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Short Communication

Temperature dependency equation for chub mackerel (*Scomber japonicus*) identified by a laboratory rearing experiment and microscale analysis

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Abstract. In this study, juveniles of chub mackerel (*Scomber japonicus*) were reared from eggs in six different temperature treatments, and their otoliths were subjected to micromilling and microvolume stable oxygen isotope ($\delta^{18}O$) analysis. We determined the $\delta^{18}O$ values of otoliths ($\delta^{18}O_{otolith}$) formed at mean temperatures of 16.3, 17.6, 18.3, 20.0, 24.0 and 26.5°C and identified a linear relationship between rearing water temperature (T, °C) and $\delta^{18}O_{otolith}$ as follows: $\delta^{18}O_{otolith\ (VPDB)} - \delta^{18}O_{water\ (VSMOW)} = -0.25\ (\pm 0.01)T + 4.46\ (\pm 0.21)$ ($R^2 = 0.96$, $P < 0.01$), where VPDB is Vienna Peedee Belemnite, VSMOW is Vienna Standard Mean Ocean Water and the error values in parentheses are standard deviations. This species-specific temperature dependency equation for chub mackerel will enable accurate reconstruction of individual thermal histories and provide essential information for effective resource management.

Additional keywords: otolith, pelagic fish, population structure, recruitment abundance, stable oxygen isotope.

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Introduction

Chub mackerel (*Scomber japonicus*) is a pelagic fish species that has a cosmopolitan distribution in subtropical and temperate waters in the Indo-Pacific Ocean (Scoles *et al.* 1998). In the northwest Pacific, this species is distributed from Japan, along the south coast of China to the Malay Archipelago (Collette and Nauen 1983) as a complex assembly of weakly diverged genetic populations (Cheng *et al.* 2015). The abundance of the Pacific stock of chub mackerel went into sharp decline around the early 1980s (Yukami *et al.* 2019) and was kept at extremely low levels in the 1990s because of heavy fishing of immature fish (Kawai *et al.* 2002). However, the stock size has been increasing since around 2005 and had recovered to its pre-decline level in 2013 (Yukami *et al.* 2019). This increase in stock size is considered to have been caused by strong year classes, which have occurred frequently since 2013 (Hashimoto *et al.* 2019). However, the reason why these strong year classes have occurred remains unclear. To keep chub mackerel resources in good condition and maintain productive fisheries, it is important to know the mechanism underlying the recent increase in recruitment abundance.

Recent studies have suggested that the recruitment abundance of chub mackerel is related to their early growth rate, which primarily depends on ambient water temperature (Kamimura *et al.* 2015; Kaneko *et al.* 2019). One of these studies was a population-level otolith study that assumed the sea surface temperature (SST) of an area abundant in chub mackerel larvae as the temperature that the larvae had experienced (Kamimura *et al.* 2015). The other study was a particle tracking study that regarded the SSTs to which particles were subjected in simulations as the thermal histories of larvae (Kaneko *et al.* 2019). Although these two studies provided important insights into the mechanism of recruitment fluctuation of chub mackerel, more studies are needed to determine the relationship between the thermal histories of chub mackerel larvae and their growth rates directly at the individual level, not indirectly at the population level as in the previous studies.

[1]These authors contributed equally to this work.

