

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

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Abstract This paper 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 the 10-m depths at 21 stations. The most dominant species was the sandlance *Ammodytes japonicus*, constituting 82% of total larval fish caught. Body size of *A. japonicus* was greater (around 9 mm total length in 2014) in eastern areas than in western areas (around 5 mm total length). This trend was also observed in rockfishes (*Sebastiscus marmoratus* and *Sebastes inermis* species complex), suggesting a common phenomenon in this region. Because water temperature was lower in eastern areas, it is likely that the longitudinal differences in larval body sizes are attributable to earlier spawning in eastern areas caused by different temperature conditions.

Keywords: oceanographic condition; timing of hatching; larval growth; spawning season

Introduction

Species-specific recruitment mechanisms are one 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 statistic of fishery and aquaculture production, Ministry of Agriculture, Forestry and Fisheries). Larvae and juveniles of these two species are targeted by commercial fisheries. Therefore, the levels of recruitment of these two species govern the fishery status in this region. *Ammodytes japonicus* are demersal spawners and demonstrate site fidelity to sandy substrate. These sandy spawning areas are additionally used for estivation during a high temperature period around summer [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 in larval and juvenile fishes collected in Ise Bay in the winter [3], indicating the importance of this species in the larval fish assemblages of some 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 with two channels. Although water current is very fast in this water, environmental factors such as temperature and dissolved oxygen 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 (around 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.

The present study aimed to elucidate the body size variation of fish larvae between eastern and western areas in the winter, and to discuss the relevance of the variation in environmental conditions such as water temperature in the Seto Inland Sea. As the larval distribution and body

size may vary not only horizontally but also vertically within the water column [7], larval collections were conducted at two depth layers of surface and 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°57' to 34°39' N, 132°34' to 134°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 January 20–23 2014 (16 stations) and January 26–30 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-third 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 depths. In 2014, towing at 10 m was operated only at 7 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 (°C), salinity, and dissolved oxygen (DO, ml l⁻¹) were measured at the surface and at 10 m at each station using a conductivity-temperature-depth (CTD) sensor (SBE-9plus, SeaBird), although no data were available for DO in 2014 owing to equipment malfunctions.

Measurements

79

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

95

96 Data analyses

97

98 The number of collected individuals per 5 min tow was regarded as catch per unit effort (CPUE),
99 and was averaged among collection depths for each of 5 major species groups (*A. japonicus*, *S.*
100 *marmoratus*, *S. inermis* species complex, *Hexagrammos otakii*, and *Hexagrammos agrammus*)
101 each year in order to determine the horizontal pattern of larval abundance. Detailed data are
102 presented in Table S1. To reveal the effects of location (longitude), collection depths, and
103 environmental factors on larval abundance, generalized linear models (GLMs) were constructed

for the CPUE of each species, using R software (www.r-project.org). Explanatory variables were collection depths (categorical data as surface and 10-m depth), longitude represented in decimal number (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 sizes, 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, 1,455 individuals from 9 taxonomic groups and 6 families were collected by 23 net-tows, consisting of 16 and 7 tows at surface and 10-m depths, respectively (Table 1). In 2015, 1,015 larvae belonging to 10 taxonomic groups of 7 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 and 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 to 12.1°C in 2015. The

temperature was lower at eastern stations each year, and increased from stations 17 to 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 to 33.0 in 2015 (Fig. 2). DO was almost constant, ranging from 4.5 to 6.9 ml l⁻¹ in 2015 (no data in 2014). No significant difference was observed between surface and 10-m depth layers 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), and DO (*t* = 2.02, *p* = 0.06 in 2015).

