INTRODUCTION

Marine fish stocks are an important food resource for humans (Crist, Mora, & Engelman, 2017) and marine predators (Crawford, Sabarros, Fairweather, Underhill, & Wolfaardt, 2008; Cury et al., 2011), although many have faced severe declines (Pauly et al., 2002). Understanding population structure is a basic and crucial requirement for efficient fisheries management (Cadrin, Karr, & Mariani, 2014) because, without it, fisheries can exert an unexpectedly high pressure on certain regional populations, leading to over-fishing of some stock components (Felix-Uraga et al., 2005; Hüssy et al., 2016). Therefore, revealing seasonal or annual changes in fish distribution at both individual and population levels has been a key topic in fisheries science (Block et al., 2005; Brennan et al., 2015; Tsukamoto & Nakai, 1998).

Several methods have been developed to track the movements of marine fish in open oceans. Electronic tagging has been valuable for reproducing the migration histories of large fish such as adult bluefin tuna based on recorded light levels and temperatures (Block et al., 2005). For early life stages in which swimming ability is negligible, numerical particle tracking experiments based on ocean models have allowed a better understanding of how fish disperse from spawning grounds (Allain, Petitgas, Lazure, & Grellier, 2007; Itoh et al., 2011). However, we still lack solid methods for small-sized, but actively swimming, juveniles that cannot be tagged, although survival rate during this stage is crucial for population structures and the environmental cause of recruitment variabilities, and to validate and improve fish movement models.

KEYWORDS

behaviour, IBM, isotope, migration, otolith, population structure, sardine, small pelagic fish
1999), although they still include assumptions that are very difficult to verify empirically, thereby presenting inherent uncertainty.

Otoliths are calcium carbonate crystals formed in the inner ear of fish, and their chemical composition is known to record ambient water chemistry (Campana, 1999; Sturrock, Trueman, Darnaude, & Hunter, 2012). In particular, the oxygen stable isotope ratio ($\delta^{18}O$), which reflects both temperature and $\delta^{13}O$ of surrounding water (Kim, O’Neil, Hillaire-Marcel, & Mucci, 2007), has often been used as a temperature proxy to discuss fish migration (e.g., Carpenter, Erickson, & Holland, 2003; Shiao, Yui, Høye, Ninnemann, & Chang, 2009). It has mainly been applied to fish species with large otoliths because conventional isotope ratio mass spectrometry required large sample amounts. Recently, however, the analysing system MICAL3c has been developed. This system requires 1/100 of the sample quantity required for conventional mass spectrometry (Ishimura, Tsunogai, & Nakagawa, 2008; Nishida & Ishimura, 2017), thereby allowing an accurate analysis of narrow growth increments in small otoliths (Sakamoto et al., 2017). Despite this drastic technical improvement, interpreting otolith $\delta^{18}O$ values to estimate fish migration history remains difficult. The variability in seawater $\delta^{18}O$, which is primarily related to salinity variation (Craig & Gordon, 1965), often confounds temperature estimation because it is essentially impossible to estimate the two parameters in a single equation. Moreover, because otolith $\delta^{18}O$ can only distinguish water masses of different temperature or salinity, estimations of fish location become impractically rough when uniform water masses are distributed broadly (Torniainen et al., 2017), which is often the case in open oceans.

Here, we describe and demonstrate a new methodology to estimate the migration history of individual small fish, by using an interdisciplinary combination of isotopic analysis and numerical simulation. The Japanese sardine was selected as the model for this demonstration because of its dynamic migration from the temperate Kuroshio region to the subarctic Oyashio region within 6 months after hatching (Kuroda, 1991), and economic and ecological importance in the western North Pacific (Ishida et al., 2009). To our knowledge, this is the first otolith microchemistry study to use numerical migration models to interpret the isotope profile. First, the distribution of the seawater $\delta^{18}O$ and its relation with salinity in the habitat area of the Japanese sardine were investigated. Using micromilling and microvolume isotope analysis, accurate otolith $\delta^{18}O$ profiles were obtained with high resolution. Furthermore, instead of estimating temperature histories from the otolith $\delta^{18}O$ profiles, we searched for migration routes that should be followed to reproduce the $\delta^{18}O$ profile, using an individual-based model in which a randomly swimming migration scheme was applied to a data-assimilated ocean model.