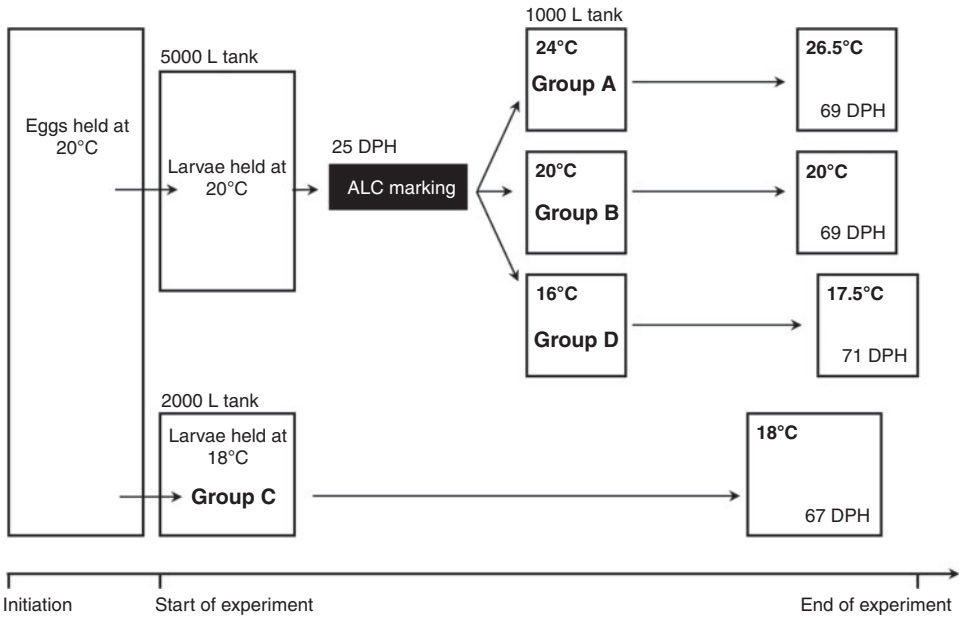

Fig. 1. Flowchart of the laboratory rearing experiment. Groups A, B, C and D represent the different temperature treatment groups. ALC, alizarin complexone; DPH, days post-hatching.

Stable oxygen isotope ratio ($\delta^{18}O$) analysis with fish otoliths, which are calcium carbonate structures in the endolymphatic sac of teleost fish that are usually composed of aragonite, is a reliable method for estimating the temperature experience of individuals because $\delta^{18}O$ can be used as a proxy of ambient water temperature (Høie *et al.* 2004; Storm-Suke *et al.* 2007; Godiksen *et al.* 2010; Sakamoto *et al.* 2017). The relationship between ambient water temperature and otolith $\delta^{18}O$ has been quantified in various fish species and is often expressed using the following simplified formula:

$$\delta^{18}O_{otolith} - \delta^{18}O_{water} = a \times T + b \quad (1)$$

where $\delta^{18}O_{otolith}$ is the $\delta^{18}O$ value of the otolith, $\delta^{18}O_{water}$ is the $\delta^{18}O$ value of ambient water and T is the temperature of ambient water, whereas a and b are constants. This type of equation shows the dependency of $\delta^{18}O$ on ambient water temperature and is herein referred to as a temperature dependency equation. The constants in the temperature dependency equation for otoliths are generally close to those in the temperature dependency equation for inorganic aragonite reported by Kim *et al.* (2007; see Kitagawa *et al.* 2013; Sakamoto *et al.* 2017).

However, the constants obtained in the $\delta^{18}O$ analysis of several species differed slightly from those of the equation for inorganic aragonite (Kitagawa *et al.* 2013; Sakamoto *et al.* 2017; Willmes *et al.* 2019). Several other studies have also suggested that the constants of temperature dependency equations differ among species (Høie *et al.* 2004; Storm-Suke *et al.* 2007; Godiksen *et al.* 2010; Kitagawa *et al.* 2013; Sakamoto *et al.* 2017). Thus, species-specific temperature dependency equations are required for precise and accurate estimates of the ambient water temperatures experienced by target species.

The aim of this study was to empirically establish a species-specific temperature dependency equation for chub mackerel. Chub mackerel juveniles were reared under six different temperature treatments. In order to minimise potential errors that could be caused by environmental fluctuations during the experimental period and indirect estimation, we used a micro-scale sampling technique and a microvolume carbonate analytical system proposed in previous studies (Ishimura *et al.* 2004, 2008) and analysed $\delta^{18}O$ data from otolith areas formed under stable water temperature and $\delta^{18}O_{water}$ conditions. This system allowed us to obtain a $\delta^{18}O$ value of as little as 0.2 μg $CaCO_3$ with an analytical precision of better than ±0.10‰.

