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Comparisons of diet and nutritional condition in *Pseudopleuronectes herzensteini* juveniles between two nursery grounds off northern Hokkaido, Japan

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Abstract

To characterise food-habits differences in *Pseudopleuronectes herzensteini* juveniles, we compared diets, prey diversity and nutritional states between two groups i.e., one in the Sea of Japan and the other in the Sea of Okhotsk around northern Hokkaido, Japan. Juveniles were collected with a sledge net along the sea bottom at the depths of 8–50 m in August 2010 and 2011. In the Sea of Japan, 63 were analysed (23 in 2010 and 40 in 2011). In the Sea of Okhotsk, 88 were analysed (55 in 2010 and 33 in 2011). There were no differences in standard lengths of juveniles (the Sea of Japan: 27.0 mm in 2010 in median; 28.8 mm in 2011; the Sea of Okhotsk: 28.3 mm in 2010; 29.2 mm in 2011) or in bottom water temperatures at the study sites. However, stomach content volume and Fulton's condition factor K were higher in the Sea of Okhotsk than in the Sea of Japan. High feeding intensities in the Sea of Okhotsk may have led to a high nutritional status in fish collected from this sea. In both seas, the diet comprised mainly harpacticoid copepods, gammarids and polychaetes, with some additional bivalves being observed in the Sea of Japan. The value of the prey-diversity index (Δ^*) was lower when the K value of juveniles was higher.

Key words: flatfish, harpacticoid copepods, condition factor K, prey diversity, Sea of Japan, Sea of Okhotsk

Introduction

Marine fish mortality is generally high during early life stages as eggs, larvae and juveniles [1], and fluctuating mortality often leads to highly unpredictable fish landings. The reasons for such fluctuations vary in different species, according to the ways in which biotic and abiotic factors affect fish populations during the early life stages [1]. For improved understanding of mortality fluctuations, it is important to gain further knowledge of fish diets and food habits.

Pseudopleuronectes herzensteini is a cold-water species of pleuronectid flatfish distributed around Japan from the Boso Peninsula to Hokkaido and the Korean Peninsula to the Tatar Strait in the western Sakhalin [2]. It is a commercially important demersal fish with annual landings that fluctuate widely [3]; the annual landing of this species in northern Hokkaido varied approximately 2,000–4,000 t during 1980–2010 [4]. The species spawn in the coastal area of Hokkaido in the Sea of Japan from May to June. Many eggs and larvae are transported to the Sea of Okhotsk by the Tsushima and Soya Warm Currents, but some remain in the Sea of Japan. Settlement at the most advanced larval stage occurs from July to August [2]. Juveniles that settle in the coastal areas in the Sea of Japan (hereinafter "J-bred juveniles") remain and mature in the Sea of Japan, whereas those that settle in the Sea of Okhotsk ("O-bred juveniles") return and spawn after 2 or 3 years in the Sea of Japan (Fig. 1) [5, 6]. Immature O-bred juveniles grow faster than immature J-bred juveniles [6, 7]. Growth differences in *P. herzensteini* juveniles will affect their survival and recruitment variation. The main reasons for growth differences in juveniles are water temperature and food availability [1]; however, experienced water temperatures show no difference between J-bred and O-bred juveniles (Joh *et al.*, unpubl. data 2014). Knowledge of food habits of immature and mature *P. herzensteini* have been described (mainly, polychaetes, gammarids and bivalves [8-10]), whereas those of juveniles are poorly known as well as the nutritional conditions. In juveniles, Yoshimura and Kiyokawa [11, 12] reported that J-bred juveniles of 10–30 mm body length fed mainly on copepods, bivalves and gammarids during 1995–1996, but the food habits of O-bred juveniles are not known. The present study aimed to characterize food habits of juveniles in the Sea of Japan and the Sea of Okhotsk, by comparing them from three perspectives: 1) diet and prey size distribution in the gut contents, 2) prey number and volume per individual as indices of feeding intensity, and 3) prey diversity index in the diet and nutritional state index of juveniles during August 2010 and 2011. We used Warwick and Clarke’s taxonomic distinctness [13] as a prey diversity index of stomach contents. This index has never, to our knowledge, been applied for the analysis of food habits of demersal fishes. We also discussed relationship between growth and food habit.

