

# Winter longitudinal variation in the body size of larval fishes in the Seto Inland Sea, Japan

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**Abstract** This study revealed the spatial variation in abundance and body size of larval fishes in the Seto Inland Sea, Japan, in January 2014 and 2015. Fish larvae were collected by a 1.3-m-diameter ring net towed at the surface and at 10-m depth at 21 stations. The most dominant species was the sandlance *Ammodytes japonicus*, constituting 82% of total larval fish caught. The body size of *A. japonicus* was greater [ca. 9 mm total length (TL) in 2014] in eastern areas than in western areas (ca. 5 mm TL in 2014). This trend was also observed in rockfishes (*Sebastes marmoratus* and *Sebastes inermis* species complex), suggesting a common phenomenon in this region. Because the water temperature was lower in eastern areas, it is likely that the longitudinal differences in larval body size are attributable to earlier spawning in eastern areas caused by different temperature conditions.

**Keywords** Oceanographic condition · Hatching timing · Larval growth · Spawning season

## Introduction

Species-specific recruitment mechanisms are some of the most important issues for sustainable fisheries. In the Seto Inland Sea, western Japan, Japanese anchovy *Engraulis japonicus* and the sandlance *Ammodytes japonicus* constituted 53% of the total catch in 2014 (Annual Statistics of Fishery and Aquaculture Production, Ministry of Agriculture, Forestry and Fisheries). Larvae and juveniles of these two species are targeted by commercial fisheries, thus, their levels of recruitment govern the status of fisheries in this region. *A. japonicus* is a demersal spawner and demonstrates site fidelity to sandy substrate. These sandy spawning areas are additionally used for estivation during a high-temperature period [1, 2]. As the available sandy ground has been reduced artificially, the stock status of this species has declined. To ensure continuous and sufficient recruitment, knowledge of the recruitment process coupled with conservation of sandy ground is essential. The sandlance is the most dominant species of larval and juvenile fishes collected in Ise Bay in the winter [3], indicating the importance of this species in the larval fish assemblages of certain regions.

The Seto Inland Sea is a highly productive [4, 5] and shallow (average depth = 38 m) semi-closed body of water connecting the Pacific Ocean by two channels. Although the current is very fast in this sea, environmental factors such as temperature and dissolved oxygen (DO) are highly variable between subareas [4]. For example, the minimum water temperature is lower in eastern areas (<9 °C; approximately 34.5°N, 134.5°E) than in western areas (ca. 11 °C; 33.7°N, 132.5°E) [6]. Such variation suggests that organisms inhabiting each subarea have different biological characteristics, such as growth and spawning season.

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The present study aimed to elucidate the body size variation of fish larvae between eastern and western areas in the winter, and to examine the relevance of the variation in environmental conditions such as water temperature in the Seto Inland Sea. As larval distribution and body size may vary not only horizontally but also vertically within the water column [7], larval collections were conducted at two depths, at the surface and at 10 m, at each collection site in the Seto Inland Sea.

