



# Migratory routes of the swordtip squid *Uroteuthis edulis* inferred from statolith analysis

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**ABSTRACT:** Despite the commercial importance of swordtip squid *Uroteuthis edulis* in Tsushima Strait, which lies between southwestern Japan and South Korea, data on its hatching grounds and migratory routes are lacking. To infer this information, we first revealed a significant negative correlation between ambient water temperatures and strontium:calcium (Sr:Ca) ratios in squid statoliths through tank experiments. Next, we counted statolith microincrements in spring and summer migratory groups of the species to elucidate their hatching dates, after measuring Sr:Ca ratios from the nucleus to the edge of each statolith. Based on these methods, spring and summer groups appear to inhabit the southern East China Sea as juveniles, and move northeastward with currents along shelf edges in the Kuroshio region. However, individuals in the spring group are apparently affected by cold waters in the northern East China Sea before reaching the Tsushima Strait, likely resulting in the unique characteristics of this seasonal group. In contrast, those in the summer group are likely unaffected because of higher water temperatures in summer than in spring. This study is the first to infer the migratory routes of the spring and summer groups of the swordtip squid.

**KEY WORDS:** Swordtip squid · Migratory route · Statolith · Sr:Ca ratio · Tsushima Strait · East China Sea · Kuroshio

## INTRODUCTION

The swordtip squid *Uroteuthis edulis* is relatively abundant in the western Pacific. Its range extends from northern (southern Sea of Japan and the East China Sea) to tropical regions (the Java Sea and coastal waters of Indonesia, Malaysia, and Thailand), and as far south as the waters off northern Australia (Jereb & Roper 2010). Approximately 10 000 tons are harvested each year during the spring, summer, and autumn from the southern Sea of Japan and the Tsushima Strait (Yoda & Fukuwaka 2015), as well as from the Pacific side of the Japanese archipelago (Sukramongkol et al. 2006). Around Tsushima Strait, 3 seasonal groups of the species are known, with individuals in each group differing in body shape and size at maturity (Okutani 2005). For example, the

spring group appears to arrive for the purpose of spawning. In this group, fin length in adults reaches up to 70 % of the mantle length, a body form referred to as 'kensaki,' whereas adult fin length in the other groups is typically ≤50 % of the mantle length. Individuals in the summer group are typical *U. edulis*, which are distributed throughout the South China Sea and other tropical waters. In contrast, the autumn group is characterized by thick bodies with large clubs, long arms, and large suckers (Jereb & Roper 2010). However, the reasons underlying these differences among seasonal groups are not understood. Furthermore, neither the species' hatching grounds nor its migratory routes to the fishing grounds have been identified.

Certain physiological characteristics of *U. edulis* may be exploited to gain greater insight into its life

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cycle. For example, the species' age and growth have been analyzed based on microincrements in statoliths, allowing the date of hatching to be estimated (Natsukari et al. 1988). In addition, the ratios of strontium to calcium (Sr:Ca) in calcified tissues of marine organisms (corals, fishes, and squids) are strongly correlated with ambient water temperature (Smith et al. 1979, Gaudie et al. 1986, Arkhipkin et al. 2004). Ontogenetic variation in the Sr:Ca ratios of statoliths was measured in 9 individuals of *Ommastrephes bartramii* (Yatsu et al. 1998), and characteristic patterns of Sr:Ca ratios in *Todarodes pacificus* statoliths suggested that statoliths could be used to monitor migratory behavior (Ikeda et al. 2003). In the present study, we reveal factors underlying the variation of Sr:Ca ratios in *U. edulis* statoliths, and infer migratory routes of the spring and summer groups in Tsushima Strait using statolith microincrement counts and variation in Sr:Ca ratios.

## MATERIALS AND METHODS

### Tank experiments

To examine the effects of water temperature and ambient seawater salinity on statolith Sr:Ca ratios, we captured *Uroteuthis edulis* (mean  $\pm$  SD mantle length  $147 \pm 16.0$  mm) with a fixed net off the shore of western Japan facing Tsushima Strait in April and May 2014. All were exposed to 5 ppm alizarin complexone (ALC), buffered to rearing pH with NaOH, for 24 h at the start of each experiment. Rearing seawater with controlled temperature or salinity was supplied at an exchange rate of 50% of the tank volume per day. Individuals were kept in the indoor tank until their deaths.

**Expt 1.** Two experimental groups, both consisting of 3 individuals, were maintained at water temperatures of 16.7–17.7°C and 19.9–20.1°C, with the salinity left uncontrolled.

**Expt 2.** Two groups, consisting of 3 and 5 individuals, were maintained at salinities of 29.6–30.3‰ and 34.2–34.7‰, respectively, and left at room temperature.