2 | MATERIALS AND METHODS

2.1 | Distribution of seawater $\delta^{18}O$ and its relationship with salinity

Surface seawater samples for water isotope analysis were collected in the western North Pacific during seven pelagic fish sampling survey cruises conducted by the National Research Institute of Fisheries Science, Fisheries Research Agency (NRIFS) in May–June 2012, September–October 2012, May–June 2013, September–October 2013, April–May 2015, May–June 2016, and September 2016, and the Shinsei-maru KS-15-11 cruise in September 2015. The sampling range encompassed the 34.00–47.48°E, 138.48–172.38°N region, which roughly covers the whole distribution of larval and juvenile Japanese sardine. In all sampling points, the salinity profile was measured with a SBE 9 Plus CTD unit (Sea-Bird Electronics, Inc.), with precision better than 0.01 in all cruises. Seawater samples for $\delta^{18}O$ analysis were taken from the sea surface using a roped plastic bucket on board, or at 5 m depth using CTD-attached Niskin bottles (General Oceanics, Inc.). Water samples were preserved in sealed glass vials to avoid evaporation. Samples obtained in 2012 and 2013 were measured at the Geo Science laboratory using the LWIA DL100 system (Los Gatos Research) with precision ±0.05‰. Samples from other cruises were analysed at the Atmosphere and Ocean Research Institute (AORI), University of Tokyo, using the Picarro L2120-i system with precision ±0.07‰. Samples analysed in AORI were membrane-filtered (pore size: 0.45 μm, Toyo Roshi Kaisha, Ltd.) before their introduction in the Picarro L2120-i system to reduce suspended particles and avoid blocking the sampling line. The correlation between seawater $\delta^{18}O$ and salinity was analysed by the least squares method using surface water $\delta^{18}O$ and salinity measured at 10 m (or 5 m if available) depth by the CTD.

2.2 | Fish sampling and otolith micromilling and $\delta^{18}O$ analyses

Six young-of-the-year Japanese sardine individuals were used. These were obtained from samples taken offshore Oyashio region in a subsurface trawl survey conducted by the NRIFS; three were sampled in October 2010 and three in September 2014. Individuals [standard length (SL): 107.7–133.7 mm] were immediately frozen after capture and defrosted just before otolith analyses. Sagittal otoliths were extracted, cleaned using a needle and a thin paintbrush under 10–20× magnification, rinsed with Milli-Q water, and air-dried for a few hours. After these procedures, otoliths were embedded in Petroproxy 154 (Burnham Petrographics LLC) resin and kept at 80°C for 12 hr to cure the resin. Embedded otoliths were ground in Petroproxy 154 (Burnham Petrographics LLC) resin and kept at 80°C for 12 hr to cure the resin. Embedded otoliths were ground with sandpaper (no. 2000) and polished with an alumina suspension (BAIKOWSKI International Corporation) in sagittal plane to reveal the daily rings from the core to the edge.

The position and number of daily rings in otoliths were examined along the axis of the postrostrum using an otolith measurement system (RATOC System Engineering Co. Ltd.). The daily age at capture was calculated by adding two to the total number of otolith daily rings (Takahashi, Nishida, Yatsu, & Watanabe, 2008), because the first daily ring is formed 2–3 days after hatching in Japanese sardine (Hayashi, Yamashita, Kawaguchi, & Ishii, 1989). At every 10 or 15 daily rings, a ring was tracked as far as possible from the axis and used as the boundary of the micromilling area. Date ranges corresponding to each milling area were back calculated from the capture
date by subtracting the number of daily increments from the edge of the otolith. Marked pictures were input to the high-precision micromilling system GEOMILL 326 that comprises a micromill, a CMOS camera, a video monitor, and an image analyser controlled by a computer. This system allows accurate sampling at 1/1,000 mm scales (Sakai, 2009), and it has been used to accurately extract the edge of sardine otoliths (Oda, Tetsu, Sakai, & Ishimura, 2016; Sakamoto et al., 2017). Each area between marked daily rings was then sequentially extracted, and the resulting powders (0.3–11.4 μg) were collected into stainless microcups (YUKO-PARTS). After each milling, the otolith was cleaned with an air-duster to avoid cross-contamination between milling paths. The micromilling depth was set at 50 μm for the two areas nearest the core and 50–120 μm for the remaining areas.

Otolith δ¹⁸O was measured using a continuous-flow isotope ratio mass spectrometry system (MICAL3c with IsoPrime 100) at the National Institute of Technology, Ibaraki College. This system allows analysis of δ¹⁸O from sub-microgram carbonate samples (>0.2 μg) with high precision and accuracy (Ishimura, Tsunogai, & Gamo, 2004; Ishimura et al., 2008; Kitagawa et al., 2013; Nishida & Ishimura, 2017; Oda et al., 2016; Sakamoto et al., 2017). Otolith powders reacted with phosphoric acid at 25°C, and the released CO₂ was purified and then introduced into the mass spectrometer. The δ¹⁸O values were reported in δ notation relative to the VPDB (Vienna Pee Dee Belemnite) scale, and given as a ‰ value. Analytical precision was better than ±0.10‰ throughout the entire analysis. The acid fractionation factor of calcite was used to facilitate comparisons with isotopic values reported in previous studies (Amano, Shiao, Ishimura, Yokouchi, & Shirai, 2015). Although we could not find errors in the purifying and analysing processes, a sharp increase was observed in the δ¹⁸O profile (* marked in Figure 1); this value was excluded from the modelling analysis and considered as a failure of isotope analysis because we could not find any migration route that reproduced such a fluctuation.

