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Title	Winter longitudinal variation in the body size of larval fishes in the Seto Inland Sea, Japan
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Citation	Fisheries Science , 83 : 373 - 382
Issue Date	2017-03-23
DOI	10.1007/s12562-017-1076-2
Self DOI	
URL	https://ir.lib.hiroshima-u.ac.jp/00049223
Right	 Japanese Society of Fisheries Science 2017 This is a post-peer-review, pre-copyedit version of an article published in Fisheries Science. The final authenticated version is available online at: https:// doi.org/10.1007/s12562-017-1076-2 This is not the published version. Please cite only the published version. この論文は出版社版ではありません。引用の 際には出版社版をご確認、ご利用ください。
Relation	



1	Winter longitudinal variation in the body size of larval fishes in the Seto Inland Sea, Japan
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16 Abstract This paper revealed the spatial variation in abundance and body size of larval fishes 17 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 18 19 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 20 in western areas (around 5 mm total length). This trend was also observed in rockfishes 21 22 (Sebastiscus marmoratus and Sebastes inermis species complex), suggesting a common 23 phenomenon in this region. Because water temperature was lower in eastern areas, it is likely 24 that the longitudinal differences in larval body sizes are attributable to earlier spawning in 25 eastern areas caused by different temperature conditions.

26

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

29 Introduction

30

31 Species-specific recruitment mechanisms are one of the most important issues for sustainable 32 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 33 34 fishery and aquaculture production, Ministry of Agriculture, Forestry and Fisheries). Larvae 35 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 36 37 are demersal spawners and demonstrate site fidelity to sandy substrate. These sandy spawning 38 areas are additionally used for estivation during a high temperature period around summer [1,2]. 39 As the available sandy ground has been reduced artificially, the stock status of this species has 40 declined. To ensure continuous and sufficient recruitment, knowledge of the recruitment 41 process coupled with conservation of sandy ground is essential. The sandlance is the most 42 dominant species in larval and juvenile fishes collected in Ise Bay in the winter [3], indicating 43 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) semiclosed 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.

51 The present study aimed to elucidate the body size variation of fish larvae between eastern 52 and western areas in the winter, and to discuss the relevance of the variation in environmental 53 conditions such as water temperature in the Seto Inland Sea. As the larval distribution and body 54 size may vary not only horizontally but also vertically within the water column [7], larval 55 collections were conducted at two depth layers of surface and 10 m at each collection site in the 56 Seto Inland Sea.

57

58 Materials and methods

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60 Study site and larval collection

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Twenty-one stations were established in the Seto Inland Sea to cover a 300-km wide area from 62 63 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 64 stations. Daytime larval collections were conducted at each station by the training and research 65 66 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 67 mesh in the anterior two-third and 0.335 mm mesh in the posterior one-third, was towed for 5 68 min at a speed over the water of 2 knots at the surface and at 10-m depths. In 2014, towing at 69 70 10 m was operated only at 7 stations out of 16 stations. Samples were sorted onboard 71 immediately after collection and larval fish were preserved in 10% formalin, 99% ethanol, or 72 by freezing with seawater.

To monitor environmental conditions, water temperature (°C), salinity, and dissolved oxygen (DO, ml 1⁻¹) 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.

77

78 Measurements

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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 observed only for A. japonicus, 44-113 larvae were subsampled and measured. The shrinkage 86 87 of larval sandlance 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 =47) and 8% (n = 9) by 99% ethanol and 10% formalin, respectively. Similarly, the shrinkage of 89 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	anal	lyses

97

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 5 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

104 for the CPUE of each species, using R software (www.r-project.org). Explanatory variables 105 were collection depths (categorical data as surface and 10-m depth), longitude represented in 106 decimal number (e.g. 133°30' E was converted to 133.5), year, and water temperature. Salinity 107 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 108 109 observed for GLM with Poisson errors, a negative binomial distribution with log-link function 110 was assumed for GLMs. The final model was determined through a stepwise model selection 111 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).

116

117 **Results**

118

119 Abundance

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In 2014, 1,455 individuals from 9 taxonomic groups and 6 families were collected by 23 nettows, 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).