### Squid collection in the field

To investigate migratory routes, we collected 15 and 16 *U. edulis* from Tsushima Strait by jigging on June 12 and August 10, 2012, with the typical characteristics of spring and summer groups, respectively

(Fig. 1; Table S1 in the Supplement at [www.int-res.com/articles/suppl/b024p053\\_supp.pdf](http://www.int-res.com/articles/suppl/b024p053_supp.pdf)). These individuals were of the most valuable commercial size for the respective seasons. In addition, 33 individuals were sampled along a shelf edge in the East China Sea using bottom-trawl surveys between May 26 and June 17, 2012 (Fig. 1; Table S2 in the Supplement), and 15 were caught with a fixed net in Sagami Bay, which is open to the northwestern Pacific, on May 23, 2014 (Fig. 1; Table S1). Mantle length (mm), body weight (g), and gonad weight (g) were recorded. Specimens were considered mature when spermatophores in the Needham sac of males or ovulated mature eggs in the oviducts of females were present.

### Statolith preparation

Statoliths were extracted after the experiments for measurement and observation. Each statolith was cleaned, dried, and mounted on a glass slide in a cylindrical silicone stub filled with acrylic resin (Shofu Ortho Palette) with the anterior side down. After hardening, the polyester block was ground from the anterior side with fine-grade carbide (240, 2000, 3000, and 4000 grade) waterproof sandpaper until the nucleus was exposed. Ground statoliths were polished with 3  $\mu$ m diamond paste before Sr and Ca measurements.

After the measurements of Sr and Ca, the dorsal and lateral domes of mounted statoliths, which faced the bottom of the polyester block, were ground until the nucleus was clearly visible in order to count the microincrements.

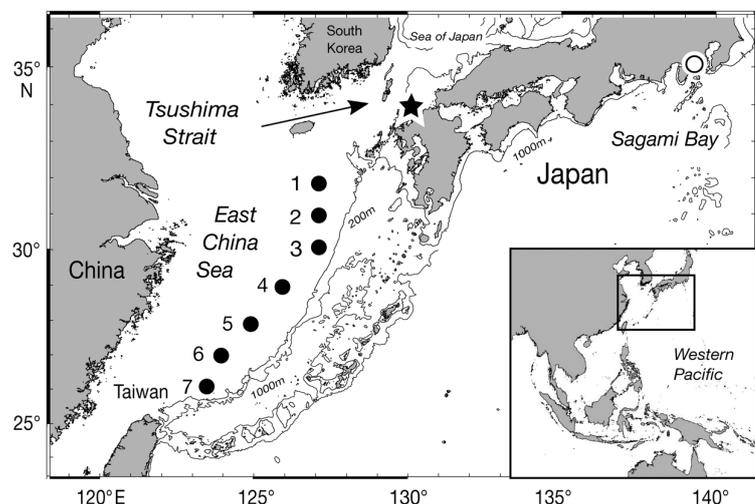


Fig. 1. *Uroteuthis edulis* sampling sites in Tsushima Strait (★), East China Sea (1–7, ●), and Sagami Bay (○)

### Sr and Ca measurements

We used a wavelength-dispersive spectrometer (JXA-8900RLS, JEOL Ltd.) for electron probe microanalysis (EPMA). The variation in Sr:Ca ratios on each statolith was assessed using line analysis, which measures a string of trace elemental peaks along a line of continuous beam spots. After each statolith was coated with carbon, each statolith measurement from the tank experiments was made across the ALC mark to the edge of the rostrum (Figs. 2 & 3). The measurement conditions were: measurement interval of 2  $\mu\text{m}$ , 1  $\mu\text{m}$  diameter focused beam, acceleration voltage of 10 kV, beam current of 100 nA, and a counting time of 20 s. Sr:Ca ratios in the statoliths from the field were measured from the nucleus to the lateral dome edge, with a measurement interval of 5  $\mu\text{m}$  and a 5  $\mu\text{m}$  diameter focused beam. The remaining measurement conditions were the same as those described above.  $\text{CaSiO}_3$  and  $\text{SrTiO}_3$  were used as standards for Ca and Sr. The results summarized in the figures are shown as running 10-point means of the Sr:Ca ratios.