Materials and Methods

The population of *P. herzensteini* in northern Hokkaido occurs mainly at depths in the range of 20–40 m [2, 14, 15], in the coastal waters off Obira and Oumu towns, facing the Sea of Japan and the Sea of Okhotsk, respectively (Fig. 1b). We set up sampling stations at sites where the bottom depths at sampling stations off Obira and Oumu, respectively, ranged from 24 to 50 m and 8 to 50 m (Fig. 1c, d). Grain sizes of bottom sediments in these waters are fine sands to rocks without silt and clay fractions (> 0.063 mm) [16, 17]. Two warm currents, the Tsushima Warm Current in the Sea of Japan, whose name changes to the Soya Warm Current in the Sea of Okhotsk, cover these areas throughout the year (Fig. 1b), with their speeds being highest from June to August and lowest from October to November [18].

Sampling was performed on board the *Hakuei-maru* (4.9 t) in the Sea of Japan and the *Seiwn-maru* (9.7 t) in the Sea of Okhotsk during the hours of 05:58–14:00, in mid and late August 2010–2011 (Table 1) as part of the annual recruitment monitoring program of flatfishes by the Hokkaido Research Organization Fisheries Research Department. Bottom water temperatures at all sampling stations were measured with a data logger (TidbiT v2, Onset Computer Corp.) in the Sea of Japan and a salinity-temperature-depth profiler (ASTD650, JFE Advantech Co., Ltd.) in the Sea of Okhotsk. Young-of-the-year juveniles were collected by bottom towing of a sledge net (1.8 m wide, 0.3 m height, and 13 mm cod-end mesh) for 10 min, after which the samples were counted and recorded on board. In 2010, the juveniles were immediately stored in 90% ethanol, and several days after sampling, they were measured and weighed. A slide calliper was used to measure the standard length (SL), to the nearest

0.01 mm, after which the fish were weighed on an electronic balance to determine wet body weight (BW) to the nearest 0.01 g. In 2011, juveniles were taken to the laboratory on ice and measured for SL and BW on the same day. After these procedures had been completed, the abdomens (which included stomachs) were preserved in 90% ethanol.

In the Sea of Japan, in 2010 25 juveniles were collected, and the stomach contents of 23, excluding two damaged juveniles, were analysed. They were grouped together (because of the small sample size) and analysed as “All”. In 2011, 61 juveniles were collected and the stomach contents of 40, excluding 21 damaged juveniles, were analysed. These were divided into two groups: “J1” and “Others”, which respectively consisted of 19 and 21 juveniles collected from J1 (31 m bottom depth) and other sampling stations (Fig. 1c).

In the Sea of Okhotsk, the stomach contents of 55 juveniles at station O1 (36 m bottom depth), O2 (43 m) and O3 (37 m) were analysed in 2010. A total of 33 juveniles at O4 (31 m) and O5 (45 m) were analysed in 2011.

The stomach contents were extracted and sorted to the lowest possible taxa, and prey items were counted. Each prey item in the diet was measured three dimensionally (Fig. 2), using a binocular microscope with an attached micrometre, marked at 0.01 mm intervals. Measurements were performed for prey-size comparison and volume estimation. Digested prey items were not counted as diet. For prey that were missing body parts, body length were estimated from linear regression formulae from prey lengths obtained from undigested prey items. The stomach content weights, parts by prey item, were not measured because they were too light (< 0.1 mg). If prey items were cut off (e.g. polychaetes), the largest length to the stump was measured (Fig. 2). Whether a prey item is swallowed by a predator is not restricted by the largest prey length (e.g. L in harpacticoid copepods; Fig. 2), but usually by the second-largest length (SLL) [19]. For this reason, we used SLLs (shown in Fig. 2) to compare prey sizes.

Data on stomach contents in each sampling station or sample group were expressed as percent occurrence frequency ($\%F_i$: the percentage of juveniles that consumed prey type i) and number and volume percent [$\%N_i$ and $\%V_i$ being respectively the percent of each prey type (of the total number), and volume of prey i]. Volumes of prey items were calculated from simple geometric formulae following Nishiyama and Hirano [20], Takatsu *et al.* [21] and Komoto *et al.* [22] (Fig. 2). An index of relative importance, $\%IRI_i$ [23] was also calculated, for each sampling station, sample group or sampling area, to determine the dominant diet as follows:

$$IRI_i = (\%N_i + \%V_i) \times \%F_i$$

$$\%IRI_i = IRI_i \times 100/\Sigma IRI$$

Prey diversity was determined by juveniles, using Warwick and Clarke’s taxonomic distinctness $\varDelta^*$ [13], which express taxonomic diversity and includes taxonomic distance between prey items as follows:

$$\varDelta^* = \sum\sum_{i<j} w_{ij} \cdot n_i \cdot n_j \Big/ \sum\sum_{i<j} n_i \cdot n_j$$

Where, w_{ij} is the taxonomic distance between species i and j; n_i and n_j are the $\%N$ of prey species i and j in stomach contents of juveniles at each station, respectively. If species i and j are within the same genus but of different species, w_{ij} is 1. Likewise, if they are within the same family but of different genera, w_{ij} is 2. $\varDelta^*$ ranges from 1 to $Lv - 1$, where Lv is the number of hierarchical taxonomic levels (which, in the present study, was 14). A large value for $\varDelta^*$ means that the diversity is high. In this study, $\varDelta^*$ values were calculated for all stomach contents comprising more than one prey type.