128 Water temperature ranged from 8.8 to 12.6 °C in 2014 and 8.8 to 12.1 °C in 2015. The

129 temperature was lower at eastern stations each year, and increased from stations 17 to 21 in 130 2015 (Fig. 2). No clear difference in water temperature between the surface and 10-m depth 131 was observed, except for station 12 in 2015. Salinity was also lower at eastern stations, ranging 132 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 1⁻¹ in 2015 (no data in 2014). No significant difference was observed between 133 134 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 135 136 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*.

142 The CPUE of A. japonicus was greater in eastern areas especially in 2014 (Fig. 3). Negative 143 relationship between its CPUE and water temperature was observed (p < 0.05; Table 2), 144 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). 145 146 Although the CPUE of S. marmoratus was suggested to be greater at higher water temperature 147 by the GLM, the effect of longitude was larger than that of water temperature. The CPUE of 148 other species was not affected by longitude nor water temperature except for *H. otakii*. CPUEs 149 of A. japonicus and Hexagrammos spp. were greater in 2014 than in 2015, while that of S. 150 marmoratus was greater in 2015 than in 2014.

151

152 Body size

154 The TL of A. japonicus was larger at eastern stations than at western stations (Fig. 4). Average 155 TL \pm standard deviation (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 ± 1.2 mm (n = 216) at Stations 13–17 in 2014. 156 157 Similarly, it was $5.2 \pm 1.1 \text{ mm}$ (*n* = 188) at Stations 1–7, $6.7 \pm 1.3 \text{ mm}$ (*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 and S. 158 159 *inermis* species complex also varied with longitudes, while no significant effect of longitude 160 was observed for H. otakii and H. agrammus (Table 3). The TLs of A. japonicus and S. 161 marmoratus were larger at lower temperatures while those of S. inermis species complex and 162 H. otakii were smaller at lower temperatures. However, the effect of water temperature on the 163 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.

170

171 **Discussion**

172

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.

190 The mechanisms driving larval size variation in winter are unclear. One possible 191 explanation is that lower temperatures in eastern areas induce an earlier spawning in winter. For 192 example, A. japonicus start their vitellogenesis when water temperature falls to 20 °C, and 193 subsequent progress of vitellogenesis is most rapid under 14 °C but final maturation completes 194 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. 195 196 comm.) and early November around Station 15 (east; Kagawa Prefecture, pers. comm.). 197 Thereafter, water temperature descended to 14 °C in early January around Station 2 and early 198 December around Station 15, and reached to 11 °C in early February around Station 2 and early 199 January around Station 15. Thus, the timing of the water temperature drops to the certain value 200 differs approximately one month between these stations. Therefore, spawning of A. japonicus 201 would begin one month earlier in eastern areas (including around Station 15) than western areas 202 (including around Station 2). In contrast, higher temperature leads to higher growth rates, as 203 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.

207 For rockfishes such as S. marmoratus, a similar explanation might be applicable for the 208 difference in larval body sizes between eastern and western areas. The reproductive pattern in 209 this species largely differs from that of A. japonicus: S. marmoratus spawn larvae directly into 210 the water column, and one female releases one to several batches [18]. The parturition period 211 of S. marmoratus continues from December to April [14], but survival of larvae reduces 212 associated with the timing of parturition [19], indicating the importance of early cohorts in S. 213 marmoratus at each area. Mature females of S. marmoratus release larvae with 4 mm TL during 214 the early night [20], and larvae grow up to 7.2 and 12.3 mm TL on 22 and 35 days after 215 parturition, respectively [21]. The collected larvae of S. marmoratus were <7 mm TL at western 216 stations in 2014 (Fig. 4), while larvae >11 mm were observed at eastern stations in 2014. Thus, 217 the parturition would start around 10 days earlier in eastern areas, leading to larger larval sizes 218 than western areas. Further examination on the mechanisms causing longitudinal difference in 219 larval sizes of rockfishes is necessary. The reason why the larval sizes of *Hexagrammos* species 220 did not differ between areas is also unknown. The larvae of H. otakii around 15 mm TL, as 221 collected in 2015, were born within 30 days, inferred from the laboratory observation [22]. This 222 indicates the short spawning period of this species [23] led to small differences in body size 223 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.