### Microincrement counts

We counted the number of microincrements on each statolith using light microscopy from the nucleus to the edge of the lateral dome. Microincrements were

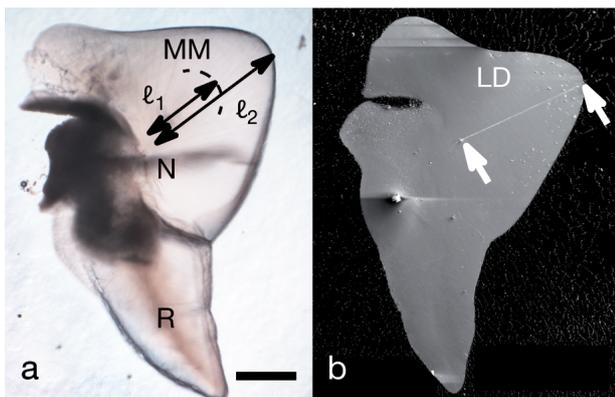


Fig. 2. *Uroteuthis edulis*. (a) Light micrograph of a polished statolith before carbon coating. N: nucleus, R: rostrum, MM: median microincrement (broken line),  $l_1$ : length between N and MM (short arrow),  $l_2$ : length between N and the edge of the statolith (long arrow), RMM (not shown; see 'Materials and methods') =  $l_1/l_2$ , scale bar: 200  $\mu\text{m}$ . (b) Scanning electron micrograph of a statolith analyzed using a wavelength-dispersive spectrometer (electron probe microanalysis, EPMA). Sr and Ca were measured between the white arrows. LD: lateral dome

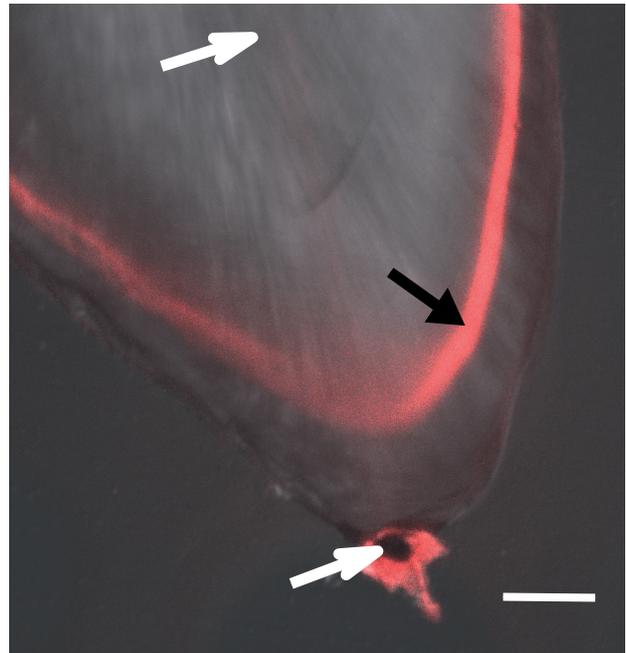


Fig. 3. Fluorescence micrograph of the rostrum of a statolith from a *Uroteuthis edulis* specimen used in the tank experiments. Sr and Ca were measured between the white arrows across the alizarin complexone (ALC) mark (black arrow) using line analysis by electron probe microanalysis (EPMA); scale bar: 20  $\mu\text{m}$

counted 3 times for each specimen. If the ratio of the difference between the maximum and minimum to the maximum of the 3 counts was  $\leq 10\%$ , we used the median. Otherwise, data from that statolith were excluded.

The ratio of the length between the nucleus and the median microincrement to the length between the nucleus and the edge of the statolith (RMM; see Fig. 2a) was calculated along the path of the Sr and Ca measurements. By multiplying the number of measurement points by RMM, we estimated the Sr:Ca ratio, which corresponded to the median day of the life of the squid.

## RESULTS

### Factors in Sr:Ca ratio variation

Based on the tank experiment results, the mean ( $\pm$ SD) differences between the average of the last 4 Sr:Ca ratios on the inside of the ALC mark and that of the last 4 ratios on the edge of the statoliths from the specimens at water temperatures of 19.9–20.1°C and 16.7–17.7°C were  $9.9 \times 10^{-4} \pm 6.5 \times 10^{-5}$  and  $2.1 \times$

$10^{-4} \pm 2.0 \times 10^{-4}$ , respectively ( $p < 0.05$ ) (Fig. 4a). Moreover,  $\sim 2.8^\circ\text{C}$  higher water temperatures, the difference between water temperatures in our experiment, corresponded to  $7.8 \times 10^{-4} \pm 2.1 \times 10^{-4}$  lower Sr:Ca ratios, as all squid in Expt 1 were caught in the same net on the same day, meaning they lived at virtually the same seawater temperature for at least their last few days. On the other hand, Expt 2 showed that the Sr:Ca ratios on the outside of the ALC mark gradually decreased for all specimens, but the mean ( $\pm$ SD) differences in Sr:Ca ratios at salinities of 29‰ and 34‰ were  $6.3 \times 10^{-4} \pm 2.7 \times 10^{-4}$  and  $6.7 \times 10^{-4} \pm 2.7 \times 10^{-4}$ , respectively ( $p = 0.86$ ), i.e. the differences in salinity had no significant effects on the ratios. In fact, the gradual decrease seemed to depend on rising water temperature (room temperature) (Fig. 4b). Thus, both results suggest that higher water temperatures yield lower Sr:Ca ratios. This supports a previous report that variation in Sr:Ca ratios in the statoliths of the Patagonian longfin squid *Loligo gahi* among geographic locations showed a generally negative correlation between Sr:Ca ratio and temperature (Arkhipkin et al. 2004). However, we found that Sr:Ca ratios were not necessarily the same even when specimens

were kept in the same tank (that is, at the same water temperature). This means that individual differences in statolith Sr:Ca ratio are so large that it is difficult to use them to accurately estimate the ambient water temperature.