2.3 Estimation of migration history

We applied an individual-based model (IBM) with a random-swimming scheme to an ocean environment reproduced by the data-assimilated ocean model FRA-ROMS. FRA-ROMS is an ocean forecast and reanalysing system developed to realistically simulate mesoscale variations over the Kuroshio–Oyashio region (Kuroda et al., 2016). A random swimming scheme was chosen to find many, ideally all, possible routes that the fish can take to reach capture location, simply based on the distance that can be covered by advection and swimming. It would be interesting to add assumptions, such as the fish preference to head the direction where they can yield higher growth rate, to further narrow route prediction. However, we avoided introducing such an assumption because the mechanism by which fish decide their heading direction is currently unknown and we wished to free our model from assumptions that are not empirically confirmed. For each of the six individual fish analysed, approximately 10⁵ simulated individuals were released on the hatching date in the survey-based spawning grounds, and advected and diffused by a surface current field reproduced using FRA-ROMS. Individuals were set to swim at a speed of 3*SL/s after metamorphosis, randomly changing their swimming direction once a day. Otolith δ¹⁸O histories were calculated for the individuals that reached the capture point, based on ambient temperature and salinity histories. The possibility of each migration route was calculated as a product of egg abundance in the grid of origin and agreement between calculated otolith δ¹⁸O history and analysed profiles. Possibility-weighted mean position and temperature and water current velocity were calculated daily and considered representatives of estimated routes.

2.3.1 FRA-ROMS configuration

The FRA-ROMS ocean forecast system was developed by the Japan Fisheries Research and Education Agency (FRA), and combines an ocean circulation model based on the Regional Ocean Modeling System (ROMS) with three-dimensional variational (3D-Var) analysis schemes. It is primarily composed of 1/2- and 1/10-degree models connected by one-way nesting, in which volume transport across the lateral boundaries is adjusted. The former parent model covers almost the entire North Pacific and has been designed to simulate basin-scale variations associated with El Nino-Southern Oscillation and the Pacific Decadal Oscillation. These are imposed as external forcing at the lateral boundaries of the child model, whose domain is limited to the western North Pacific to simulate mesoscale variations over the Kuroshio–Oyashio region. The vertical structure of this system comprises 48 layers defined by the specific S-coordinate function in both models. Model specifications and a detailed methodology of numerical simulation can be found in Kuroda et al. (2013, 2016). In situ temperature-salinity profiles and satellite sea surface height and temperature are assimilated into the models by the 3D-Var method using a weekly time window.

Comparison with several oceanographic datasets indicates that FRA-ROMS is able to reproduce representative features of mesoscale variations such as the position of the Kuroshio path and the variability in the Kuroshio Extension (Kuroda et al., 2016), which might have crucial effects on the migration route of Japanese sardine. It should be emphasized that position errors are acceptable between ocean drifters and particles passively transported by currents estimated by FRA-ROMS (Kuroda et al., 2016). The accuracy of reanalysed daily sea surface temperature (SST) was evaluated by comparing it with a daily gridded SST dataset (AVHRR_OI) with a horizontal resolution of 0.25° (National Climatic Data Center, 2007) for the Kuroshio–Oyashio transition area, and the root-mean-square differences (RMSDs) estimated at monthly intervals were in the range 0.63–1.10 (Kuroda et al., 2016), corresponding to 0.11‰–0.20‰ in otolith δ¹⁸O. The accuracy of reanalysed salinity was evaluated by comparing it with a monthly mean dataset of global oceanic salinity derived from Argo float observations with a horizontal resolution of 2.5° × 5° (Hosoda, Ohira, & Nakamura, 2008), for the area from 30°N to 50°N and 130°E to 180°E. The RMSDs estimated for monthly means from 2010 to 2014 at 10 m depth were below 0.20, corresponding to 0.12‰ in seawater δ¹⁸O (Eq. 1, see Results) in areas
where the Japanese sardine is distributed (Supporting Information Figure S1).

2.3.2 IBM simulation design and route selection

The survey-based monthly egg abundance data (Oozeki, Takasuka, Kubota, & Barange, 2007), 1/4° grid scale for individuals from 2010 and 1/2° for individuals from 2014, were used to set the starting points of particle tracking. In the grid cells in which egg abundance was positive in the month that targeted individuals hatched, 120 × 120 particles were laid at regular intervals on the hatch date. The number of egg-positive grid cells in the southern coast of Japan was 37 and 33 for 2010 and 2014, respectively. The horizontal movement of particles was regulated with advection, diffusion, and active swimming terms using the Euler scheme:

\[
(x_{n+1}, y_{n+1}) = (x_n, y_n) + (u_n, v_n) \Delta t + \left( x'_n, y'_n \right) + \left( \text{mig}_x^n, \text{mig}_y^n \right) \Delta t,
\]

where \((x_n, y_n)\) is the position of a particle at time step \(n\), \((u_n, v_n)\) is the surface current velocity at \((x_n, y_n)\) interpolated linearly from the surface velocity reanalysed by FRA-ROMS, and \((x'_n, y'_n)\) is the random walk steps representing horizontal diffusion parameterized by the scheme of Smagorinsky (1963). The term \(\text{mig}_x^n, \text{mig}_y^n\) corresponds to the active swimming velocity at time step \(n\), which was updated daily as

\[
\left( \text{mig}_x^n, \text{mig}_y^n \right) = C \times \text{BSL} \times \cos(2\pi \theta) \times \sin(2\pi \theta)
\]