Total numbers and volumes of prey items per juvenile were used to indicate feeding intensities, with the aim of comparing results among sampling stations and sample groups.

Fulton’s condition factor K was used as a nutritional condition index and was calculated as follows:

$$K = Bw \times 100/Sl^3$$

where Bw is body weight of the juvenile in g and Sl is standard length in cm. K values among sampling stations and sample groups were compared in the same year, because BW measurements were performed under different storage conditions in 2010 (ethanol solution) and 2011 (cooling on ice).

The Kruskal-Wallis test was used to compare SLs among sampling stations and sample groups, and to compare the SLL of prey items among prey types. Scheffe’s multiple comparison was used to compare Ks and feeding intensities between the two areas. Mann-Whitney U test was used to compare SLLs between prey types by area or year. Spearman's rank correlation was used to compare the relationship between $\varDelta^*$ and

K. Statistical analyses were conducted using R 3.1.0 (The R Foundation for Statistical Computing) or Microsoft Office Excel 2007 (Microsoft Corporation).

Results

Water temperature and body length

A total of 86 *P. herzensteini* juveniles in the Sea of Japan and 558 in the Sea of Okhotsk were collected in August in 2010 and 2011 (Table 1). Median bottom temperatures of all sampling stations where juveniles were collected in 2010 were 20.1°C and 20.0°C in the Sea of Japan and the Sea of Okhotsk, respectively. Those in 2011 were 17.1°C and 18.8°C in the Sea of Japan and the Sea of Okhotsk, respectively. Temperature differences were smaller between areas than between years.

In 2010, median SLs of juveniles collected were 27.0 mm in the Sea of Japan and 28.3 mm in the Sea of Okhotsk. In 2011, those were 28.8 mm in the Sea of Japan and 29.2 mm in the Sea of Okhotsk. Juvenile SLs did not differ between areas in both years (*U* test; $p = 0.13$ in 2010 and $p = 0.31$ in 2011).

In 2010, the median SLs of juveniles that had been subjected to stomach content analysis were 27.0 mm (All), 27.5 mm (O1), 28.5 mm (O2), and 29.7 mm (O3). In 2011, they were 28.8 mm (J1), 30.9 mm (Others), 29.6 mm (O4) and 29.3 mm (O5). The SLs of juveniles that had been subjected to stomach content analysis did not differ among sampling stations and sample groups in 2010 (Kruskal-Wallis test; $p = 0.18$) and 2011 ($p = 0.13$).

Prey items

Juveniles from the Sea of Japan and the Sea of Okhotsk fed on 51 taxa + 2 unidentifiable crustaceans and 82 taxa + 15 unidentifiable crustaceans and eggs, respectively (both years combined, Online Resource 1).

In the Sea of Japan, *%IRI* showed that harpacticoid copepods comprised 11.0% and 34.0% of the diets in 2010 and 2011, respectively. Polychaetes accounted for relatively high *%IRI*, 61.5% and 7.7%. These values were followed by bivalves (22.0% and 13.6%) and gammarids (3.9% and 8.8%).

In the Sea of Okhotsk, harpacticoid copepods (*%IRI*: 19.3% and 81.7%) and gammarids (40.2% and 18.5%) dominated, and these values were higher than those of polychaetes (12.2% and 7.0%) and other prey items.

Bivalves showed higher representation in the Sea of Japan with respect to their *%F* and *%N* values (*%F* = 74 and 65 and *%N* = 33.8 and 17.6) than in the Sea of Okhotsk (*%F* = 47 and 18 and *%N* = 4.1 and 0.5). In the juvenile diet, all bivalve prey were found in their shells, indicating that the juveniles swallowed them whole.

Among harpacticoid prey, *Halectionosoma* spp. showed the highest values for *%F* and *%V* in the Sea of Japan (*%F* = 26 and 35, *%V* = 0.2 and 2.4, Online Resource 1), and *Amphiascus* spp. showed the highest values for *%N* (*%N* = 1.0 and 26.2). In the Sea of Okhotsk, *Longipedia* spp. represented the highest percentages in harpacticoid copepods (*%F* = 64 and 76, *%N* = 11.1 and 45.4, *%V* = 1.6 and 26.5).