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). Negative relationship between its CPUE and water temperature was observed (*p* < 0.05; Table 2), indicating that the CPUE was greater at lower temperature. 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 nor 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 standard deviation (SD) of this species was 4.7 ± 1.6 mm ($n = 97$) at Stations 1–7, 8.4 ± 1.6 mm ($n = 178$) at Stations 8–12, and 9.4 ± 1.2 mm ($n = 216$) at Stations 13–17 in 2014. Similarly, it was 5.2 ± 1.1 mm ($n = 188$) at Stations 1–7, 6.7 ± 1.3 mm ($n = 92$) at Stations 8–12, and 9.4 ± 1.8 mm ($n = 328$) at Stations 13–21 in 2015. The TLs of *S. marmoratus* and *S. inermis* species complex also varied with longitudes, 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 layers than at the 10 m depths while those of *A. japonicus* and *H. otakii* were larger at the surface layers. 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 species varies longitudinally within the study area in the Seto Inland Sea. The effect of sampling dates on the body sizes of larvae was not tested. Samplings in the eastern areas (Stations 13–21) were operated 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 sizes, 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 d⁻¹ during 30 d after hatching under laboratory condition [12, 13], indicating that >4 mm difference of in average size of larvae is comparable to >18 days difference in hatching dates. Similarly, growth rates of *S. marmoratus* were around 0.1 mm d⁻¹ within 10 d after hatching under laboratory condition [14,15], indicating that the 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 lower temperatures than in western areas. The lower-temperature surface layers in eastern areas have typically been observed in this area from November to March (6th 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 explanation is that lower temperatures in eastern areas induce an earlier spawning in winter. For example, *A. japonicus* start their vitellogenesis when water temperature falls to 20 °C, and subsequent progress of vitellogenesis is most rapid under 14 °C but final maturation completes around 11°C [16]. In the period from October 2013 to March 2014, bottom water temperature of 20 °C was observed in late November around Station 2 (west; Ehime Prefecture, pers. comm.) and early November around Station 15 (east; Kagawa Prefecture, pers. comm.). Thereafter, water temperature descended to 14 °C in early January around Station 2 and early December around Station 15, and reached to 11 °C in early February around Station 2 and early January around Station 15. Thus, the timing of the water temperature drops to the certain value differs approximately one month between these stations. Therefore, spawning of *A. japonicus* would begin one month earlier in eastern areas (including around Station 15) than western areas (including around Station 2). In contrast, higher temperature leads to higher growth rates, as observed in *A. japonicus* [17]. If the larvae with small sizes in western areas continued to expose

themselves to higher water temperature than that in eastern areas subsequently, the larvae in western areas would grow up with higher rates, resulting in mitigating the body size difference later.

For rockfishes such as *S. marmoratus*, a similar explanation might be applicable for the difference in larval body sizes 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 reduces associated with the timing of parturition [19], indicating the importance of early cohorts in *S. marmoratus* at each area. Mature females of *S. marmoratus* release larvae with 4 mm TL during the early night [20], and larvae grow up to 7.2 and 12.3 mm TL on 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, the parturition would start around 10 days earlier in eastern areas, leading to larger larval sizes than western areas. Further examination on the mechanisms causing longitudinal difference 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* around 15 mm TL, as collected in 2015, were born within 30 days, inferred from the laboratory observation [22]. This indicates 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 larval size of *A. japonicus* is the passive eastward transport of larvae. Nakata [24] revealed that strong westerly wind causes eastward transport of larval *A. japonicus* within a relatively small scale (from St. 15 to St. 19 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 might result in the difference in body size between areas. However, the larval transport within a greater scale, from 133° to 134 °E in longitude, is unlikely because it has not been suggested by the model simulation (Yamamoto H. et al., unpublished data). Longitudinal gradients in both temperature and salinity (Fig. 2) indicate the low mixture of waters between eastern (around 133° E) and western (around 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. Greater catch and abundant distribution in eastern areas have been well recognized 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 future. Furthermore, higher temperature and higher salinity in western areas were observed in the present study (Fig. 2), indicating the formation of the thermohaline front. Around the thermohaline front, a high concentration of larvae such as *Hexagrammos* species and prey organisms often took place [30–32]. Such 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 preference in the water column during daytime. It differs from the past study showing the vertical distribution of *S. marmoratus* larvae which were the most abundant at surface layer

compared to 25 and 50 m layers [33]. 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 *A. hexapterus* shows abundant distribution around 15–45 m than 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 *A. marinus* larvae were abundant in surface waters during the day at 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, winter longitudinal differences 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 sizes, and to understand how this variation influences recruitment dynamics.