where \(C\) is a constant coefficient to estimate cruising speed from body length, \(\text{BSL}\) is a back calculated SL on that day, and \(\theta\) is a random number between 0 and 1. Back calculated SL was based on the linear relationship between SL and otolith radius using a biological intercept method (Campana, 1990; Takahashi et al., 2008). Particles were tracked until the capture day and their position, ambient temperature, and salinity were output daily. This trial was repeated 2,000 times with different random number sequences. Hara (1987) reported that the cruising speed of the adult Japanese sardine is 1.2–4.1 body length/s. Although low swimming ability of sardine larvae would be negligible (Silva, Faria, Teodósio, & Garrido, 2014), we assumed that metamorphosed juveniles, compared to adults, swim equally or slightly faster in proportion to their body size because smaller sized fish have generally higher tail beat frequency (e.g., Bainbridge, 1958; Hunter & Zweifel, 1971). Therefore, \(C\) was set to 0 when BSL is under 30 mm, and changed to 3 when BSL exceeded 30 mm. Additional experiments were conducted with \(C\) for BSL > 30 mm equal to 2 or 4, aiming to test the sensitivity of the results to the value of \(C\), using 1,000 replicates. As the scheme is essentially a random walk, the scale of dispersal is larger for smaller frequencies of direction changes. To check the sensitivity of the results to the frequency of direction change, further experiments with \(C\) equal to 3 were conducted with frequency equal to 2 and 0.5 times/day, using 1,000 replicates.

The possibility of each route was calculated as follows. First, the particles with horizontal position out of the ±0.5° range from the captured location on the capture date were regarded as unrelated and excluded from further analysis. For particles that reached the capture location, egg abundance at the grid of origin was set as the initial weight. Calculation of the \(\delta^{18}O\) profile was conducted using averaged ambient temperature and salinity of the particle during the date corresponding to each milled otolith area. Salinity was converted into seawater \(\delta^{18}O\) using a regression between seawater \(\delta^{18}O\) and salinity in the habitat of the Japanese sardine (Equation 1, see Section 3). Otolith \(\delta^{18}O\) was then calculated by substituting seawater \(\delta^{18}O\) and temperature into the equation for the relationship among otolith \(\delta^{18}O\), temperature, and seawater \(\delta^{18}O\) recently proposed for the Japanese sardine (Sakamoto et al., 2017; \(\delta_{\text{otolith}}^{18}O = \delta_{\text{seawater}}^{18}O - 0.18T + 2.69\)). The agreement of the calculated \(\delta^{18}O\) for the required period was computed by substituting the calculated otolith \(\delta^{18}O\) value into a probability density function of normal distribution \(N(\delta^{18}O_{\text{analyzed}}, 0.18)\). The overall possibility for each route was calculated as the product of initial weight and agreement for each date range. Routes with possibilities higher than 1/100 of the highest possibility were considered possible routes. For these possible routes, possibility-weighted mean positions, ambient water temperature and water current velocity were calculated daily to discuss the details of selected routes.

3 RESULTS

3.1 Seawater \(\delta^{18}O\) and salinity

Regarding seawater \(\delta^{18}O\) in the habitat of the Japanese sardine, LeGrande and Schmidt (2006) summarized archived global seawater \(\delta^{18}O\) data and proposed a seawater \(\delta^{18}O\)-salinity relationship for the North Pacific. More regionally, Yamamoto, Tanaka, and Tsunogai (2001) and Oba and Murayama (2004) proposed a

FIGURE 1 Comparison of seawater \(\delta^{18}O\) and salinity in the habitat area of Japanese sardine. Closed squares, open circles, and closed circles represent data collected south of 36°N, between 36°N and 40°N, and north of 40°N, respectively. The solid line is the linear regression line for all plots.
relationship for the Oyashio and the Kuroshio–Oyashio system, respectively, from near shore seawater sampling, although Japanese sardine are also abundant in offshore regions. In this study, the distribution of the seawater $\delta^{18}O$ and its relation with salinity in the habitat area of the Japanese sardine were investigated with increased spatial resolution and coverage. The results are summarized in Figure 1 and S2. Surface seawater $\delta^{18}O$ had a clear spatial variation, showing higher values (> +0.3‰) in the Kuroshio region, lower values (<−0.6‰) in the Oyashio region, and medium values in the transition zone (Supporting Information Figure S2). A positive correlation was observed between seawater $\delta^{18}O$ and salinity (Figure 1). Compared to the previously proposed relationships, data obtained north of 40°N had similar values to the equations for the North Pacific (LeGrande & Schmidt, 2006) or to the near shore Kuroshio–Oyashio system (Oba & Murayama, 2004). However, data obtained south of 36°N showed higher $\delta^{18}O$, close to that of the line for the Tropical Pacific (LeGrande & Schmidt, 2006), suggesting that the previous equations for the North Pacific (LeGrande & Schmidt, 2006), the Oyashio region (Yamamoto et al., 2001), and the Kuroshio–Oyashio system (Oba & Murayama, 2004) would underestimate seawater $\delta^{18}O$ in the Kuroshio region. Linear regression analysis by the least squares method resulted in a seawater $\delta^{18}O$–salinity ($S$) relationship ($r^2 = 0.86$, $p < 0.01$) for the Japanese sardine habitat as follows:

$$\delta^{18}O_{\text{seawater}} = 0.56 \times S - 19.06$$ (1)