## Materials and methods

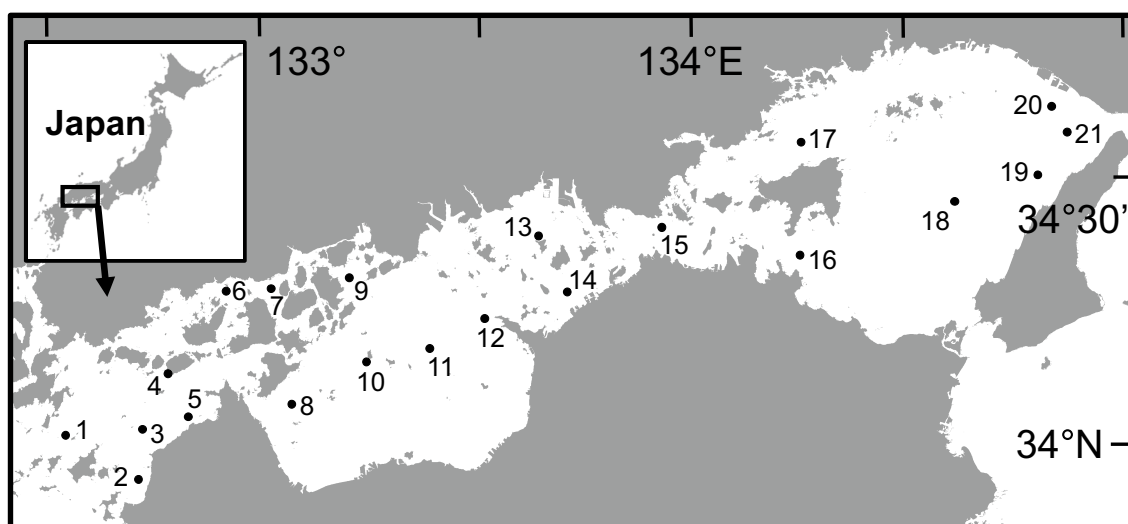
### Study site and larval collection

Twenty-one stations were established in the Seto Inland Sea to cover a 300-km-wide area from west to east ( $33^{\circ}57'–34^{\circ}39'N$ ,  $132^{\circ}34'–134^{\circ}52'E$ ; Fig. 1; ESM Table S1). Station numbers were assigned along longitudes from west to east. Bottom depths ranged from 11 to 59 m at all stations. Daytime larval collections were conducted at each station by the training and research vessel Toyoshiomaru (256 tons) from 20 to 23 January 2014 (16 stations) and 26–30 January 2015 (21 stations) (Table S1). A ring net with a 1.3-m-diameter mouth, 4.5-m length, and 2-mm mesh in the anterior two-thirds and 0.335-mm mesh in the posterior one-third, was towed for 5 min at a speed over the water of 2 knots at the surface and at 10-m depth. In 2014, towing at 10 m was operated only at seven stations out of 16 stations. Samples were sorted onboard immediately after collection and larval fish were preserved in 10% formalin, 99% ethanol, or by freezing with seawater.

To monitor environmental conditions, water temperature (degrees Celsius), salinity, and DO (milliliters per liter) were measured at the surface and at 10-m depth at each station using a conductivity-temperature-depth sensor (SBE-9plus, SeaBird), although no data were available for DO in 2014 owing to equipment malfunctions.

### Measurements

Larval fish were sorted in the laboratory by species according to Okiyama [8] and other literature for flatfish [9, 10]. Although juvenile/adult *Sebastes inermis* were classified into three species [11], the larvae were regarded as *S. inermis* species complex because of difficulty in visual identification of larval species. Total length (TL) was measured to the nearest 0.1 mm using a digital caliper under a microscope. Larvae that were broken or inadequate for measurement were omitted. When the number of larvae per sample exceeded 60 (62–344), as observed only for *A. japonicus*, 44–113 larvae were subsampled and measured. The shrinkage of larval sandlance by the preservatives was determined by measuring TL onboard immediately after collection and again after more than 1 month of preservation. Shrinkage was 10% ( $n = 47$ ) and 8% ( $n = 9$ ) by 99% ethanol and 10% formalin, respectively. Similarly, the shrinkage of other larvae were determined using rockfish (*S. inermis* species complex and *Sebastes marmoratus*) as 6% ( $n = 6$ ) and 3% ( $n = 5$ ) by ethanol and formalin, respectively. The TL at collection was calculated using these shrinkage rates. No shrinkage was assumed for frozen samples. Effects of collection dates on TL of each species were assumed to be negligible (see “Discussion”).



**Fig. 1** Map of the study site and location of sampling stations in the Seto Inland Sea. Numbers indicate station numbers assigned along longitudes

## Data analyses

The number of collected individuals per 5-min tow was regarded as catch per unit effort (CPUE), and was averaged among collection depths for each of five major species groups (*A. japonicus*, *S. marmoratus*, *S. inermis* species complex, *Hexagrammos otakii*, and *Hexagrammos agrammus*) each year in order to determine the horizontal pattern of larval abundance. Detailed data are presented in Table S1. To reveal the effects of location (longitude), collection depths, and environmental factors on larval abundance, generalized linear models (GLMs) were constructed for the CPUE of each species, using R software (<http://www.r-project.org>). Explanatory variables were collection depths (categorical data as surface and 10-m depth), longitude represented by decimal numbers (e.g. 133°30'E was converted to 133.5), year, and water temperature. Salinity was not included because of collinearity with water temperature and longitude (tolerance, longitude = 0.26, water temperature = 0.29, and salinity = 0.17). Because over-dispersion was observed for GLM with Poisson errors, a negative binomial distribution with log-link function was assumed for GLMs. The final model was determined through a stepwise model selection based on the Akaike information criterion.

To reveal factors affecting larval body size, GLMs with Gaussian family and identity function (equivalent to simple linear models) were constructed for TL of each species following stepwise model selection. Initial explanatory variables were the same with GLMs for CPUE (depth, longitude, year, and water temperature).