Materials and methods

Egg hatching

Eggs were obtained from induced spawning of captive broodstock maintained at the Hakatajima Station, National Research Institute of Fisheries and Environment of Inland Sea (Imabari, Japan) using the procedure reported by Nyuji *et al.* (2012). A group of suitable 2-year-old chub mackerel (53–59 individuals of each sex) was injected intramuscularly with 400 μg kg^{-1} of bodyweight gonadotropin-releasing hormone analogue (GnRHa) on 28 May 2018 and was maintained in a 20 000-L square tank with circulating seawater. The first spawning was observed ~36 h after injection, and subsequent daily spawning occurred. Eggs from the first and second spawns were placed and incubated in 5000- and 2000-L fibre-reinforced plastic tanks at mean temperatures of 20 and 18°C respectively under a 14-h light–10-h dark cycle (Fig. 1). The larvae were fed with a mixture of rotifers (*Brachionus*) and planktonic algae (*Isochrysis galbana* or *Nannochloropsis oculata*) once daily until 16 days post-hatching (DPH) (18°C tank) or 12 DPH (20°C tank). From these timings onward, larvae were also fed with newly hatched brine shrimp (*Artemia salina*) once per day. After 27 DPH (18°C tank) and 21 DPH (20°C tank), larvae were fed with ~3% of their bodyweight (g) of commercial dry pellets composed of 52% protein, 11% oil, 18% ash and 3% fibre (New Arteck, Marubeni Nisshin Feed, Tokyo, Japan).

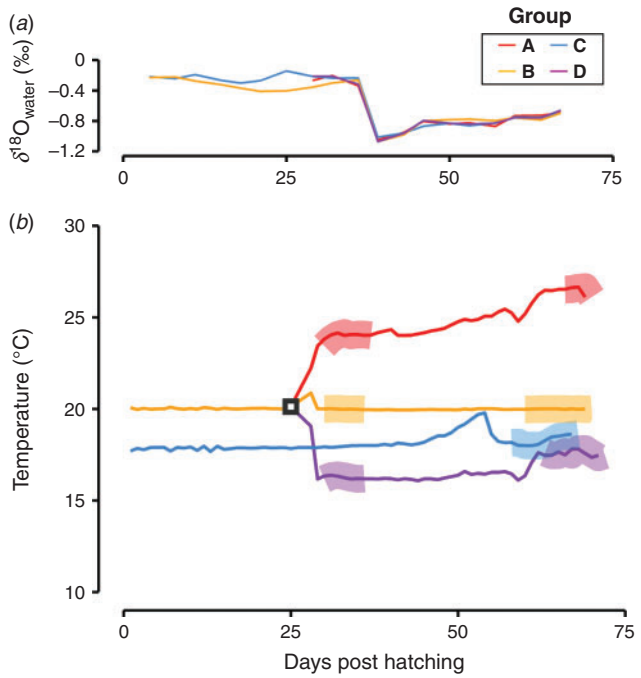

Fig. 2. (*a*) $\delta^{18}O_{water}$ values and (*b*) water temperatures in the four different temperature treatment groups (A–D). The otolith areas formed during the shaded periods were used for isotope analysis.

Rearing in different temperature treatments

Fish were reared in four different temperature treatments, hereafter referred to as Groups A, B, C and D (Fig. 1). The fish in Groups A, B and D were reared in the 20°C tank until they grew into juveniles. All individuals metamorphosed into juveniles by 25 DPH. At this point, the individuals in these groups were immersed in 15-ppt alizarin complexone (ALC), which deposited visibly distinguishable fluorescent marks on their otoliths to facilitate precise dating. Then, the individuals were evenly divided and introduced into three different 1000-L tanks (80 individuals in each tank). The water temperature of Group A was kept at ~24.0°C for 17 days, then raised to ~26.5°C and maintained at this temperature until the end of the rearing experiment. The water temperature of Group B was maintained at 20.0°C throughout the experimental period. The water temperature of Group D was kept at ~16.0°C for 20 days, then raised to ~17.5°C and maintained at this temperature until the end of the rearing experiment. Fish in Group C were kept at ~18.0°C from the egg stage until the end of the rearing experiment in the 2000-L tank. At the end of the rearing experiment, 45–60 individuals were randomly sampled from each tank. The fork length (FL) and bodyweight of the sampled individuals were measured before freezing. Rearing water samples for $\delta^{18}O$ analysis were taken from all the tanks twice a week throughout the experimental period. The water samples were placed in 50-mL sealed glass vials and refrigerated before isotopic analysis to prevent evaporation.