240 Larval abundance was not necessarily higher in eastern areas. Greater catch and abundant 241 distribution in eastern areas have been well recognized for A. japonicus [29], resulting from 242 heavier sand removal in western areas in the past. However, longitude was not necessarily the 243 most important variable affecting the number of collected larvae of even A. japonicus. Spatial 244 relationships in habitats between adults and larvae of each species or larval connectivity 245 between areas are issues that should be investigated in future. Furthermore, higher temperature 246 and higher salinity in western areas were observed in the present study (Fig. 2), indicating the 247 formation of the thermohaline front. Around the thermohaline front, a high concentration of 248 larvae such as *Hexagrammos* species and prey organisms often took place [30-32]. Such 249 hydrographic structure should be considered as a potential factor affecting larval assemblages. 250 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 254 compared to 25 and 50 m layers [33]. Depth preference of rockfish larvae should be investigated 255 further. Collection depth was irrelevant to the CPUE of A. japonicus, but this differs from the 256 past observation that A. japonicus larvae prefer depths of 5–15 m during daytime [34]. Similarly, 257 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 258 259 for these differences. Actually, the congeneric A. marinus larvae were abundant in surface 260 waters during the day at in areas without vertical environmental gradients, whereas the larvae 261 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.

268

269 Acknowledgements

We are grateful to Dr. H. Hashimoto and Y. Yamada for motivating this study by their preliminary research. We thank staff of TRV Toyoshiomaru and members of the Laboratory of Biology of Aquatic Resources, Hiroshima University, for their support in field samplings. We also thank Dr. Y. Kurita and anonymous reviewers for their critical comments on the manuscript. This work was partly supported by the Environment Research and Technology Development Fund (S-13) granted by the Ministry of the Environment, Japan.

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374 Figure captions

375

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

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- 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.
- 383

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*).

389

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 (a) *Ammodytes japonicus*

2015

(Fig. 3)

0

1 5

10



(b) Sebasticus marmoratus





(c) Sebastes inermis species complex



(d) Hexagrammos otakii





(e) Hexagrammos agrammus





Table 1

		2014				2015		
Family	Species	Ns*	N10*	TL range	Ne*	N10*	TL range	
				(mm)	INS		(mm)	
Ammodytidae	Ammodytes japonicus	866	430	2.6-13.1	455	251	3.1-16.6	
Scorpaenidae	Sebastiscus marmoratus	5	19	2.5-11.2	74	121	2.3-21.1	
	Sebastes inermis species complex	7	45	3.7-8.5	11	51	3.3-18.1	
	Sebastes pachycephalus	1	3	6.2-9.8	0	5	6.7-16.1	
	Sebastes oblongus	0	0		0	1	9.4	
	Unidentified Sebastes	2	0	No data	0	0		
Hexagrammidae	Hexagrammidae Hexagrammos otakii		1	6.0-11.4	22	4	8.0-14.9	
	Hexagrammos agrammus	26	0	6.3-11.4	5	0	8.4-11.6	
Lateolabracidae	Lateolabrax japonicus	0	1	9.0	0	4	6.0-11.6	
Pleuronectidae	leuronectidae Pseudopleuronectes vokohamae		0		3	3	3.0-6.8	
	Platichthys bicoloratus	0	0		0	5	6.9-7.8	
	Pleuronichthys lighti	0	1	20.6	0	0		

List of species collected in January 2014 and 2015

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	р	Variable	Estimate	SE	р
Ammodytes jap	onicus						
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
Sebastiscus marmoratus							
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
Sebastes inermis 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
Hexagrammos	otakii						
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
Hexagrammos agrammus							
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

Analysis of Deviance				Summary				
Error source	Sum of square	df	р	Variable	Estimate	SE	р	
Ammodytes jap	onicus							
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	
Sebastiscus ma	rmoratus							
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	
Sebastes inermis species complex		Σ.						
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	
Hexagrammos	otakii							
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	
Hexagrammos	agrammus							
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	

of each species

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.