## Results

### Abundance

In 2014, a total of 1455 individuals from nine taxonomic groups and six families were collected by 23 net tows, consisting of 16 and seven tows at surface and 10-m depths, respectively (Table 1). In 2015, a total of 1015 larvae belonging to ten taxonomic groups of seven families were collected by 42 net tows (21 tows at both surface and 10-m depth). The most dominant species was the sandlance *A. japonicus*, which constituted 89 and 70% of larvae collected in 2014–2015, respectively. Rockfishes *S. marmoratus* and *S. inermis* species complex and greenlings *H. otakii* and *H. agrammus* were also abundant (Table 1).

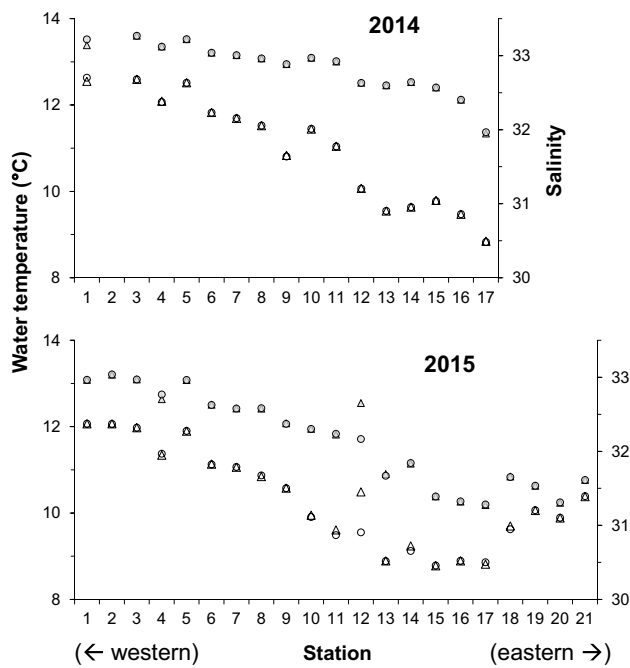
Water temperature ranged from 8.8 to 12.6 °C in 2014 and 8.8–12.1 °C in 2015. The temperature was lower at eastern stations each year, and increased from stations 17–21 in 2015 (Fig. 2). No clear difference in water temperature between the surface and 10-m depth was observed, except for station 12 in 2015. Salinity was also lower at eastern stations, ranging from 31.9 to 33.3 in 2014 and 31.3–33.0 in 2015 (Fig. 2). DO was almost constant, ranging from 4.5 to 6.9 ml l<sup>-1</sup> in 2015 (no data in 2014). No significant difference was observed between the surface layer and 10-m depth for water temperature (paired *t*-test; *t* = 0.06, *p* = 0.96 in 2014; *t* = 1.20, *p* = 0.24 in 2015), salinity (*t* = 1.20, *p* = 0.25 in 2014; *t* = 0.80, *p* = 0.43 in 2015), or DO (*t* = 2.02, *p* = 0.06 in 2015).

**Table 1** List of species collected in January 2014 and 2015

Family	Species	2014			2015		
		<i>n<sub>s</sub></i>	<i>n<sub>10</sub></i>	TL range (mm)	<i>n<sub>s</sub></i>	<i>n<sub>10</sub></i>	TL range (mm)
Ammodytidae	<i>Ammodytes japonicus</i>	866	430	2.6–13.1	455	251	3.1–16.6
Scorpaenidae	<i>Sebastiscus marmoratus</i>	5	19	2.5–11.2	74	121	2.3–21.1
	<i>Sebastes inermis</i> species complex	7	45	3.7–8.5	11	51	3.3–18.1
	<i>Sebastes pachycephalus</i>	1	3	6.2–9.8	0	5	6.7–16.1
	<i>Sebastes oblongus</i>	0	0		0	1	9.4
	Unidentified <i>Sebastes</i>	2	0	No data	0	0	
Hexagrammidae	<i>Hexagrammos otakii</i>	48	1	6.0–11.4	22	4	8.0–14.9
	<i>Hexagrammos agrammus</i>	26	0	6.3–11.4	5	0	8.4–11.6
Lateolabracidae	<i>Lateolabrax japonicus</i>	0	1	9.0	0	4	6.0–11.6
Pleuronectidae	<i>Pseudopleuronectes yokohamae</i>	0	0		3	3	3.0–6.8
	<i>Platichthys bicoloratus</i>	0	0		0	5	6.9–7.8
	<i>Pleuronichthys lighti</i>	0	1	20.6	0	0	

A total of 1455 individuals of larvae were collected in 2014, and 1015 individuals were collected in 2015. The number of tows was 16 for the surface and seven for 10-m depth at 16 stations in 2014, while it was 21 for both the surface and 10-m depth at 21 stations in 2015