$\delta^{18}O$ analysis of otoliths and rearing water

Sagittal otoliths were dissected out from 17 individuals from the different temperature treatments ranging in size from 58.4 to 135.6 mm FL; adherent bits of tissue were removed using a needle and a thin paintbrush under a stereomicroscope. The otoliths were rinsed with Milli-Q water and air dried. The otoliths were then embedded in epoxy resin (Polyester Solidifier; Nichika, Kyoto, Japan) and polished with sandpaper (2000 grit) and lapping film (4000 grit).

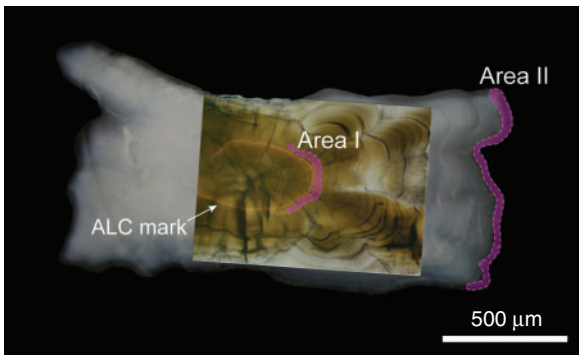

Fig. 3. Otolith Areas I and II. ALC, alizarin complexone.

Values of $\delta^{18}O_{water}$ decreased markedly on approximately Day 35 of the experiment (Fig. 2*a*) because the salinity of the sea water around the Hakatajima Station dropped significantly due to heavy rain. In addition, extremely hot days caused some fluctuations in water temperature (Fig. 2*b*). To avoid periods of such unstable $\delta^{18}O_{water}$ and temperatures, otoliths were milled using a high-precision micromilling system (GEOMILL326; Izumo-web, Izumo, Japan) and two areas formed under stable conditions were extracted: Area I, adjacent to ALC marks, and Area II near the otolith edges (coloured areas in Fig. 3). These areas were formed under relatively stable temperature and $\delta^{18}O_{water}$ conditions (standard deviations <0.25°C and <0.07‰ for temperature and $\delta^{18}O_{water}$ respectively) and were easy to extract because of their visible boundaries, namely the ALC marks and the otolith edges (Fig. 3). As shown in Fig. 2*b*, Areas I and II in Group A were formed at mean temperatures of 24.0 and 26.5°C respectively. Areas I and II in group B were formed at a mean temperature of 20.0°C. Area II in Group C was formed at a mean temperature of 18.0°C. Areas I and II in Group D were formed at mean temperatures of 16.0 and 17.5°C respectively. The width of each area was determined using the daily otolith growth rate. The daily growth rate of each otolith was calculated by dividing the otolith radius by DPH (Group C) or days after ALC marking (Groups A, B and D). These areas were extracted along daily increments, the daily deposition of which was verified in a previous study (Takahashi *et al.* 2014). Irregular otolith microstructure, which is a typical signature of vaterite formation, was not observed. The weight and width of the extracted otolith areas were 0.5–3.6 µg and 40–160 µm respectively. The milling depth was 50 µm for all extracted otolith areas. The $\delta^{18}O_{otolith}$ value of each otolith area ($n = 10$ for Area I, $n = 14$ for Area II) was determined using a continuous-flow isotope ratio mass spectrometry system proposed in previous studies (Ishimura *et al.* 2004, 2008) at the National Institute of Technology, Ibaraki College (Hitachitanaka, Japan) and $\delta^{18}O_{otolith}$ values are reported in delta notation relative to Vienna Peedee Belemnite (VPDB). Detailed analytical procedures have been reported by Nishida and Ishimura (2017) and Sakamoto *et al.* (2017). The otolith