3.2 | Otolith $\delta^{18}O$ profiles

Figure 2 shows the otolith $\delta^{18}O$ profiles analysed for the six individuals examined. The temporal resolutions of the otolith $\delta^{18}O$ profiles were 20–30 days for the sample nearest to the core and 10–15 days for all other samples. Unfortunately, some samples nearest to the core or at the edge of the otolith could not be analysed precisely due to their small amount or handling failure. None of the profiles, except one from 2014, showed a remarkable trend, fluctuating between −1‰ and +0.2‰ throughout the fish life (Figure 2a–e). A profile from 2014 showed a decreasing trend (Figure 2f), starting higher than 0‰ and ending lower than −0.8‰, with a small increase in June to July peaking at about −0.1‰.

3.3 | Migration routes estimated using randomly swimming IBM

Figure 3 shows the high possibility routes found for each individual using random swimming in the IBM and calculated otolith $\delta^{18}O$ histories for each route. Routes that well reproduced the otolith $\delta^{18}O$ profile were crowded in a certain range, successfully showing the
area that the fish should have passed. Although starting points varied between 133 and 140°E, the overall migration patterns were consistent within a year but different between years. Individuals from 2010 (Figure 3a,c,e) were transported by the Kuroshio until ~150°E then started to migrate northeast, while those from 2014 (Figure 3b,d,f) took more offshore routes, being advected as far as ~165°E before heading north.

These routes seemed to be reasonable as, for most individuals analysed, the possibility-weighted mean routes from May to June, corresponding to 40-100 days post hatch, coincided with the area where late-larvae and juvenile sardines were caught during sampling surveys conducted in the corresponding period (Figure 4a,b). Mean temperature and water current velocity were also calculated to examine key timings and features of the migration. Sardines were

**FIGURE 3** High possibility routes for each individual according to random swimming model estimation. The thicker and darker coloured routes are the routes with higher possibilities. The possibility of each route was divided by the highest possibility for each individual. Capture locations are presented as green stars. The left upper panel within each picture shows calculated otolith δ¹⁸O history for each migration route (yellow-black) and the analysed otolith δ¹⁸O (green).
Initially transported along the Kuroshio until departing to the north in late May to mid-June (Figure 4c,d). They entered the Oyashio feeding ground dominated by subarctic water (surface water temperature <15°C) from the end of June to early July (Figure 4e,f), and reached the highest latitude (47–48°N) in late August (Figure 4c,d). The substantial contribution of the northward water current for sardines reaching the feeding ground was suggested by the positive northward speed of this current in May and June (Figure 4g,h). Selected routes were similar when swimming speed was changed, but moved slightly inshore with C = 2 (Supporting Information Figure S3). Similarly, selected routes were robust to changes in the frequency of swimming direction, but shifted inshore with high frequency of these changes (Supporting Information Figure S4).

4 | DISCUSSION

Here, we reproduced the migration history of the small pelagic Japanese sardine using the combination of high-resolution otolith δ¹⁸O analysis and numerical migration simulation without any ad hoc assumptions. Accurate micromilling and microvolume isotope analysis showed the remarkable capability of providing otolith δ¹⁸O profiles in a resolution of several 10-day periods, even for small otolith species such as sardine. Although otolith δ¹⁸O profiles did not show apparent signs of migration, this analysis combined with randomly swimming IBM simulations showed clear northward migration heading for the capture point in the feeding ground, revealing the true utility of otolith δ¹⁸O profiles.

The neutral or decreasing trends of otolith δ¹⁸O profiles contradicted the hypothesis that an increasing trend would appear due to migration from the warm Kuroshio to the cold Oyashio water, and the negative correlation between otolith δ¹⁸O and temperature. In fact, the signals resulting from decreasing temperature seem to be less important than those resulting from the variation in seawater δ¹⁸O, which is approximately 0.8‰ lower in the Oyashio than in the Kuroshio region (Figure 1). Under such strong compensation by seawater δ¹⁸O, it is difficult to estimate temperature history and migration route from otolith δ¹⁸O profiles alone, and salinity data are also required for a comprehensive analysis.