### Age determination

The average ages of *Uroteuthis edulis* captured in Tsushima Strait on June 12 and August 10, 2012 were  $231 \pm 17$  d ( $n = 12$ ) and  $218 \pm 20$  d ( $n = 12$ ), respectively, with estimated hatching in October to November 2011 and December 2011 to January 2012, respectively. The average age of the specimens caught along the shelf edge in the East China Sea between May 26 and June 17, 2012 was  $202 \pm 31$  d ( $n = 28$ ), with estimated hatching in November 2011 to February 2012. The average age of specimens collected from Sagami Bay on May 23, 2014 was  $171 \pm 15$  d ( $n = 10$ ), with estimated hatching around December 2013. Thus, most sampled squid hatched between the previous autumn and early spring of the year in which they were caught (Fig. 5).

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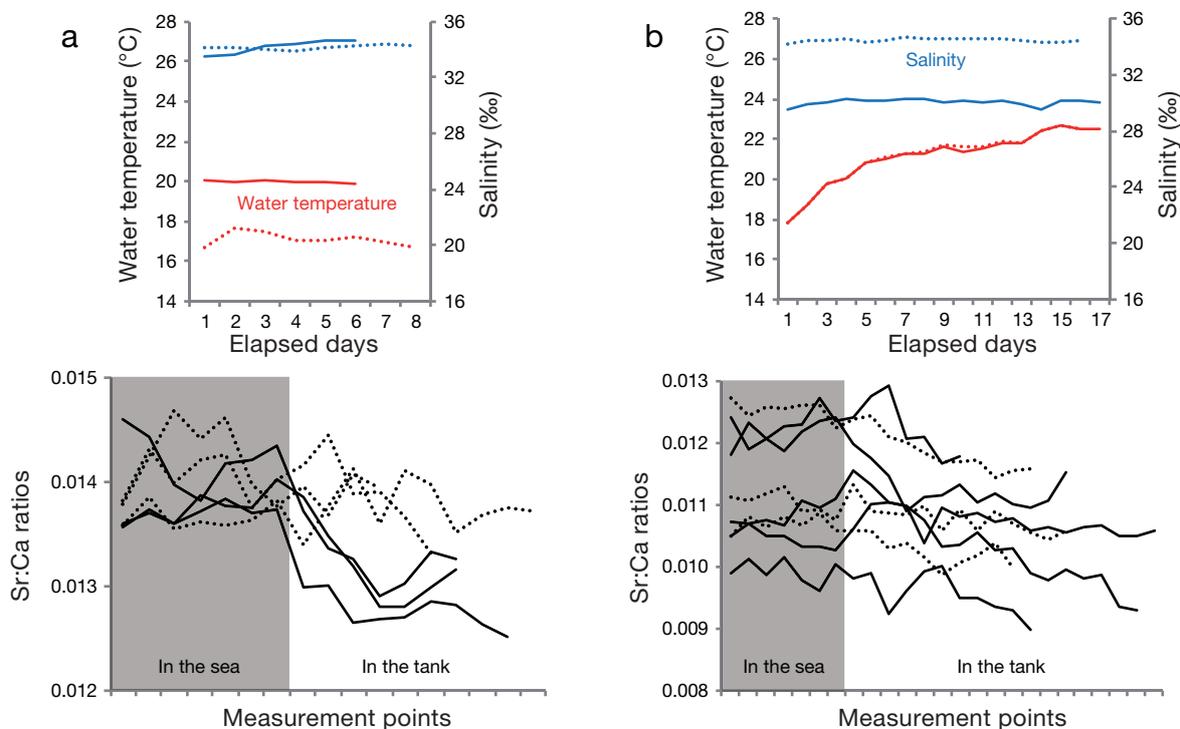


Fig. 4. Variation in the Sr:Ca ratios in statoliths of *Uroteuthis edulis* treated with alizarin complexone (ALC) at the start of the tank experiments, (a) under controlled water temperatures (16.7–17.7°C and 19.9–20.1°C) and original salinity, and (b) under uncontrolled water temperature (room temperature) and regulated salinity (29.6–30.3‰ and 34.2–34.7‰). Sr and Ca were measured in the rostrum of each statolith at intervals of 2  $\mu\text{m}$ . Measurement points in the bottom graphs show 7 consecutive points on the inside of the ALC mark and all points of outside of the mark on a line. Red and blue lines represent water temperature and salinity, respectively, and solid and dotted lines show different conditions and specimens in 2 tanks in each experiment

The means ( $\pm$ SD) of the RMMs of the statoliths from Tsushima Strait in June and August and Sagami Bay were  $0.53 \pm 0.083$ ,  $0.55 \pm 0.028$ , and  $0.52 \pm 0.050$ , respectively. Microincrements in the lateral dome were nearly evenly spaced, though the distance between them narrowed slightly near the edge.