*n<sub>s</sub>* Number of collected larvae at the surface, *n<sub>10</sub>* number of collected larvae at 10-m depth, *TL* total length



**Fig. 2** Water temperature and salinity, measured by a conductivity-temperature-depth sensor at the surface and 10-m depth, at each station each year. *Open triangles* Water temperature at the surface, *open circles* water temperature at 10-m depth, *solid triangles* salinity at the surface, *solid circles* salinity at 10-m depth

Larvae of *Hexagrammos* spp. were found mostly at the surface, whereas more larvae of *S. inermis* species complex were found at 10-m depth than at the surface (Table 1). CPUE was significantly greater for surface tows for *H. otakii* (GLM,  $p < 0.01$ ; Table 2), and at 10-m depth tows for both *S. marmoratus* ( $p < 0.001$ ) and *S. inermis* species complex ( $p < 0.001$ ). Collection depth was not adopted as an explanatory variable in the model for the CPUE of *A. japonicus*.

The CPUE of *A. japonicus* was greater in eastern areas, especially in 2014 (Fig. 3). A negative relationship between its CPUE and water temperature was observed ( $p < 0.05$ ; Table 2), indicating that the CPUE was greater at lower temperature. A significant effect of longitude on the number of collected individuals was observed only for *S. marmoratus* ( $p < 0.05$ ; Table 2). Although the CPUE of *S. marmoratus* was suggested to be greater at higher water temperature by the GLM, the effect of longitude was larger than that of water temperature. The CPUE of other species was not affected by longitude or water temperature, except for *H. otakii*. CPUEs of *A. japonicus* and *Hexagrammos* spp. were greater in 2014 than in 2015, while that of *S. marmoratus* was greater in 2015 than in 2014.

## Body size

The TL of *A. japonicus* was larger at eastern stations than at western stations (Fig. 4). Average TL  $\pm$  SD of this species was  $4.7 \pm 1.6$  mm ( $n = 97$ ) at stations 1–7,  $8.4 \pm 1.6$  mm ( $n = 178$ ) at stations 8–12, and  $9.4 \pm 1.2$  mm ( $n = 216$ ) at stations 13–17 in 2014. Similarly, it was  $5.2 \pm 1.1$  mm ( $n = 188$ ) at stations 1–7,  $6.7 \pm 1.3$  mm ( $n = 92$ ) at stations 8–12, and  $9.4 \pm 1.8$  mm ( $n = 328$ ) at stations 13–21 in 2015. The TLs of *S. marmoratus*, *S. inermis* species complex also varied with longitude, while no significant effect of longitude was observed for *H. otakii* and *H. agrammus* (Table 3). The TLs of *A. japonicus* and *S. marmoratus* were larger at lower temperatures while those of *S. inermis* species complex and *H. otakii* were smaller at lower temperatures. However, the effect of water temperature on the TL of *S. inermis* species complex was smaller than that of longitude.

Significant effects of collection depth on the body size of larvae were observed for *A. japonicus*, *S. marmoratus*, and *H. otakii*; larvae of *S. marmoratus* were smaller at the surface layer than at 10-m depth, while those of *A. japonicus* and *H. otakii* were larger at the surface layer. Significant effects of year on the TLs of larvae were detected except for *S. marmoratus* (Table 3). Larvae of *A. japonicus* were smaller in 2015, while those of other species were larger in 2015 than in 2014.

## Discussion

This study revealed that the body size of larvae of some fish species varies longitudinally within the study area in the Seto Inland Sea. The effect of sampling dates on the body size of larvae was not tested. Sampling in the eastern areas (stations 13–21) was undertaken on the third and fourth days (except for station 14 on the second day) during both cruises in 2014 and 2015, indicating that the growth from the first day to the fourth day (3 days) might be included in the result of larval size variation between areas. However, longitudinal difference in body size, e.g., 4.2–4.7 mm difference in average size of *A. japonicus* between stations 1–7 and 13–21, was considerably greater. Growth rates of *A. japonicus* were  $0.15$ – $0.23$  mm day<sup>-1</sup> during 30 days after hatching under laboratory conditions [12, 13], indicating that >4-mm difference in the average size of larvae is comparable to that of the >18-day difference in hatching dates. Similarly, growth rates of *S. marmoratus* were ca.  $0.1$  mm day<sup>-1</sup> within 10 days after hatching under laboratory conditions [14, 15], indicating that sampling dates can be negligible in these surveys.