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Figure captions

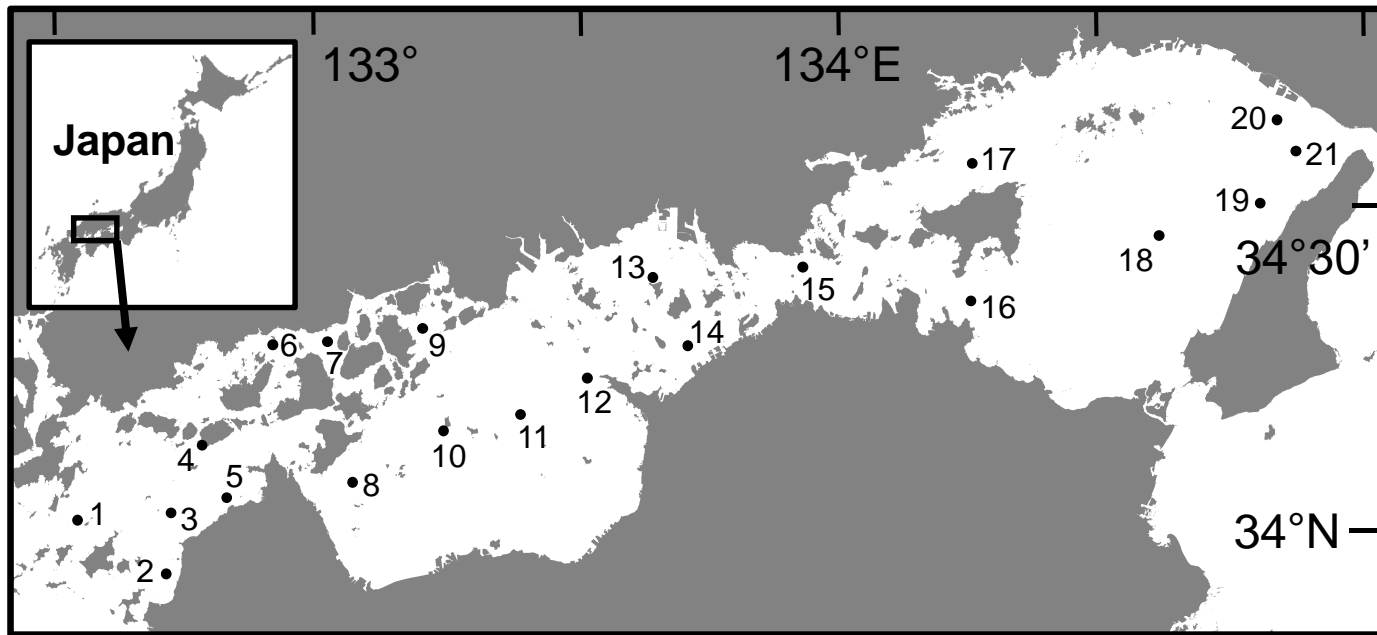
Fig. 1. Map of the study site and location of sampling stations in the Seto Inland Sea. Numerals indicate station numbers assigned along longitudes.

Fig. 2. Water temperature and salinity, measured by a CTD sensor at surface and 10-m depths at each station each year. Open triangles and circles denote water temperature at the surface and 10-m depth, respectively. Solid triangles and circles denote salinity at the surface and 10-m depth, respectively.