As such, we employed a simple individual-based migration model to find possible migration routes between the spawning ground and the capture location, which showed the capability of providing detailed movements. Route selection in this estimation can be explained by several processes. Otolith δ¹⁸O variations can directly reflect the corresponding latitudinal movements, because temperature and salinity are generally uniform along zonal directions but differ meridionally in open oceans. On the contrary, longitudinal positions cannot be estimated from otolith δ¹⁸O and horizontal distributions of temperature and salinity. However, for the Japanese sardine spawning around the Kuroshio, the time at which the northward movement is initiated controls the period of larvae advection by the Kuroshio, thereby determining the transported distance. Furthermore, when fish have low swimming ability but need to move north, they require strong northward cross-jet currents. In the Kuroshio Extension (KE), a cross-frontal northward current is frequently observed between the trough and the crest of the meander (Sainz-Trápaga & Sugimoto, 2000), as is the case of the Gulf Stream (Bower & Rossby, 1989). Warm streamers are also spread intermittently from the KE (Sainz-Trápaga & Sugimoto, 2000) and quasi-stationary jets extend northward in the transitional area between the KE and the Oyashio fronts (Isoguchi, Kawamura, & Oka, 2006), probably providing conditions for longitudinal selection. Although these processes seem unique for the KE, similar processes may occur in other regions as many fish larvae depend on regional flows, such as the coastal jets in the Benguela Current (Hutchings et al., 2002) or the eddies in the California Current (Logerwell, Laviniegos, & Smith, 2001), to effectively reach food-rich feeding grounds.

The method used here revealed new aspects of feeding migration of the Japanese sardine. Our estimations suggested that it is from the middle to end of May that sardines start to move northward departing from KE, and it is from the end of June to early July that they enter the Oyashio feeding ground north of 42°N. Although the spawning grounds and transportation during the larval stage have been well documented through a number of surveys (e.g., Kuroda, 1991), these key timings in the feeding migration are the first to be clarified because this type of information can only be obtained by continuously tracking fish movement. The estimation provided here also showed that sardines utilise the northward current during their northward migration, supporting the hypothesis of Isoguchi et al. (2006), who pointed out that warm tongues and meanders from KE might be the direct routes for the northward migration of pelagic fishes based on their analyses of surface flow field. Considering all individuals analysed in this study are the survivors that reached the feeding ground, riding the northward current near KE might be an important condition for the sardine to recruit and thus the strength of such currents can significantly affect the recruitment rate. Between the 2 years analysed, the selected routes in 2014 were more offshore than those in 2010. This shift may be related to the seven-times larger population size in 2014 (Yukami et al., 2017), as sardines tend to expand their habitat area offshore when biomass is increased (Barange et al., 2009). All these detailed descriptions of migration patterns would be useful for narrowing down the season and areas that are important for recruitment variability, studying how fish decide their swimming direction, and testing and improving migration models, which will be the scopes of future studies.

It should be noted that the accuracy of route estimation using such processes largely relies on the reproducibility of the ocean model. The model we used was developed to realistically simulate the environment by assimilating numerous satellite and in situ observation data, although the number of observations is still limited, especially for salinity, as this is not measured by satellites. Further accurate estimation requires both expansion of the monitoring network and improvement of simulation models. It is also noteworthy that model schemes require some assumptions on the swimming depth. Because age-0 Japanese sardine vertically migrate mainly within the surface mixed layer (e.g., Takahashi et al., 2008), we
FIGURE 4  Possibility-weighted mean data obtained from the individual-based migration model. (a, b) Possibility-weighted means and SD obtained for individual positions and their comparison to the results of the sampling surveys conducted in (a) 26 May–20 June, 2010 and (b) 24th May–18th June, 2014. Points at which larvae or juvenile sardines were captured are indicated by blue circles. Mean estimated positions in the date range corresponding to the survey period are shown as thick lines. (c-h) Time series of and likelihood-weighted means and SD of (c), (d) latitude, (e), (f) temperature and (g), (h) northward water current speed. The same colour in the same year indicates the same individual.
assumed they experience an environment similar to that on the water surface. When applying this methodology to species distributed in wider depth range, some adjustments, such as averaging the temperature and salinity within the water column, or introducing vertical migrations into IBM, may be needed. In addition, due to spatially and temporally dense observations of Japanese sardine spawning, these data were used as starting points for IBM estimation, but this is not always the case. In the absence of such survey datasets, modelled spawning grounds can be used (e.g., Zwolinski, Emmett, & Demer, 2011).

Overall, the method presented here would be a great alternative to electronic tags understanding movements of fish during early life history or for fish that are otherwise too small to accommodate electronic tags. It would also be useful not only to reveal population structure but also to validate and improve movement models that have been lacking detailed reference data to discuss their accuracy. Moreover, this method has the unique and strong advantage of examining the environmental history of successfully recruited individuals. This is crucial information to understand the environmental conditions necessary for fish to survive, providing clues on how environmental variabilities are driving fish population fluctuations. Because otolith $\delta^{18}O$ is generally recognized as temperature dependent (Heie, Otterlei, & Folkvord, 2004; Kim et al., 2007; Kitagawa et al., 2013; Sakamoto et al., 2017; Storm- Suke, Dempson, Reist, & Power, 2007), the method presented here will notably improve the knowledge on the survival and migration ecology of early life stages of numerous fish species.

**ACKNOWLEDGEMENTS**

The authors gratefully acknowledge the support from Grant-in-Aid for JSPS Fellows 17J00556, JSPS KAKENHI grants number JP15H04541, 16H02944, and 18H04921, and from grants for marine fisheries stock assessment and evaluation for Japanese waters from the Fisheries Agency and Fisheries Research and Education Agency of Japan. We thank S. Itoh for technical advices on numerical simulation and insightful comments to improve the manuscript. We thank Mr. Zhang who provided the seawater $\delta^{18}O$ data in 2012 and 2013. There are no conflicts of interest to declare.