The larval sizes of *A. japonicus*, *S. marmoratus* and *S. inermis* species complex were larger in eastern areas with

**Table 2** Generalized linear models (family = negative binomial, link = log) for the catch per unit effort (CPUE) of individuals of each species

Analysis of deviance				Summary			
Error source	LR $\chi^2$	df	p	Variable	Estimate	SE	p
<i>Ammodytes japonicus</i>							
Error		62		Intercept	7.85	1.97	<0.001
WT	4.42	1	0.036	WT	−0.37	0.18	0.036
Year	7.93	1	0.005	Year (2015)	−1.17	0.44	0.008
<i>Sebastes marmoratus</i>							
Error		60		Intercept	−124.69	53.08	0.019
Layer	10.85	1	<0.001	Layer (10-m depth)	1.28	0.38	<0.001
WT	2.53	1	0.11	WT	0.37	0.24	0.12
Longitude	7.27	1	0.007	Longitude	0.90	0.38	0.019
Year	9.93	1	0.002	Year (2015)	1.40	0.44	0.001
<i>Sebastes inermis</i> species complex							
Error		63		Intercept	−0.72	0.34	0.035
Layer	18.86	1	<0.001	Layer (10-m depth)	1.95	0.46	<0.001
<i>Hexagrammos otakii</i>							
Error		61		Intercept	12.86	3.60	<0.001
Layer	8.34	1	0.004	Layer (10-m depth)	−2.43	0.82	0.003
WT	7.88	1	0.005	WT	−1.09	0.33	<0.001
Year	5.11	1	0.024	Year (2015)	−1.91	0.74	0.010
<i>Hexagrammos agrammus</i>							
Error		62		Intercept	0.49	0.53	0.36
Layer	12.00	1	<0.001	Layer (10-m depth)	−19.58	2682.3	0.99
Year	5.83	1	0.016	Year (2015)	−1.92	0.81	0.018

Initial explanatory variables were collection depths (*Layer*), longitude, water temperature (*WT*), and year. Effects of layer and year were tested on the basis of surface layer and year 2014, respectively. Analysis of deviance by type II Wald  $\chi^2$ -test. All explanatory variables were selected based on the Akaike information criterion

LR Likelihood ratio

lower temperatures than in western areas. A lower temperature of the surface layer in these eastern areas has typically been observed from November to March (Sixth Regional Coast Guard Headquarters, unpublished data). Therefore, the winter variation in larval size could be related to water temperature.

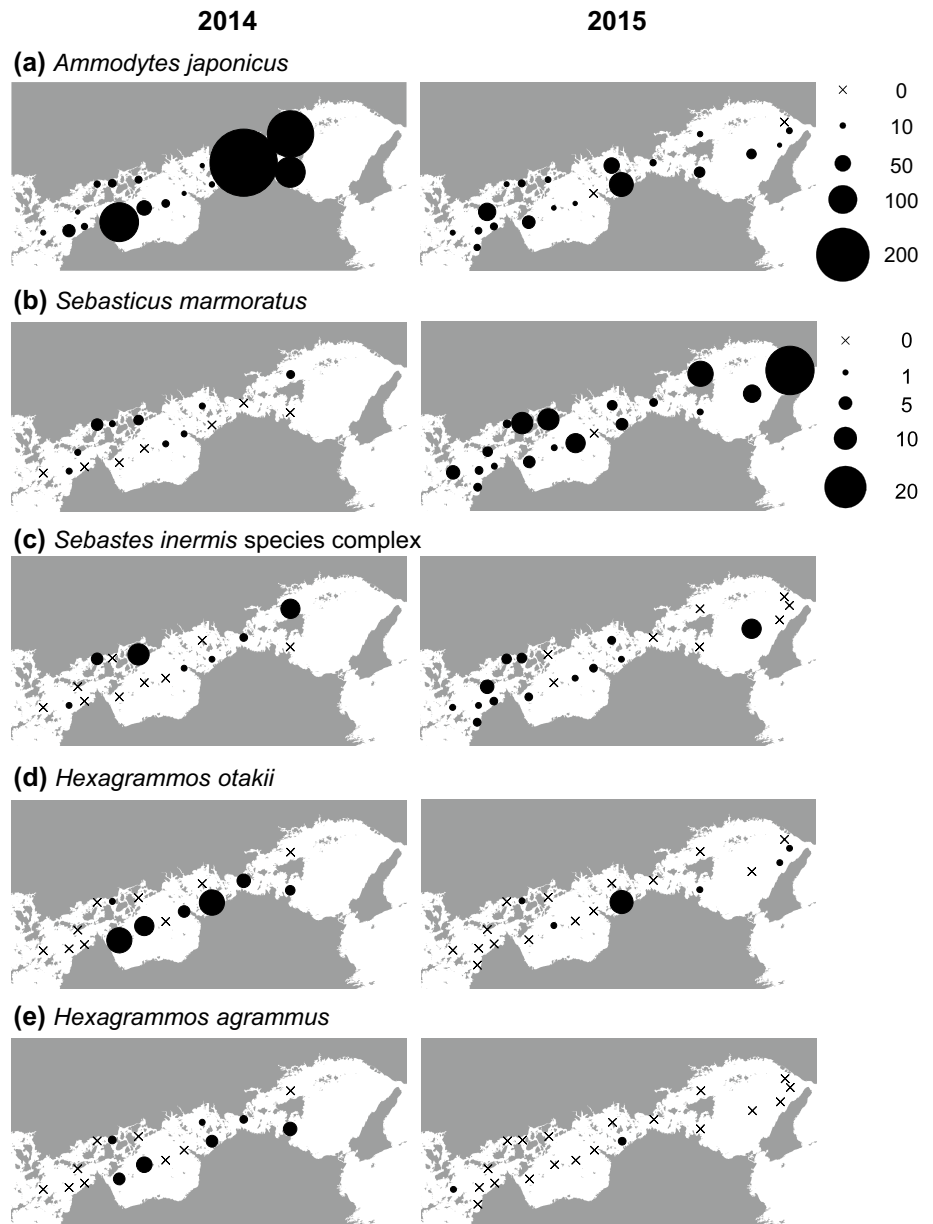
The mechanisms driving larval size variation in winter are unclear. One possible mechanism is that lower temperatures in eastern areas induce earlier spawning in winter. For example, *A. japonicus* start their vitellogenesis when the water temperature falls to 20 °C; the subsequent progress of vitellogenesis is most rapid at < 14 °C, but final maturation completes at ca. 11 °C [16]. In the period from October 2013 to March 2014, the lowest water temperature of 20 °C was observed in late November around station 2 (west; Ehime Prefecture, personal communication) and early November around station 15 (east; Kagawa Prefecture, personal communication). The water temperature descended to 14 °C in early January around station 2 and in early December around station 15, and reached 11 °C in early February around station 2 and early January around