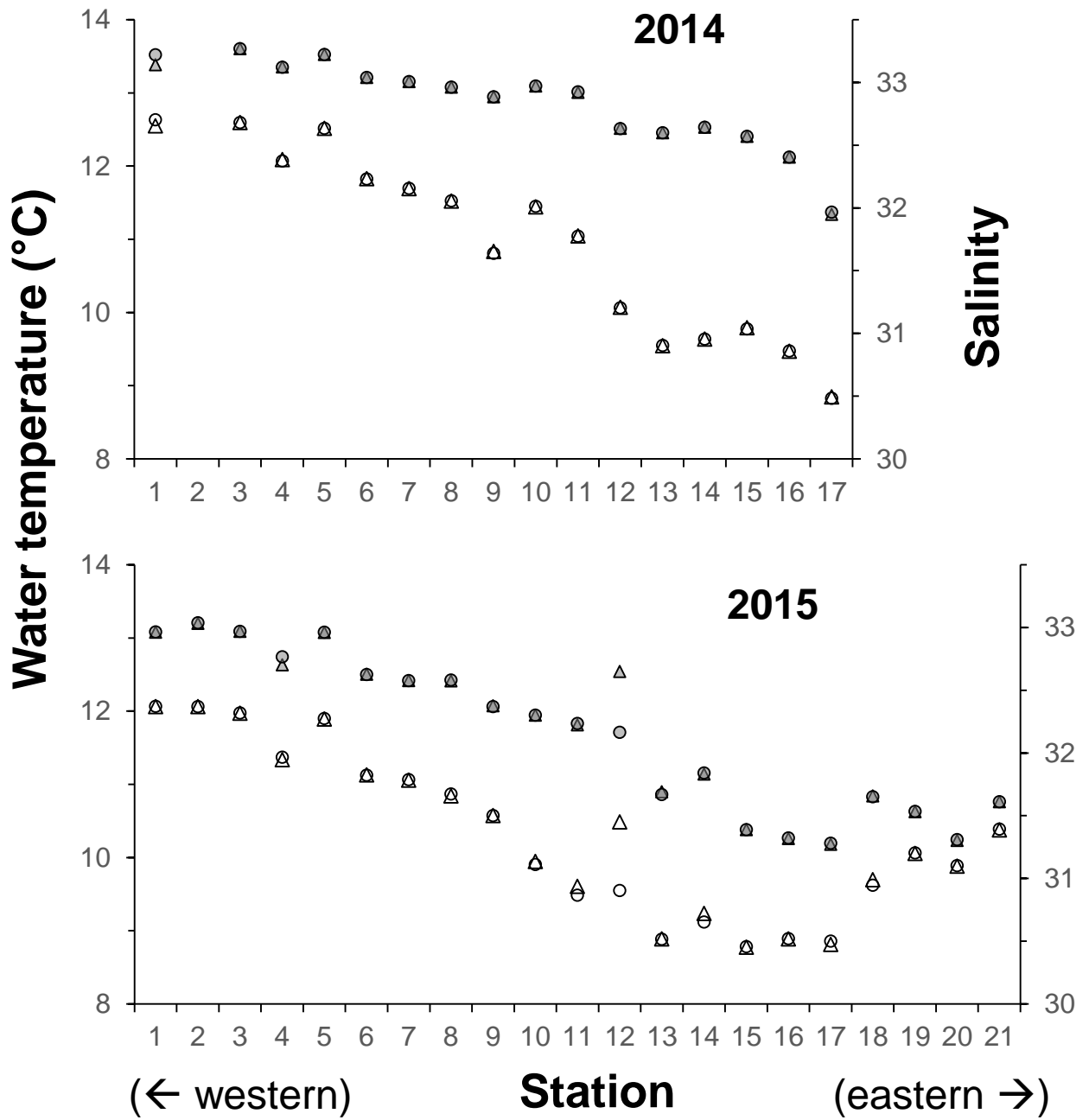
Fig. 3. Geographical pattern in catch per unit effort (CPUE) of larvae of 5 major species groups. CPUE is defined as the number of collected individuals per 5 min tow of a 1.3-m mouth ring net. The CPUE at surface and 10-m depths were averaged. Scales are standard for 4 of the species groups (*S. marmoratus*, *S. inermis* species complex, *H. otakii*, and *H. agrammus*).

Fig. 4. Total length of collected larvae of 5 major species groups at each station in 2014 and 2015. Open triangles and circles denote larvae collected at surface and 10-m depths, respectively. Details of the number of individuals are shown in Table S1.

(Fig. 1)



(Fig. 2)

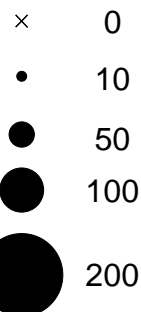
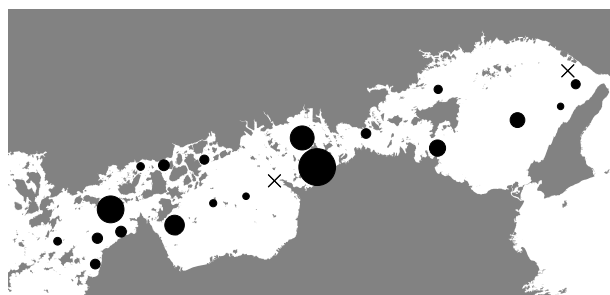
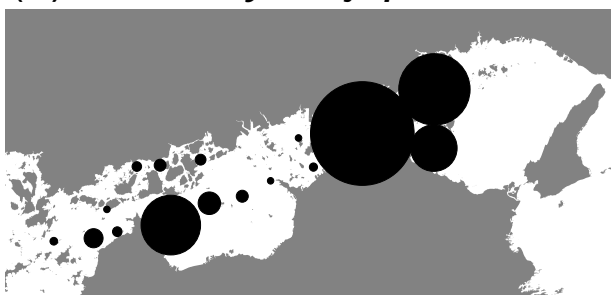