**AUTHORS’ CONTRIBUTIONS**

T.S. and K.K. designed and conceived the study. T.S., T.H., and T.I. performed isotope analyses. T.S. and K.K. wrote the program and performed the numerical simulations. T.Setou provided ocean model data and validated its accuracy. Y.K., C.W., and A.K. provided fish samples. All authors contributed to manuscript editing. T.S., K.K., and K.S. wrote the manuscript.

**DATA ACCESSIBILITY**

Seawater and otolith $\delta^{18}O$ data: Dryad Digital Repository entry https://doi.org/10.5061/dryad.9k0v2nn (Sakamoto et al., 2018).

**REFERENCES**

Allain, G., Petitgas, P., Lazure, P., & Grellier, P. (2007). Biophysical modelling of larval drift, growth and survival for the prediction of anchovy (Engraulis encrasicholus) recruitment in the Bay of Biscay (NE Atlantic). *Fisheries Oceanography*, 16, 489–505. https://doi.org/10.1111/j.1365-2419.2007.00443.x

Amano, Y., Shia, J., Ishimura, T., Yokouchi, K., & Shirai, K. (2015). Otolith geochemical analysis for stock discrimination and migratory ecology of tunas. In T. Kitagawa & S. Kimura (Eds.), *Biological and ecology of bluefin tuna* (pp. 225–257). Boca Raton, FL: CRC Press.

Anderson, J. T. (1988). A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fishery Science*, 5, 55–66. https://doi.org/10.2960/J.v8.a6

Bainbridge, R. (1958). The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *Journal of Experimental Biology*, 35, 109–133.

Barange, M., Coetzee, J., Takasuka, A., Hill, K., Gutierrez, M., Oozeki, Y., ... Agostini, V. (2009). Habitat expansion and contraction in anchovy and sardine populations. *Progress in Oceanography*, 83, 251–260. https://doi.org/10.1016/j.pocean.2009.07.027

Block, B. A., Teo, S. L., Walli, A., Boustany, A., Stokesbury, M. J., Farwell, C. J., ... Williams, T. D. (2005). Electronic tagging and population structure of Atlantic Bluefin tuna. *Nature*, 434, 1121. https://doi.org/10.1038/nature03463

Bower, A., & Rossby, T. (1989). Evidence of cross-frontal exchange processes in the Gulf stream based on isopycnal RAFOs float data. *Journal of Physical Oceanography*, 19, 1177–1190. https://doi.org/10.1175/1520-0485(1989)019<1177:EOCFEP>2.0.CO;2

Brennan, S. R., Zimmerman, C. E., Fernandez, D. P., Cerling, T. E., McPhee, M. V., & Wooler, M. J. (2015). Strontium isotopes delineate fine-scale natal origins and migration histories of Pacific salmon. *Science Advances*, 1, e1400124. https://doi.org/10.1126/sciadv.1400124

Cadrin, S. X., Karr, L. A., & Mariani, S. (2014). Chapter one – Stock identification methods: An overview. In S. X. Cadrin, L. A. Kerr, & S. Mariani (Eds.), *Stock identification methods* (2nd ed., pp. 1–5). San Diego, CA: Academic Press.

Campana, S. E. (1990). How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Science*, 47, 2219–2227. https://doi.org/10.1139/f90-246

Campana, S. E. (1999). Chemistry and composition of fish otoliths: Pathways, mechanisms and applications. *Marine Ecology Progress Series*, 188, 263–297. https://doi.org/10.3354/meps188263

Carpenter, S. J., Erickson, J. M., & Holland, F. Jr (2003). Migration of a late cretaceous fish. *Nature*, 423, 70. https://doi.org/10.1038/nature01575

Craig, H., & Gordon, L. I. (1965). Deuterium and oxygen 18 variations in oceanographic studies and paleotemperatures (pp. 9–130). Spoleto, Italy: Cons. Naz. di Rech.

Crawford, R., Sabarros, P., Fairweather, T., Underhill, L., & Wolfardt, A. (2008). Implications for seabirds off South Africa of a long-term change in the distribution of sardine. *African Journal of Marine Science*, 30, 177–184. https://doi.org/10.2989/AJMS.2008.30.1.18.468

Crist, E., Mora, C., & Engelman, R. (2017). The interaction of human population, food production, and biodiversity protection. *Science*, 356, 260–264. https://doi.org/10.1126/science.aal2011

Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilsen, T., Crawford, R. J., Furness, R. W., ... Sydeman, W. J. (2011). Global seabird response to forage fish depletion—one-third for the birds. *Science*, 334, 1703–1706. https://doi.org/10.1126/science.1212928

**ORCID**

Tatsuya Sakamoto http://orcid.org/0000-0003-0672-4168

**AUTHORS’ CONTRIBUTIONS**

T.S. and K.K. designed and conceived the study. T.S., T.H., and T.I. performed isotope analyses. T.S. and K.K. wrote the program and performed the numerical simulations. T.Setou provided ocean model data and validated its accuracy. Y.K., C.W., and A.K. provided fish samples. All authors contributed to manuscript editing. T.S., K.K., and K.S. wrote the manuscript.