### Ontogenetic variation in statolith Sr:Ca ratios

Fig. 6 shows the results of Sr and Ca measurements, i.e. 10-point running means of Sr:Ca ratios in the statoliths of specimens from Tsushima Strait in June and August, from the East China Sea, and from Sagami Bay. To eliminate individual differences in ontogenetic variation in Sr:Ca ratios in Fig. 6a,b,d, the lines in each graph were vertically translated so that the final Sr:Ca ratios could be adjusted to the average of the original Sr:Ca ratios, because each specimen from Tsushima Strait in June and August and Sagami Bay was caught under almost identical conditions. Next, we averaged the translated 10-point running means of the Sr:Ca ratios (Fig. 7). Based on these figures, variations from the nucleus to the edge of the statolith can be classified into 2 patterns: a decline-reversal pattern in specimens from Tsushima Strait in June and from Sagami Bay in May, and a pattern of small change in those from Tsushima Strait in August. The former appeared to decrease in the first part of the ontogenetic ratios and increase again later, while the latter was generally flat or downward trending. Of 33 lines in the specimens from the East China Sea (Fig. 6c), 13 displayed the decline-reversal pattern and 20 the small-change pattern (Fig. 8). Specimens with the decline-reversal pattern were caught only above 29°N latitude in the East China

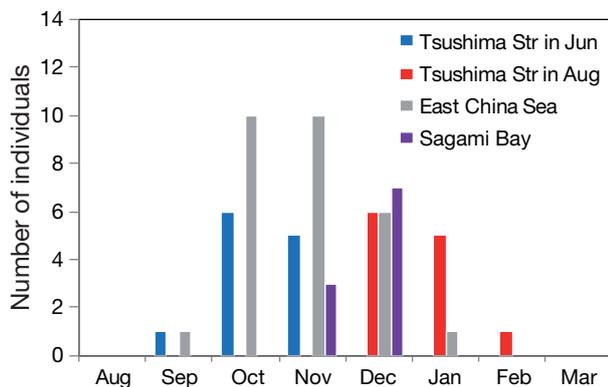


Fig. 5. Monthly hatching number of *Uroteuthis edulis* caught each month, from left to right, in Tsushima Strait in June and August ( $n = 12$  each), East China Sea ( $n = 28$ ), and Sagami Bay ( $n = 10$ )

Sea, whereas those with the small-change pattern were found at all sampling sites (Fig. 9).

## DISCUSSION

*Uroteuthis edulis* from the Tsushima Strait in June likely experienced about 1.8°C warmer water in February than in June. This is because the Sr:Ca ratios in the microincrements formed in February were about  $5.1 \times 10^{-4}$  lower than those from June (Fig. 7a), and, based on the tank experiments, a  $5.1 \times 10^{-4}$  increase in the ratio corresponds to a ~1.8°C decrease in temperature. Our monthly marine observations showed that water temperatures in the eastern part of the Tsushima Strait (33–43°N and 129–27°E) on June 4, 2012 were 18.5°C at 50 m in depth (17.1–20.6°C over a depth range of 0–96 m; details not shown), virtually identical marine conditions as when the squid were captured (Table S1 in the Supplement). Thus, the squid would experience water temperatures of 20–22°C in February. To this end, Fig. S1a (in the Supplement), which represents water temperatures at depths <100 m in the East China Sea and Tsushima Strait in winter due to vertical mixing (Furey & Bower 2005), shows that such warm water occurred only around the Kuroshio, which is the western boundary current of the North Pacific subtropical gyre (Isobe & Imawaki 2002). Therefore, *U. edulis* found in the strait in June would move northward via the Kuroshio region, as would the 13 specimens collected in the northern East China Sea, which showed the same decline-reversal pattern in ontogenetic variation in Sr:Ca ratios (Figs. 8a & 9). Additionally, this same decline-reversal pattern shows that the October and November hatching ground was probably located not in the Kuroshio region but in the southern East China Sea, as the juvenile squid would have inhabited waters whose temperatures were almost the same as when they were captured in the Tsushima Strait in June; i.e. ~18–19°C. Fig. S2 (in the Supplement) shows that appropriate waters were located in the southern part of the East China Sea, supported by reports that a spawning ground was located northeast of Taiwan in spring (March–April) and autumn (October–November) (Wang et al. 2008, 2010). Thus, we can hypothesize that some juvenile *U. edulis* that hatched in the southern East China Sea would be transported by currents either along or east of sampling sites 5, 6, and 7 (Fig. S3 in the Supplement), as the Taiwan Warm Current, which mainly consists of throughflow in the Taiwan Strait and the Kuroshio intrusion