station 15. Thus, the time at which the water temperature drops to a certain value differs by approximately 1 month between these stations. As a consequence, the spawning of *A. japonicus* would begin 1 month earlier in eastern areas (including around station 15) than western areas (including around station 2). In contrast, a higher temperature leads to higher growth rates, as observed in *A. japonicus* [17]. If small-sized larvae in western areas continue to be exposed to a higher water temperature than that in eastern areas, the larvae in the former areas would grow at higher rates, resulting in mitigation of the body size difference later.

For rockfishes such as *S. marmoratus*, there might be a similar explanation for the difference in larval body size between eastern and western areas. The reproductive pattern in this species largely differs from that of *A. japonicus*: *S. marmoratus* spawn larvae directly into the water column, and one female releases one to several batches [18]. The parturition period of *S. marmoratus* continues from December to April [14], but survival of larvae is associated with the timing of parturition [19], indicating the importance of early cohorts in *S. marmoratus* in



**Fig. 3a–e** Geographical pattern of catch per unit effort (CPUE) of larvae of five major species groups. CPUE is defined as the number of collected individuals per 5-min tow of a 1.3-m-mouth ring net. The CPUE at the surface and 10-m depth were averaged. Scales are standard for four of the species groups (*Sebasticus marmoratus*, *Sebastes inermis* species complex, *Hexagrammos otakii*, and *Hexagrammos agrammus*)