samples were reacted with phosphoric acid at 25.0°C. Most of the isotope values of carbonate in previous studies (e.g. Kim *et al.* 2007; Kitagawa *et al.* 2013; Sakamoto *et al.* 2017) were calculated using isotope fractionation factors for calcite. Therefore, to facilitate comparison with these studies, we used a commonly accepted calcite acid fractionation factor of 1.01025 (Sharma and Clayton 1965). We prepared a 24-point dataset of $\delta^{18}O_{otolith}$ from the 17 otoliths; two data points (i.e. otolith Areas I and II) obtained from 7 individuals and one data point (i.e. otolith Area I or II) obtained from the remaining 10 individuals. Detailed information about all the otolith areas analysed is given in Table S1, available as Supplementary material to this paper. The $\delta^{18}O$ value of each rearing water sample was determined using a Picarro L2130-i Analyzer (Sanyo Trading, Tokyo, Japan) at the National Institute of Technology, Ibaraki College, with a long-term analytical precision of ±0.05‰ for seawater; these $\delta^{18}O_{water}$ values are reported relative to Vienna Standard Mean Ocean Water (VSMOW).

All experimental procedures followed the guidelines for animal welfare of the Fisheries Research and Education Agency, Japan (50322001) and were approved by the Committee of Animal Welfare of the National Research Institute of Fisheries and Environment of Inland Sea (Number 2016-3).

Statistical analysis

Because no significant effect of otolith areas on $\delta^{18}O_{otolith} - \delta^{18}O_{water}$ was detected with multiple regression analyses ($P = 0.743$), all 24 data points for $\delta^{18}O_{otolith}$ obtained from Areas I and II were pooled. Multiple regression analysis also showed that different widths and different weights did not have any significant effects on $\delta^{18}O_{otolith}$ ($P = 0.64$ and $P = 0.47$ respectively). A linear regression model was applied to the pooled data to determine the relationship between rearing water temperature and $\delta^{18}O_{otolith} - \delta^{18}O_{water}$ for chub mackerel. The response variable was $\delta^{18}O_{otolith} - \delta^{18}O_{water}$, where $\delta^{18}O_{otolith}$ was the $\delta^{18}O$ value of each otolith area and $\delta^{18}O_{water}$ was the mean $\delta^{18}O$ value of rearing water during the formation of the otolith area. The explanatory variable was the mean water temperature at which each otolith area was formed. All statistical procedures were conducted using R (ver. 3.4.1, R Foundation for Statistical Computing, Vienna, Austria, see http://www.R-project.org/, accessed 7 September 2018). Figures were generated using ggplot2 (ver. 3.0.0, see https://cloud.r-project.org/package=ggplot2), and multiple regression analysis was conducted using the lm function.

Unless indicated otherwise, data are given as the mean ± s.d.

Results

During the period of formation of otolith Area I, the mean water temperatures in Groups A, B and D were 24.0 ± 0.2, 20.0 ± 0.0 and 16.3 ± 0.1°C respectively, and the $\delta^{18}O_{water}$ values of Groups A, B and D were −0.27 ± 0.07, −0.33 ± 0.04 and −0.21 ± 0.00‰ respectively. During the period of formation of otolith Area II, the mean water temperatures in Groups A, B, C and D were 26.5 ± 0.22, 20.0 ± 0.01, 18.3 ± 0.25 and 17.6 ± 0.15°C respectively, whereas the mean $\delta^{18}O_{water}$ values were −0.69 (single piece of data), −0.75 ± 0.05, −0.76 ± 0.05 and −0.71 ± 0.07‰ respectively.

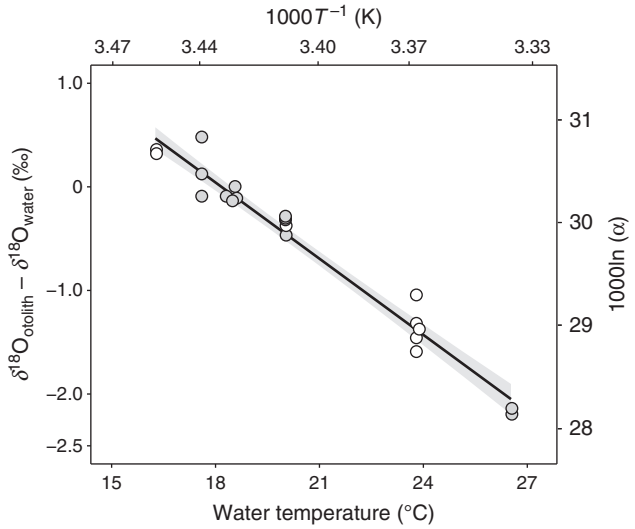

Fig. 4. Relationship between water temperature and $\delta^{18}O_{otolith} - \delta^{18}O_{water}$ for chub mackerel. The open and shaded symbols represent the $\delta^{18}O$ values of Areas I and II respectively. The solid line represents the regression line of all the samples from Areas I and II, with the grey shading on either side of the line indicating the 95% confidence interval. *T*, temperature in Kelvin; α, the fractionation factor between otolith and water.