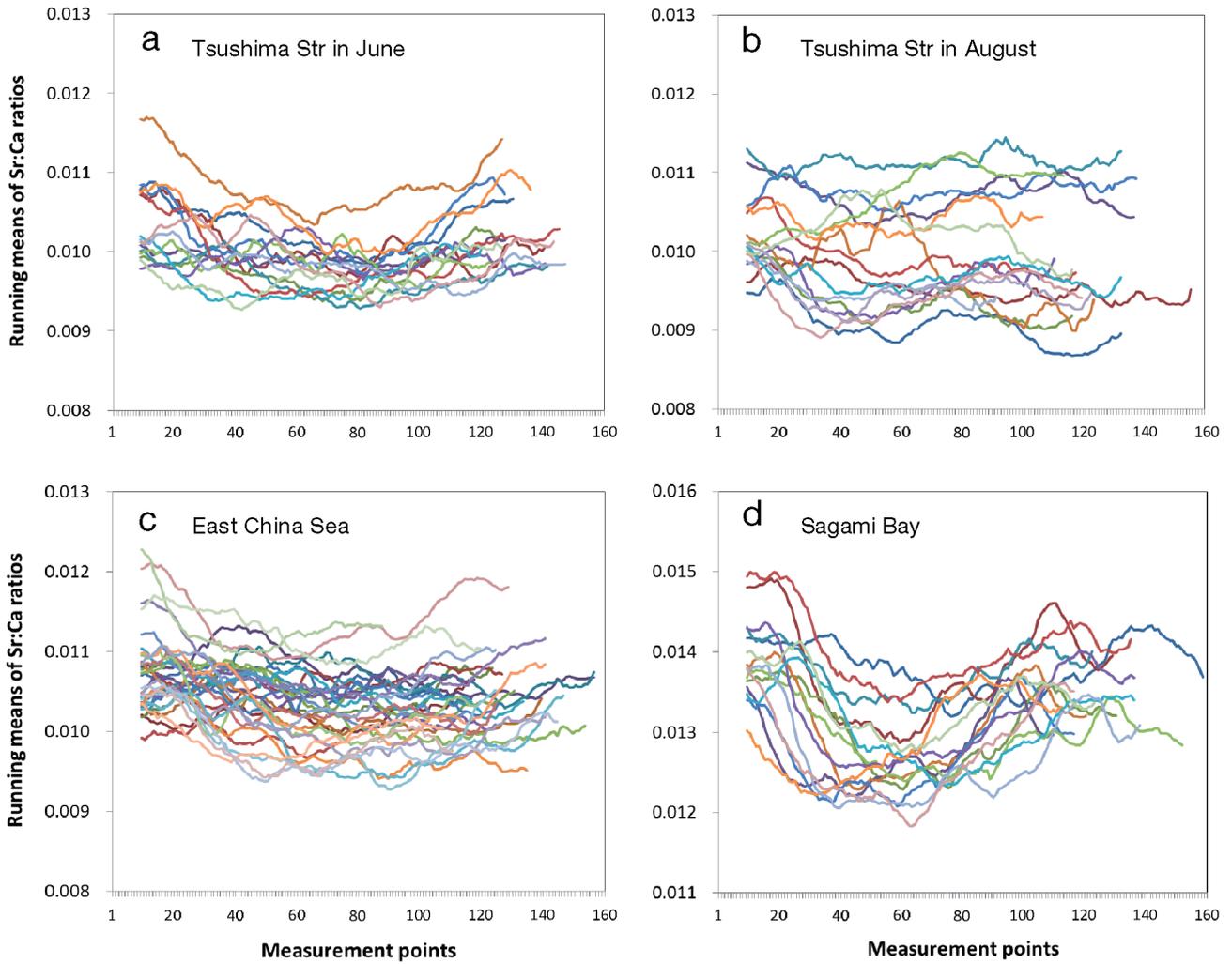


Fig. 6. Ten-measurement-point running means of ontogenetic variation in the Sr:Ca ratios of *Uroteuthis edulis* statoliths from (a) 15 specimens from Tsushima Strait in June, (b) 16 from Tsushima Strait in August, (c) 33 from the East China Sea, and (d) 15 from Sagami Bay. Sr and Ca were measured from the nucleus to the lateral dome edge at intervals of 5  $\mu\text{m}$