Among gammarid prey, *Cerapus* spp. represented the highest percentages in the Sea of Okhotsk in 2010 (*%F* = 47, *%N* = 20.4, *%V* = 34.8). There were no dominant gammarids in the Sea of Japan.

Harpacticoid copepods (in two stations and one group), gammarids (in three stations) and polychaetes (in one station and one group) represented the highest percentage (> 30%) of *%IRI* in eight stations or groups (Fig. 3). Bivalves did not dominate (show the highest *%IRI*) in any stations or groups, and *%IRI* values of bivalves in the Sea of Japan showed higher *%IRI* values (16.2–23.6%) than those in the Sea of Okhotsk (0.02–4.7%).

Prey size

Median SLLs of all prey items were 240 μm in the Sea of Japan and 223 μm in the Sea of Okhotsk in 2010, and SLLs were not significantly different between seas (*U* test; $p = 0.57$). In 2011, median SLLs were 374 μm in the Sea of Japan and 250 μm in the Sea of Okhotsk, and SLLs in the Sea of Japan were significantly larger than those in the Sea of Okhotsk (*U* test; $p = 0.003$).

Median (range) SLLs of major prey taxa were as follows: harpacticoid copepods, 180 μm (90–380 μm); gammarids, 220 μm (110–1040 μm); polychaetes, 265 μm (51–2282 μm) and bivalves, 403 μm (210–1300 μm). Among these SLLs, there was a significant difference (Kruskal-Wallis test, $p < 0.001$), harpacticoid copepods being the smallest and bivalves being the largest. The size range of polychaetes was greater than those of other prey taxa (Fig. 4). There was no significant difference among SLLs of bivalves between the Sea of Japan (median, 420 μm; range, 210–1300 μm) and the Sea of Okhotsk (370 μm and 217–1260 μm; U test; $p = 0.18$). As juveniles grew, they fed on an increasingly larger size range of prey. Larger juveniles fed on both small and large prey.

Feeding intensity

In 2010, feeding intensities (number of prey individuals per stomach) of juveniles in O1, O2 and O3 in the Sea of Okhotsk [medians: 26, 21 and 42 individuals (inds.) juvenile^{-1}] were significantly higher than those in “All” in the Sea of Japan (7 inds. Juvenile^{-1}; Scheffe’s multiple comparison: $p < 0.001$; Fig. 5a). Similarly, in 2011, those in O4 and O5 (68 and 21 inds. juvenile^{-1}) were significantly higher than those in J1 and “Others” (6 and 3 inds. juvenile^{-1}; $p < 0.001$). Feeding intensities, indicated by prey volume per stomach in the Sea of Okhotsk (median: 0.81, 1.76 and 2.07 mm^3 juvenile^{-1}), were significantly higher in the Sea of Japan in 2010 (0.40 mm^3 juvenile^{-1}; Scheffé’s multiple comparison: $p = 0.02$; Fig. 5b). Similarly, in 2011, those in the Sea of Okhotsk (1.06 and 1.19 mm^3 juvenile^{-1}) were significantly higher than those in the Sea of Japan (0.66 and 0.08 mm^3 juvenile^{-1}; $p = 0.003$).

Condition factor

Fulton’s condition factor K values were significantly higher in O1, O2 and O3 in the Sea of Okhotsk (median: 1.33, 1.38 and 1.26) than in “All” in the Sea of Japan (0.97) in 2010 (Scheffé’s multiple comparison; $p < 0.001$; Fig. 5c). In 2011, the K values in O4 and O5 (1.54 and 1.51) were also significantly higher than those in J1 and “Others” (1.41 and 1.45; $p = 0.008$).

The taxonomic distinctness Δ^* in juvenile stomach showed significantly negative correlation with K value in 2010 (Spearman's rank correlation; $\rho = -0.32$; $p = 0.006$; Fig. 6) and in 2011 ($\rho = -0.27$; $p = 0.03$). The median Δ^* values for prey in 2010 were 12.43 at All, 10.71 at O1, 9.09 at O2, and 11.56 at O3. In 2011, the median Δ^* values were 11.94 at J1, 11.00 at Others, 8.28 at O4 and 10.32 at O5. The highest median of Δ^* was recorded at All where the highest *%N* was 33.8% for bivalves, followed by 23.2% for harpacticoid copepods. The lowest median Δ^* value was recorded at O4 in 2011, where harpacticoid copepods dominated, with a *%N* of 81.5%, whereas other taxa comprised < 18.5%.