For Area I, mean $\delta^{18}O_{otolith}$ values were +0.07 ± 0.02‰ at 16.3°C, and −0.61 ± 0.07‰ at 20.0°C, −1.58 ± 0.20‰ at 24.0°C; for Area II, mean $\delta^{18}O_{otolith}$ values were −0.52 ± 0.23‰ at 17.6°C, −0.84 ± 0.07‰ at 18.3°C −1.09 ± 0.07‰ at 20.0°C, and −2.85 ± 0.01‰ at 26.5°C. Using the least squares method, the linear regression relationship between water temperatures in the range 16.3–26.5°C and $\delta^{18}O$ was expressed in the form of a temperature dependency equation:

$$\delta^{18}O_{otolith(VPDB)} - \delta^{18}O_{water(VSMOW)} = -0.25(\pm 0.01)T + 4.46(\pm 0.21)\left(R^2 = 0.96, P < 0.01\right) \quad (2)$$

where *T* is temperature (°C) and the errors in parentheses are standard deviations (Fig. 4).

Fractionation expressed as 1000ln(α) was calculated as follows:

$$1000\ln(\alpha) = 21.40\left(1000T^{-1}\right) - 43.03$$

where *T* is temperature (K) and α is the fractionation factor between otolith and water.

Discussion

We succeeded in obtaining a reliable temperature dependency equation with a small standard deviation as the $\delta^{18}O$ thermometer of chub mackerel (Fig. 4). The equation obtained in this study showed a lower temperature than the equation for inorganic aragonite reported by Kim *et al.* (2007) at every $\delta^{18}O_{otolith} - \delta^{18}O_{water}$ value within the temperature range tested. Therefore, the application of the equation for inorganic aragonite to chub mackerel would lead to errors in the estimation of their temperature experience, as suggested by previous studies

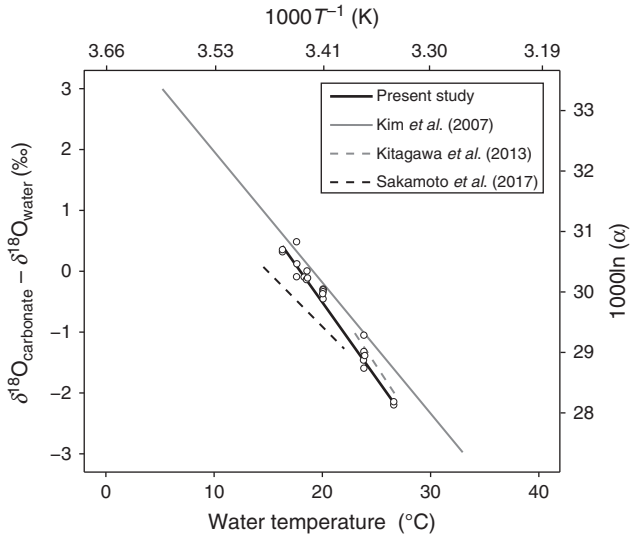

Fig. 5. Comparison of the temperature dependency equations for chub mackerel (present study), other fish species (Kitagawa *et al.* 2013; Sakamoto *et al.* 2017) and inorganic carbonate (Kim *et al.* 2007). The solid grey line corresponding to the equation of Kim *et al.* (2007) was recalculated using a calcite acid fractionation factor of 1.01025 to facilitate comparison (Sharma and Clayton 1965). The open symbols represent the values of $\delta^{18}O_{otolith} - \delta^{18}O_{water}$ for chub mackerel obtained from the present study. *T*, temperature in Kelvin; α, the fractionation factor between otolith and water.