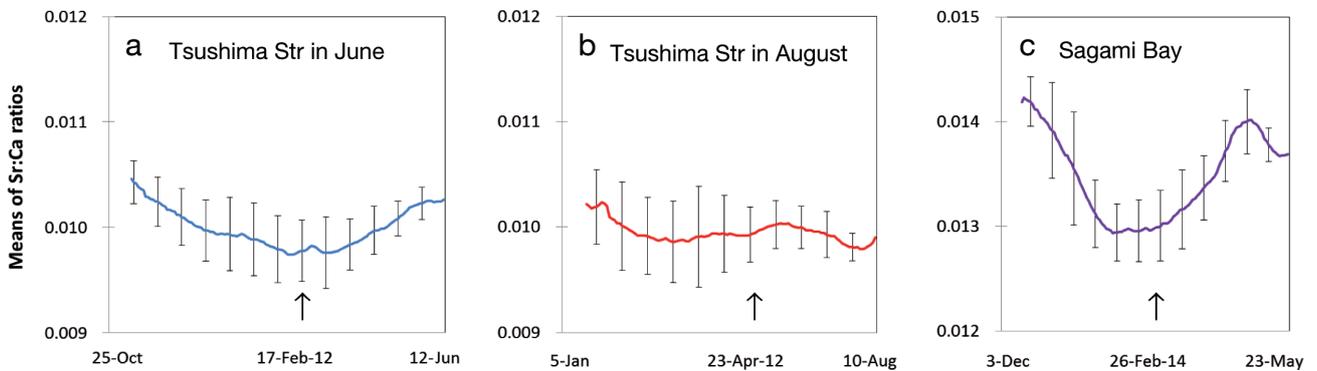


Fig. 7. Average ontogenetic running means ( $\pm\text{SD}$ ) of the Sr:Ca ratios of statoliths from *Uroteuthis edulis* specimens from Tsushima Strait in (a) June and (b) August, and (c) from Sagami Bay. Each ratio was calculated after vertical translation of lines in Fig. 6a,b,d so that the last Sr:Ca ratios might be adjusted to the mean. From left to right, dates under each horizontal axis show the average hatching date, the average intermediate date (arrow), and the sampling date. The Sr:Ca ratios corresponding to the average inter-mediate date were specified through RMM (see 'Materials and methods' and Fig. 2a)

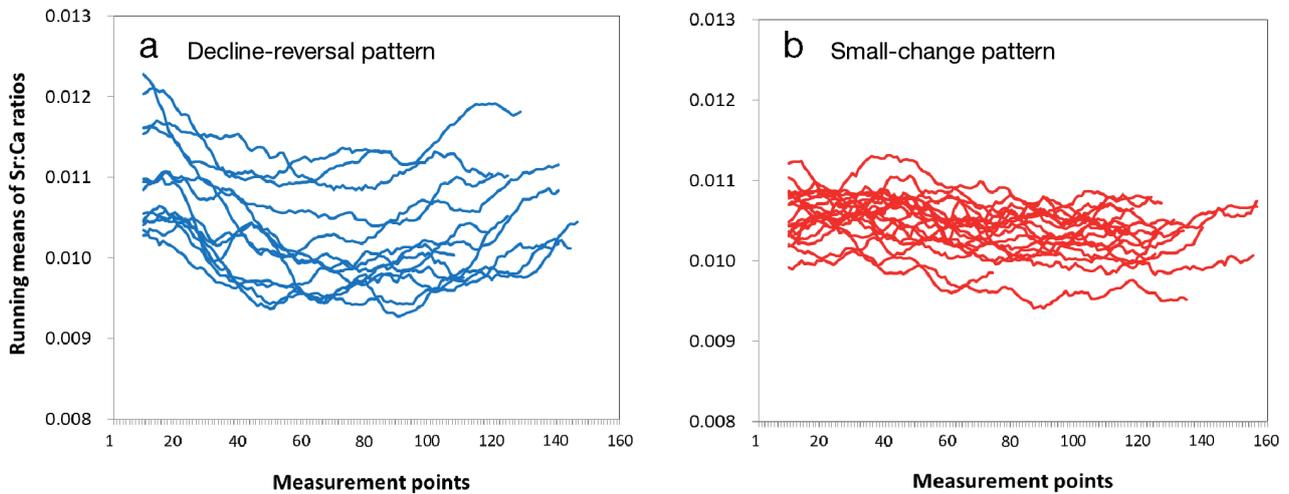


Fig. 8. Two patterns of running means of ontogenetic variation in the Sr:Ca ratios of statoliths from 33 *Uroteuthis edulis* specimens in the East China Sea (see Fig. 6c). Variation can be assigned to 1 of 2 patterns: (a) 13 specimens with a decline-reversal pattern, or (b) 20 with a small-change pattern

northeast of Taiwan, flows northeast in the southern East China Sea (Isobe 2008). Juveniles transported along the sites would show the small-change pattern in their statoliths, while those transported east of the sites would show the decline-reversal pattern. However, some juveniles in the current east of the sites would have been transported to the Pacific by the Kuroshio Current. Such squid could comprise those caught in Sagami Bay on the Pacific side, whose

statoliths show a clear decline-reversal pattern. This means that they may have been affected by the warm current.

