juveniles in this study (Fig. 3), indicating that earlier spawning with warming in late winter in the northern ECS caused earlier hatching of *T. japonicus* juveniles in recent decades.

4.2. Effects of earlier hatching on the growth and temperature trajectories

Combining high-resolution isotopic analysis with growth increment analyses of archived otoliths enabled us to reconstruct the growth and temperature/metabolic trajectories of *T. japonicus* juveniles. The seasonal change in the otolith radius demonstrated that body size at given dates in the 2000s–2010s were significantly larger than those in the 1960s–1970s throughout life, indicating that earlier hatching in the 2000s–2010s caused a larger body size and higher daily age of *T. japonicus* juveniles captured in the summer and fall than those in the 1960s–1970s. As $\delta^{13}\text{C}_{\text{oto}}$ is a negative function of the field metabolic rate (Chung et al. 2019), the sharp increase in the $\delta^{13}\text{C}_{\text{oto}}$ values during the early life stages up to 50 dph indicated an exponential decrease in the field metabolic rate. As body-mass-specific respiration rates exponentially decrease with somatic growth during the early life stages of various fish species (Post & Lee 1996), the higher $\delta^{13}\text{C}_{\text{oto}}$ values at given dates in the 2000s–2010s than those in the 1960s–1970s, after subtracting the effect of the $\delta^{13}\text{C}$ -DIC decline by the Suess effect, may support a different energy balance, resulting in a different growth trajectory depending on the hatch dates. Additionally, as $\delta^{18}\text{O}_{\text{oto}}$ is also a negative function of the temperature experienced (Høie et al. 2004, Geffen 2012, Kitagawa et al. 2013,

Sakamoto et al. 2017), the seasonal trend in the $\delta^{18}\text{O}_{\text{oto}}$ values indicates that in both study periods, *T. japonicus* juveniles experienced seasonal increases in temperature from May to August after a declining temperature, with a habitat shift from the surface to the near-bottom layers in April (Enomoto et al. 2022). No significant difference in the $\delta^{18}\text{O}_{\text{oto}}$ values was found between the study periods from April to August, suggesting that *T. japonicus* juveniles experienced comparable thermal conditions during the 2 study periods. Similar thermal histories may have been caused by the different hatching periods, as discussed in the previous section.

From the viewpoint of ontogenetic changes in somatic growth and temperature, there was a significant difference in temperature and growth trajectories between the 2 periods. As *T. japonicus* larvae metamorphose from the larval to juvenile morphs during 30–40 dph at approximately 12 mm SL (Xie & Watanabe 2005), the $\delta^{18}\text{O}_{\text{oto}}$ and $\delta^{13}\text{C}_{\text{oto}}$ values at given ages indicated that *T. japonicus* juveniles in the 2000s–2010s experienced a lower temperature and lower field metabolic rate during the larval and early juvenile stages than those in the 1960s–1970s, and the different temperature trajectories caused a slower growth rate and smaller size at ages in the recent decades compared with those in the 1960s–1970s. The significant relationships between the otolith increment width and $\delta^{18}\text{O}_{\text{oto}}$ values suggest that growth rates are strongly affected by thermal conditions during the late larval and early juvenile stages (20–50 dph). The maximum width of the otolith growth increments during the larval and early juvenile stages is related to temperature in various marine fishes, including *T. japonicus* (Takahashi & Watanabe 2004, Xie & Watanabe 2005, Baumann et al. 2006). Enomoto et al. (2022) demonstrated that based on individual $\delta^{18}\text{O}_{\text{oto}}$ values, the *T. japonicus* habitat layer shifts from the surface to the near-bottom layers began at 23 dph in the late larval stage and ended at 54 dph in the early juvenile stage in the ECS. The habitat shift during the early life stages of *T. japonicus* may have affected the growth and temperature trajectories between the study periods, although after the habitat shift, food availability, rather than thermal conditions, may strongly affect the growth rate in the near-bottom layer, as indicated by the lack of clear relationships between the otolith increment width and $\delta^{18}\text{O}_{\text{oto}}$ values after 60 dph and significant relationships between the otolith increment width and $\delta^{13}\text{C}_{\text{oto}}$ values at 110 and 120 dph.

The patterns in $\delta^{18}\text{O}_{\text{oto}}$ trajectories in the waters adjacent to the study area may provide insights into

the causes of ontogenetic differences in temperature trajectories between the 2 study periods. The $\delta^{18}\text{O}_{\text{oto}}$ trajectory of the March-hatched *T. japonicus* juveniles in the northern ECS (Enomoto et al. 2022) was comparable to that in the 2000s–2010s in this study to up to 60 dph, while it diverged after 60 dph, indicating that *T. japonicus* juveniles in the 2000s–2010s experienced thermal conditions similar to those in the northern ECS. After 60 dph, the juveniles in this study experienced seasonal increases in temperature in the coastal study area, whereas juveniles in the upstream waters in the northern ECS experienced a decrease in temperature in the Yellow Sea Cold Water (Sassa et al. 2009). Meanwhile, the $\delta^{18}\text{O}_{\text{oto}}$ trajectory of the April-hatched juveniles in the southwestern Sea of Japan (Muto et al. 2022) was lower than that in the 2000s–2010s, indicating that the thermal conditions experienced during the early life stages were higher in the downstream waters of the Tsushima Warm Current in recent decades. The $\delta^{18}\text{O}_{\text{oto}}$ trajectory in the 1960s–1970s was comparable to that in the southwestern Sea of Japan, indicating that the April-hatched juveniles experienced similar thermal conditions during their early life stages, even though the juveniles in recent decades have been distributed in downstream waters. Given that the spatial gradient of the experienced temperature is associated with the habitat layer shift depending on the hatching period, comparable trends in the temperature trajectory between the southwestern Sea of Japan in recent decades and the northern ECS in the 1960s–1970s are plausible. Thus, the expansion of the potential spawning area in March into the study area would affect not only earlier hatching but also the growth and temperature trajectories associated with the habitat layer shift in *T. japonicus*.

The effects of ocean warming on fish ecology have been reported based on the changes in their distribution ranges (Perry et al. 2005, Poloczanska et al. 2013) and timing of life events (Wedekind & Küng 2010, McQueen & Marshall 2017) at various spatiotemporal scales. Although the spatial scale of this study area was limited to the entire distribution range of *T. japonicus*, our results demonstrated that the hatching period in recent decades was clearly different from that in the 1960s–1970s. However, the temperature trajectory was comparable between the 2 periods due to earlier hatching, except for that in the larval and early juvenile stages, which might have been associated with the habitat layer shift. Archived otoliths have revealed the growth and temperature trajectories under climate variability over the twentieth century in Atlantic cod (Denechaud et al. 2020, von

Leesen et al. 2020) and species-specific strategies for enhancing growth and survival under climate variability in sardines in the North Pacific (Sakamoto et al. 2022). It would have been impossible to address the responses of fish ecology to climate variability in previous studies or to the warming ocean in this study without archived otoliths. Therefore, archiving otoliths at the present age is necessary to determine the impact of future warming on fish ecology in marine ecosystems.

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