(e.g. Kitagawa *et al.* 2013; Sakamoto *et al.* 2017; Willmes *et al.* 2019). For example, suppose $\delta^{18}O_{otolith} - \delta^{18}O_{water}$ is −2.0‰. In this case, the temperature experienced by the fish is estimated to be 28.5°C using the equation for inorganic aragonite of Kim *et al.* (2007), whereas it is estimated to be 26.0°C using the species-specific equation for chub mackerel developed in the present study (Eqn 2). This difference is not negligible in identifying the migration routes of chub mackerel.

Chub mackerel and Japanese sardine are pelagic species that inhabit approximately the same area and use similar migration routes. However, the slope of the species-specific temperature dependency equation for chub mackerel is steeper than that of the equation for Japanese sardine reported by Sakamoto *et al.* (2017; Fig. 5). In addition, the equation for bluefin tuna proposed by Kitagawa *et al.* (2013) shows a 0.6–0.9°C higher temperature than our equation for chub mackerel at every $\delta^{18}O_{otolith} - \delta^{18}O_{water}$ value within the temperature range tested for bluefin tuna (Fig. 5), even though these species belong to the same family Scombridae. Given the fact that these three otolith studies were conducted under the same analytical settings and using the same data processing methods, it is unlikely that these interspecies differences were caused by systematic errors arising from differences in methodology. Therefore, neither the ecological similarity nor the phylogenetic distance between species seems to be a reliable criterion for predicting the similarity of the equations. Thus, we agree with the suggestion made previously by some authors that species-specific temperature dependency equations should be empirically determined for an accurate reconstruction of individual thermal histories (Kalish 1991; Thorrold *et al.* 1997; Høie *et al.* 2004; Godiksen *et al.* 2010).

Unpredictable fluctuations in rearing environments are inherent in any long-term rearing experiment unless it is conducted in a closed recirculating system such as the one used by Kikuchi *et al.* (2006). In the present experiment, $\delta^{18}O_{water}$ fluctuations associated with salinity fluctuations were observed. This study accomplished precise dating by reading daily increments of the ALC-marked otoliths of hatchery-reared individuals. This allowed us to pinpoint the otolith areas formed under stable environmental conditions. In addition, the aforementioned micromilling technique and microvolume analysis enabled us to precisely extract the targeted otolith areas and determine the $\delta^{18}O_{otolith}$ value of each area. In this way, we successfully obtained a reliable equation even from fish that had experienced unexpected environmental changes. The robustness against environmental fluctuations would be another advantage of this methodology, in addition to its applicability to small fish species pointed out by Sakamoto *et al.* (2017).

For precise estimation of the temperature history of chub mackerel, the salinity of ambient water should also be considered because it affects $\delta^{18}O_{water}$, as does water temperature. Most chub mackerel belonging to the Pacific stock inhabit offshore areas, which are not subjected to freshwater input and are unlikely to undergo large fluctuations in $\delta^{18}O_{water}$ associated with salinity change. Nevertheless, a minor portion of the Pacific stock migrates to inshore areas (Yukami *et al.* 2019), where $\delta^{18}O_{water}$ can possibly be affected by freshwater input. Thus, some caution is required when applying the equation obtained in this study to individuals captured from inshore areas.

The equation for chub mackerel obtained from this study provides essential information for effective resource management through an accurate reconstruction of individual thermal histories. For example, a comparison of the thermal histories of fast- and slow-growing individuals can facilitate further understanding of the thermal mechanism that accounts for the difference in growth rate between the individuals, which is a possible cause of the significant annual variation in recruitment abundance and the recent occurrence of strong year classes (Kamimura *et al.* 2015; Kaneko *et al.* 2019).

In addition, a recent study proposed a new method that combines microscale $\delta^{18}O$ analysis with numerical simulation to reconstruct the early migration routes of fishes at the individual level (Sakamoto *et al.* 2019). The simulation in this method is based on ocean data assimilation models that include both temperature and salinity data. Thus, by combining the $\delta^{18}O$ thermometer presented in this study with the new method, the possible migration history of chub mackerel can be estimated. This will contribute to an understanding of the interaction among chub mackerel populations in the north-west Pacific and of the ecological processes that shape the contemporary genetic population structure of chub mackerel in this region.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

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