**ACKNOWLEDGEMENTS**

The authors gratefully acknowledge the support from Grant-in-Aid for JSPS Fellows 17J00556, JSPS KAKENHI grants number JP15H04541, 16H02944, and 18H04921, and from grants for marine fisheries stock assessment and evaluation for Japanese waters from the Fisheries Agency and Fisheries Research and Education Agency of Japan. We thank S. Itoh for technical advices on numerical simulation and insightful comments to improve the manuscript. We thank Mr. Zhang who provided the seawater $\delta^{18}O$ data in 2012 and 2013. There are no conflicts of interest to declare.
Sakai, S. (2009). Micromilling and sample recovering techniques using high-precision micromill GEOMILL326. JAMSTEC-Reports, Japan Agency for Marine–Earth Science and Technology, 10, 4–5.

Sakamoto, T., Komatsu, K., Yoneda, M., Ishimura, T., Higuchi, T., Shirai, K., ... Kawabata, A. (2017). Temperature dependence of δ18O in otolith of juvenile Japanese sardine: Laboratory rearing experiment with micro-scale analysis. Fisheries Research, 194, 55–59. https://doi.org/10.1016/j.fishres.2017.05.004

Sakamoto, T., Komatsu, K., Shirai, K., Higuchi, T., Ishimura, T., Setou, T., ... Kawabata, A. (2018). Data from: Combining micro-volume isotope analysis and numerical simulation to reproduce fish migration history. Dryad Digital Repository, https://doi.org/10.5061/dryad.9k0v2nn

Shiao, J., Yui, T., Høie, H., Ninnemann, U., & Chang, S. (2009). Otolith O and C stable isotope compositions of southern Bluefin tuna Thunnus maccocyii (Pisces: Scombridae) as possible environmental and physiological indicators. Zoological Studies, 48, 71–82.

Silva, L., Faria, A., Teodósio, M. A., & Garrido, S. (2014). Ontogeny of swimming behaviour in sardine sardina pilchardus larvae and effect of larval nutritional condition on critical speed. Marine Ecology Progress Series, 504, 287–300. https://doi.org/10.3354/meps10758

Smagorinsky, J. (1963). General circulation experiments with the primitive equations: I. the basic experiment. Monthly Weather Review, 91, 99–164. https://doi.org/10.1175/1520-0493(1963)091<0099:GCEWTP>2.3.CO;2

Storm-Suke, A., Dempson, J. B., Reist, J. D., & Power, M. (2007). A field-derived oxygen isotope fractionation equation for Salvelinus species. Rapid Communications in Mass Spectrometry, 21, 4109–4116. https://doi.org/10.1002/rcm.2301

Sturrock, A., Trueman, C., Darnaude, A., & Hunter, E. (2012). Can otolith elemental chemistry retrospectively track habitat in fully marine fishes? Journal of Fish Biology, 81, 766–795. https://doi.org/10.1111/j.1095-8649.2012.03372.x

Takahashi, M., Nishida, H., Yatsu, A., & Watanabe, Y. (2008). Year-class strength and growth rates after metamorphosis of Japanese sardine (Sardinops melanostictus) in the western north Pacific ocean during 1996–2003. Canadian Journal of Fisheries and Aquatic Science, 65, 1425–1434. https://doi.org/10.1139/F08-063

Torniainen, J., Lensu, A., Vuorinen, P. J., Sonninen, E., Keinänen, M., Jones, R. I., ... Kiljunen, M. (2017). Oxygen and carbon isoscapes for the Baltic Sea: Testing their applicability in fish migration studies. Ecology and Evolution, 7, 2255–2267. https://doi.org/10.1002/ece3.2841

Tsukamoto, K., & Nakai, I. (1998). Do all freshwater eels migrate? Nature, 396, 635. https://doi.org/10.1038/25264

Yamamoto, M., Tanaka, N., & Tsunogai, S. (2001). Okhotsk sea intermediate water formation deduced from oxygen isotope systematics. Journal of Geophysical Research: Oceans, 106, 31075–31084. https://doi.org/10.1029/2000JC000754

Yukami, R., Watanabe, C., Kamimura, Y., Furuichi, S., Akamine, T., & Kishida, T. (2017) Stock assessment and evaluation for the Pacific stock of Japanese sardine (fiscal year 2016). In Marine fisheries stock assessment and evaluation for Japanese waters (fiscal year 2016/2017) (pp. 15–52). Tokyo, Japan: Fisheries Agency and Fisheries Research and Education Agency of Japan (in Japanese).

Zwolinski, J. P., Emmett, R. L., & Demer, D. A. (2011). Predicting habitat to optimize sampling of Pacific sardine (Sardinops sagax). ICES Journal of Marine Science, 68, 867–879. https://doi.org/10.1093/icesjms/fsr038

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Sakamoto T, Komatsu K, Shirai K, et al. Combining microvolume isotope analysis and numerical simulation to reproduce fish migration history. Methods Ecol Evol. 2019;10:59–69. https://doi.org/10.1111/2041-210X.13098