2014

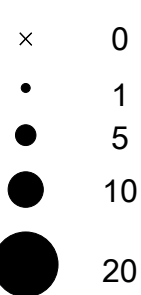
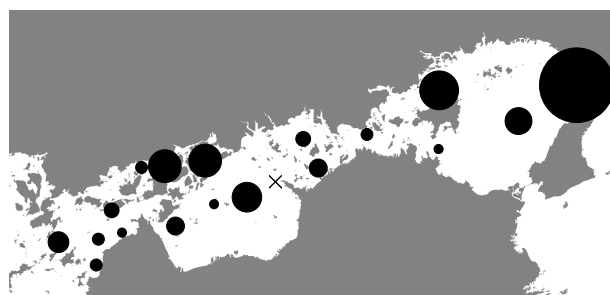
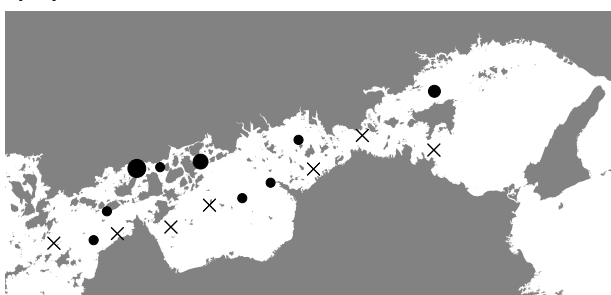
2015

(Fig. 3)

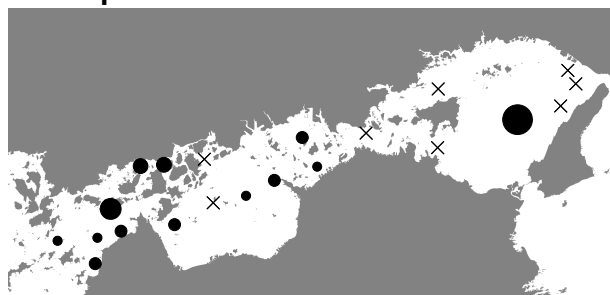
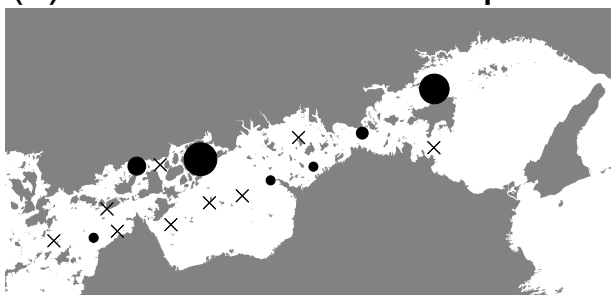
(a) *Ammodytes japonicus*



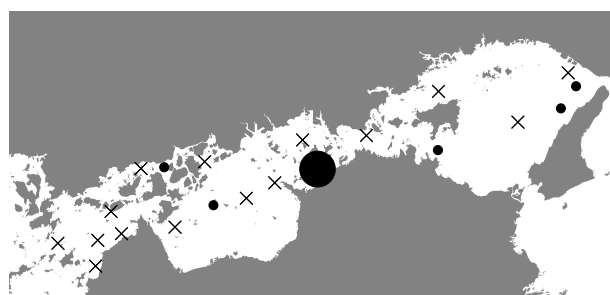
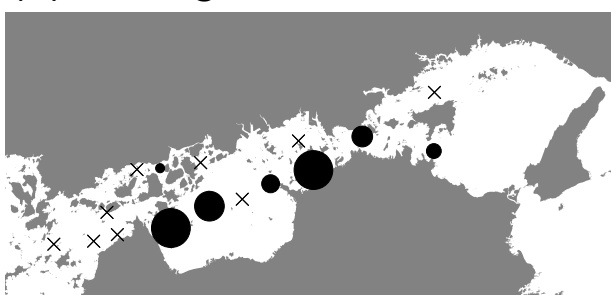
(b) *Sebasticus marmoratus*