In addition, the migratory route we inferred could explain the characteristics of the squid we sampled. Thirty-three specimens in the East China Sea revealed that both female and male maturity rates of those with the decline-reversal pattern were significantly higher than those with the small-change pattern ( $p < 0.05$ ; Fig. S4 in the Supplement), despite water temperatures in the northern East China Sea being lower than in the southern part (see bottom water temperatures in Table S2, Fig. S1b). It is reasonable to assume that the Kuroshio region, i.e. warm waters, should accelerate squid maturation. Moreover, this route could explain the group's 'kensaki' growth form, wherein a longer body implies that more resources were used for growth as maturation was suppressed by the cold waters of the northern East China Sea. To this end, *Sepioteuthis lessoniana* (Jackson & Moltchanivskyj 2002) and *Loligo vulgaris reynaudii* (Olyott et al. 2006) both grow longer in mantle length in colder water.

As for *U. edulis* collected from the Tsushima Strait in August, Sr:Ca ratios in microincrements formed at the juvenile stage were  $3.0 \times 10^{-4}$  higher than those when the squid were captured (Fig. 7b). This means that the juveniles inhabited waters where the water temperature in January was only  $1.3^\circ\text{C}$  lower than that in the Tsushima Strait in August. On August 3, 2012, water temperatures in the eastern part of the Tsushima Strait ( $33\text{--}43^\circ\text{N}$  and  $129\text{--}27^\circ\text{E}$ ) were  $22.3^\circ\text{C}$  at a depth of 50 m ( $17.5\text{--}27.3^\circ\text{C}$  over a depth range of 0–96 m). In this case, the water temperature

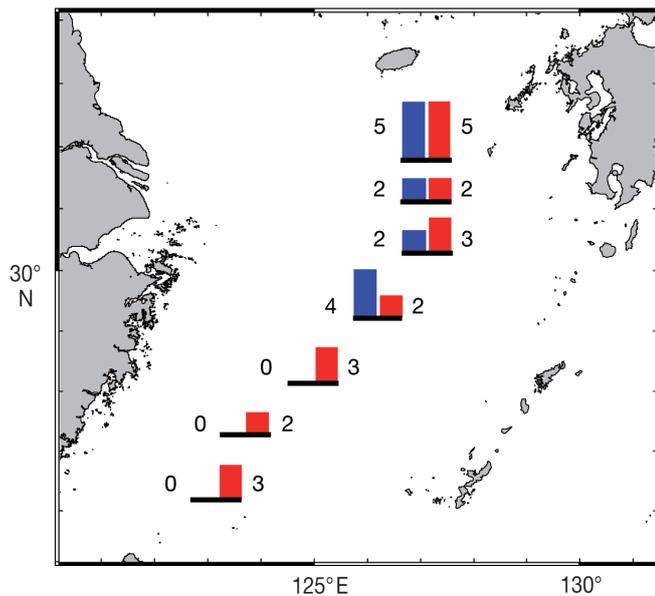


Fig. 9. Spatial distribution of *Uroteuthis edulis* specimens exhibiting 1 of 2 patterns among 7 sampling sites in the East China Sea. At each site, the number of specimens with the decline-reversal pattern (blue; see Fig. 8a) vs. the number of specimens with the small-change pattern (red; see Fig. 8b) is shown

in the hatching or nursery ground can be estimated to be 21°C (16.2–26.0°C, as a result of subtracting 1.3°C from water temperatures above), which is quite high for winter. Fig. S5 (in the Supplement) indicates that the southern East China Sea is the most likely hatching ground of the squid caught in Tsushima Strait in August. The juveniles were certainly transported by the currents just as potential individuals in the spring group were transported in October (Fig. S6 in the Supplement). Because water temperatures in the northern East China Sea were higher in summer than in spring, Sr:Ca ratios in the statoliths of the squid captured in August showed the small-change pattern. Such stable warm conditions would determine the characteristics of the summer group, whose individuals were relatively small and mature.

Several questions remain. The first is why ontogenetic Sr:Ca ratios in the statoliths of the specimens from Sagami Bay were always higher than those from the other sampling sites (Fig. 6). This may be due to differences in the waters in which they hatched. To quantify these, we must clarify the relationship between water temperature and the Sr:Ca ratio. Second, if our inferred 1-way migratory routes for the 2 seasonal groups of *U. edulis* are correct, how does this species reproduce in the East China Sea and southern Sea of Japan? To reveal this is a vital step toward sustainable fisheries management. Furthermore, we should also infer the migratory routes of the autumn group found in the Tsushima Strait.

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