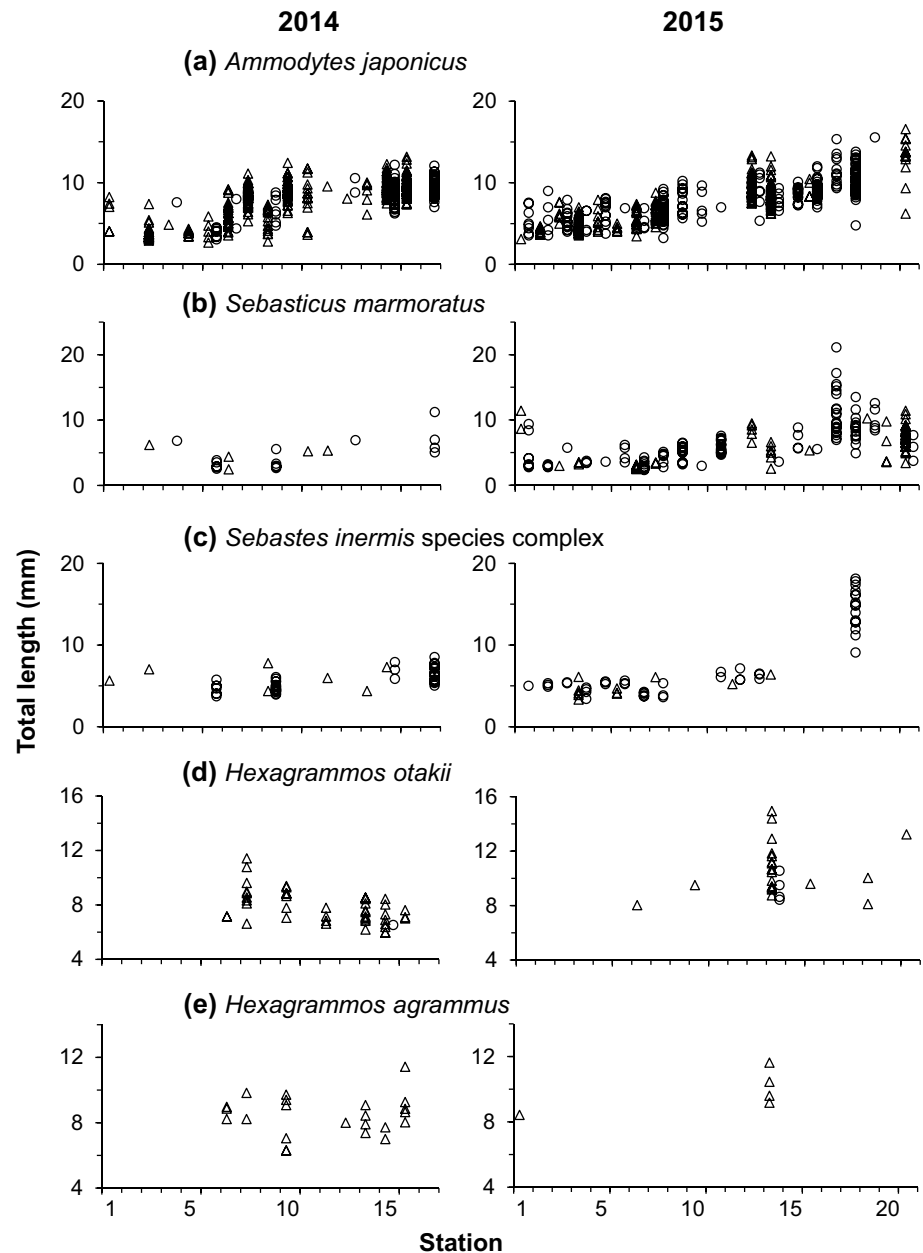


each area. Mature females of *S. marmoratus* release larvae of 4-mm TL during the early night [20], and larvae grow to 7.2 and 12.3 mm TL 22 and 35 days after parturition, respectively [21]. The collected larvae of *S. marmoratus* were <7 mm TL at western stations in 2014 (Fig. 4), while larvae >11 mm were observed at eastern stations in 2014. Thus, parturition should start ca. 10 days earlier in eastern areas, which would lead to larger larval sizes than in western areas. Further examination of the mechanisms causing longitudinal differences in larval sizes of rockfishes is necessary. The reason why the larval sizes of *Hexagrammos* species did not differ between areas is also unknown. The larvae of *H. otakii* of ca. 15-mm TL, as collected in 2015, were born within 30 days, as inferred from laboratory

observations [22]. This indicates that the short spawning period of this species [23] led to small differences in body size between collection sites.

Another possible explanation for the longitudinal variation in the larval size of *A. japonicus* is the passive eastward transport of larvae. Nakata [24] revealed that a strong westerly wind causes eastward transport of larval *A. japonicus* on a relatively small scale (15–19 stations were used in this study). Such wind-induced transport of larvae from spawning sites to other areas might play a role in reducing adult predation on larvae [25]. If a principal spawning ground is located in a western area, the earlier cohorts with larger body sizes might be transferred to eastern areas and this might result in the difference in body size between

**Fig. 4** Total length of collected larvae of five major species groups at each station in 2014 and 2015. *Open triangles* Larvae collected at the surface, *open circles* larvae collected at 10-m depth. Details of the number of individuals are shown in Table S1



areas. However, larval transport on a greater scale, from 133° to 134°E in longitude, is unlikely because it has not been suggested by modeled simulations (Yamamoto et al., unpublished data). Longitudinal gradients in both temperature and salinity (Fig. 2) indicate the low mixture of waters between eastern (ca. 133°E) and western (ca. 134°E) areas.