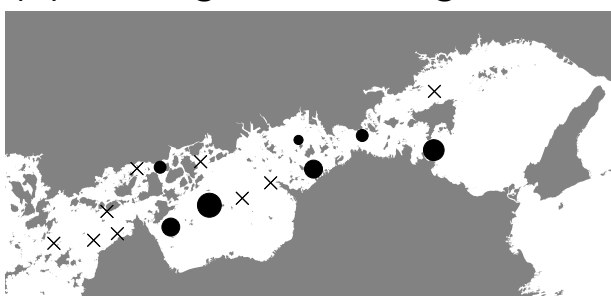
(c) *Sebastes inermis* species complex



(d) *Hexagrammos otakii*



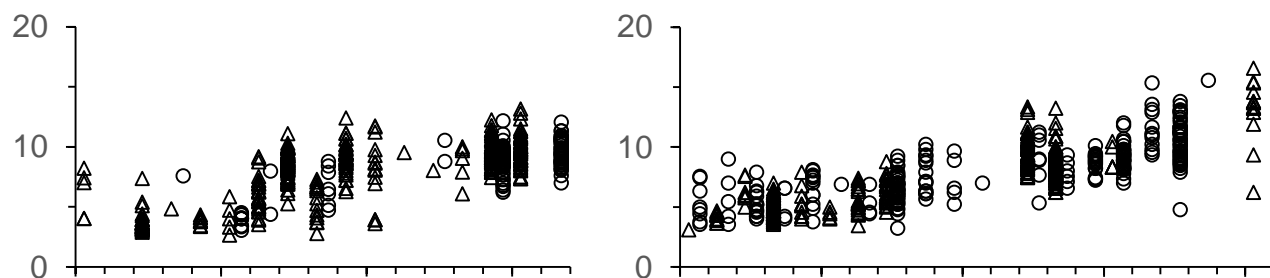
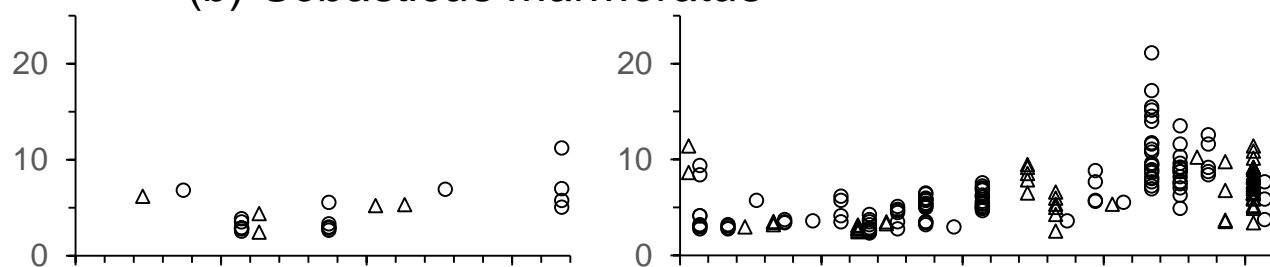
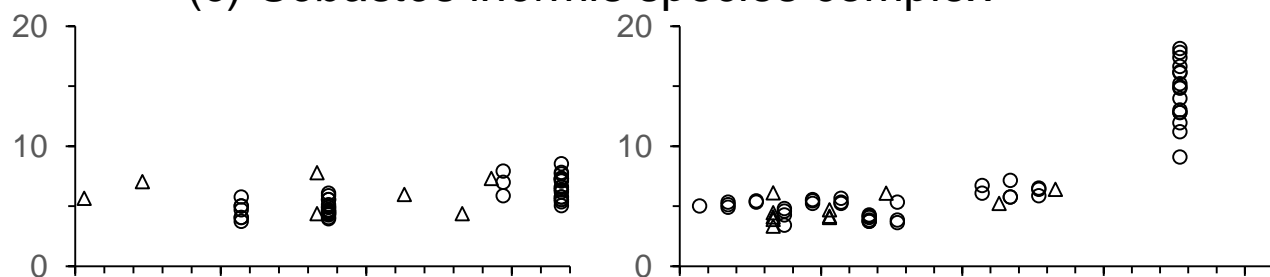
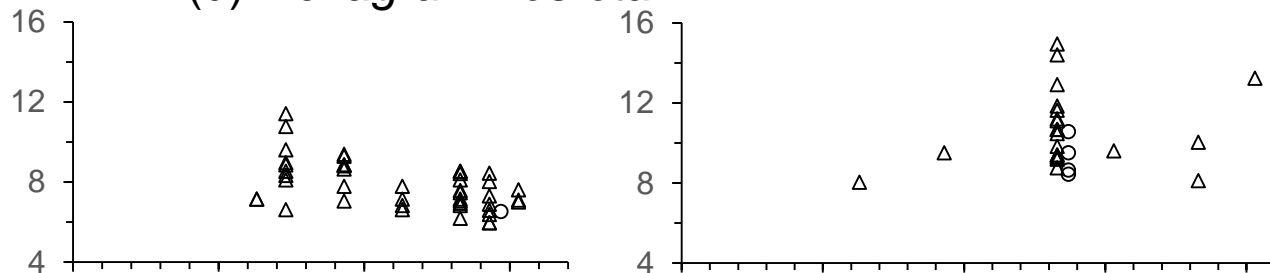
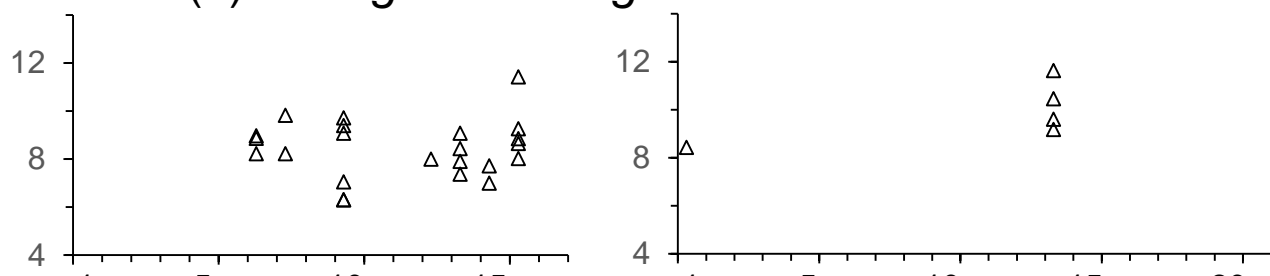
(e) *Hexagrammos agrammus*



2014

2015

(Fig. 4)

(a) *Ammodytes japonicus*(b) *Sebasticus marmoratus*(c) *Sebastes inermis* species complex(d) *Hexagrammos otakii*(e) *Hexagrammos agrammus*

Station

Table 1

List of species collected in January 2014 and 2015

Family	Species	2014			2015		
		Ns*	N10*	TL range (mm)	Ns*	N10*	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 1,455 individuals of larvae were collected in 2014 and 1,015 individuals were collected in 2015. The number of tows was 16 for surface and 7 for 10-m depth at 16 stations in 2014, while it was 21 for both surface and 10-m depths at 21 stations in 2015

* Ns, number of collected larvae at surface layers; N10, number of collected larvae at 10-m depth layers.

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 Chisq*	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>Sebastiscus marmoratus</i>							
Error		60		Intercept	-124.69	53.08	0.019
Layer	10.85	1	<0.001	Layer (10-m)	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)	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)	-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)	-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 was operated by Type II Wald chi-square test.

All explanatory variables were selected based on Akaike information criterion.

*Likelihood ratio Chi square

Table 3

Generalized linear models (family = gaussian, link = identity) for total length of collected larvae of each species

Analysis of Deviance				Summary			
Error source	Sum of square	df	p	Variable	Estimate	SE	p
<i>Ammodytes japonicus</i>							
Error	2817.3	1094		Intercept	-381.15	23.13	<0.001
Layer	42.57	1	<0.001	Layer (10-m)	-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>Sebastiscus marmoratus</i>							
Error	1175.0	214		Intercept	-211.32	37.97	<0.001
Layer	31.03	1	0.018	Layer (10-m)	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>Hexagrammos otakii</i>							
Error	129.48	68		Intercept	2.43	2.26	0.29
Layer	5.49	1	0.094	Layer (10-m)	-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>Hexagrammos 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 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 was operated by Type II test.

All explanatory variables were selected based on Akaike information criterion.