Because *Ammodytes* species exhibit strong site fidelity and small-scale movement after settlement [26–28], longitudinal segregation might occur in *A. japonicus* populations in the Seto Inland Sea. Further studies are necessary to determine whether the *A. japonicus* population is composed of more than two subpopulations with different spawning seasons and other biological traits.

Larval abundance was not necessarily higher in eastern areas. A greater catch and abundant distribution in eastern areas have been well documented for *A. japonicus* [29], resulting from heavier sand removal in western areas in the past. However, longitude was not necessarily the most important variable affecting the number of collected larvae of even *A. japonicus*. Spatial relationships in habitats between adults and larvae of each species or larval connectivity between areas are issues that should be investigated in the future. Furthermore, a higher temperature and higher salinity in western areas were observed in the present study (Fig. 2), indicating the formation of a thermohaline front. Around the thermohaline front, a high concentration of larvae such as

**Table 3** Generalized linear models (family = Gaussian, link = identity) for TL of collected larvae of each species

Analysis of deviance				Summary			
Error source	Sum of square	df	p	Variable	Estimate	SE	p
<i>A. japonicus</i>							
Error	2817.3	1094		Intercept	−381.15	23.13	<0.001
Layer	42.57	1	<0.001	Layer (10-m depth)	−0.45	0.11	<0.001
WT	5.26	1	0.15	WT	−0.12	0.084	0.15
Year	29.44	1	<0.001	Year (2015)	−0.37	0.11	<0.001
Longitude	785.53	1	<0.001	Longitude	2.93	0.17	<0.001
<i>Sebastes marmoratus</i>							
Error	1175.0	214		Intercept	−211.32	37.97	<0.001
Layer	31.03	1	0.018	Layer (10-m depth)	0.91	0.38	0.018
WT	100.66	1	<0.001	WT	−0.90	0.21	<0.001
Longitude	211.46	1	<0.001	Longitude	1.69	0.27	<0.001
<i>Sebastes inermis</i> species complex							
Error	223.68	108		Intercept	−1066.6	58.16	<0.001
WT	212.46	1	<0.001	WT	2.60	0.26	<0.001
Year	98.38	1	<0.001	Year (2015)	1.92	0.28	<0.001
Longitude	725.86	1	<0.001	Longitude	7.83	0.42	<0.001
<i>H. otakii</i>							
Error	129.48	68		Intercept	2.43	2.26	0.29
Layer	5.49	1	0.094	Layer (10-m depth)	−1.13	0.67	0.094
WT	10.93	1	0.019	WT	0.52	0.22	0.019
Year	124.48	1	<0.001	Year (2015)	3.32	0.41	<0.001
<i>H. agrammus</i>							
Error	37.16	26		Intercept	8.42	0.25	<0.001
Year	8.57	1	0.021	Year (2015)	1.44	0.59	0.021

Initial explanatory variables were layer, longitude, WT, and year. Effects of layer and year were tested on the basis of surface layer and year 2014, respectively. Analysis of deviance by type II test. All explanatory variables were selected based on Akaike information criterion. For abbreviations, see Tables 1 and 2

*Hexagrammos* species and prey organisms often occur [30–32]. Such a hydrographic structure should be considered as a potential factor affecting larval assemblages.

The CPUE of larvae, which was greater at the surface in *Hexagrammos* species, but greater at 10-m depths in *S. marmoratus* and *S. inermis* species complex, could reflect species' depth preferences in the water column during daytime. It differs from that of a past study showing the vertical distribution of *S. marmoratus* larvae, which were most abundant in the surface layer compared to 25 and 50-m depths [33]. Thus, the depth preference of rockfish larvae should be investigated further. Collection depth was irrelevant to the CPUE of *A. japonicus*, but this differs from the past observation that *A. japonicus* larvae prefer depths of 5–15 m during daytime [34]. Similarly, congeneric *Ammodytes hexapterus* shows abundant distribution at depths of ca. 15–45 m compared to 0–15 m throughout the day [7]. The strong current in the study

area and vertical disturbance in winter might account for these differences. Actually, the congeneric *Ammodytes marinus* larvae were abundant in surface waters during the day in areas without vertical environmental gradients, whereas the larvae were abundant at midwater with high food availability in a stratified water column [35].

In conclusion, longitudinal differences in winter in the abundance and body size of larvae were observed in some species, such as *A. japonicus* and *S. marmoratus*, but not in all species. It is suggested that differences in water temperature between areas (lower in eastern areas in winter) affect longitudinal variation. Future studies are necessary to elucidate the mechanisms underlying the variation in larval size, and to understand how this variation influences recruitment dynamics.

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