Discussion

The diet of *P. herzensteini* juveniles in the Sea of Okhotsk was clarified for the first time. Stomach content analyses revealed that the major prey taxa were harpacticoid copepods, gammarids and polychaetes in both the Sea of Japan and the Sea of Okhotsk, with bivalves being a major prey taxon in the Sea of Japan around northern Hokkaido in August 2010 and 2011. In addition, the juveniles fed on a wide size range of prey. Yoshimura and Kiyokawa [11, 12] reported that *P. herzensteini* juveniles of 10–30 mm in body length fed mainly on copepods, bivalves and gammarids in the Sea of Japan during 1995–1996, and these items were confirmed as important prey organisms for maintaining juveniles in the Sea of Japan. These results agree with that of the present study.

In previous study, off Niigata prefecture, *P. herzensteini* juveniles (ca. 30 mm in body length) fed on polychaetes with > 70% in *%F* [24]. However, in our study, we found that juveniles were not highly dependent on polychaetes in *%F* (70% and 33% in the Sea of Japan, and 58% and 61% in the Sea of Okhotsk; Online Resource 1). Juveniles in both seas around northern Hokkaido fed on various prey items, and prey items differed geographically.

Prey items were larger in the Sea of Japan than in the Sea of Okhotsk in 2011. This size difference may have been due to the relatively high dietary composition of bivalves in the Sea of Japan (22.0% and 13.6% in *%IRI*; Online Resource 1). Bivalves represent large prey (Fig. 4), and thus are important prey items for *P. herzensteini* juveniles.

However, the maximum *%IRI* value for bivalves was 24% in the Sea of Japan, where the opportunity of feeding may have been lower than that for harpacticoid copepods, gammarids or polychaetes. It is not clear why prey sizes did not differ significantly between the two seas in 2010.

One-year-old fish grow faster in the Sea of Okhotsk than in the Sea of Japan [6, 7]. Juvenile sizes (SLs) were similar between the two seas in August during both years of our study period, but the juveniles in the Sea of Okhotsk showed larger nutritional condition (*K*) than those in the Sea of Japan (Fig. 5c). Thus, growth differences may start from the difference in feeding intensities in the juvenile stage (0 year; Fig. 5a, b). The difference in feeding intensities between the two seas is the most reasonable factor accounting for differences in nutritional difference. Different feeding intensities are generally caused by differences in predator size, time of day, prey size, water temperature and prey abundance in the environment [25]. In the present study, the predator size (SLs) difference in both seas was detected during August, and this explains the difference in feeding intensities. There may have been no differences in feeding time between the two seas, given that *P. herzensteini* is a visual day feeder [26] and we sampled juveniles at similar times during the daytime. The active feeding temperature of immature and mature *P. herzensteini* individuals is within the range of 17.8–19.0°C [27] and bottom temperatures in both seas were within or near this temperature range. Thus, the temperature difference cannot explain the cause of the difference in feeding intensity.

Mean calorie consumption per day positively correlates with the nutritional condition factor *K* and growth rate in the winter flounder *P. americanus* [28]. Growth differences of 0-year plaice, *Pleuronectes platessa*, in the Wadden Sea were affected by food availability, but not by temperature [29]. Growth differences in the northern rock sole *Lepidopsetta polyxystra* around Kodiak Island in Alaska were affected not only by temperature but also by food availability [30].

We propose that taxonomic diversity in diet affects the nutritional condition of predators. The nutritional condition (*K*) of *P. herzensteini* juveniles was higher when the value of Δ^* was lower in each sampling year (Fig. 6). Various animals, including fishes, tend to concentrate their predation on a specific prey taxon, if available prey in the environment are abundant. *P. herzensteini* juveniles with low values of Δ^* showed feeding success on a narrow taxonomic range of prey items, which might have a lower catch cost than feeding on a wide taxonomic range of prey. Future studies should compare the growth of juveniles in both seas by examining otolith and also examining stomach contents.

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Fig. 1 Study locations in the Sea of Japan and the Sea of Okhotsk; **a** schematic illustration of distribution of juveniles or immature fish; **b** spawning area of *Pseudopleuronectes herzensteini* (modified from Maruyama and Yamamoto [14], Watanobe [2, 15]); **c**, **d** sampling stations with isobaths. Stars indicate the locations of Oumu Town and Obira Town; open and solid circles indicate sampling stations, and solid circles indicate stations where stomach content analyses of collected *P. herzensteini* were performed. J1 and O1–O5 show station numbers. Bottom isobaths are based on data from the Japan Oceanographic Data Centre (http://www.jodc.go.jp/index_j.html; accessed 5 December 2012)

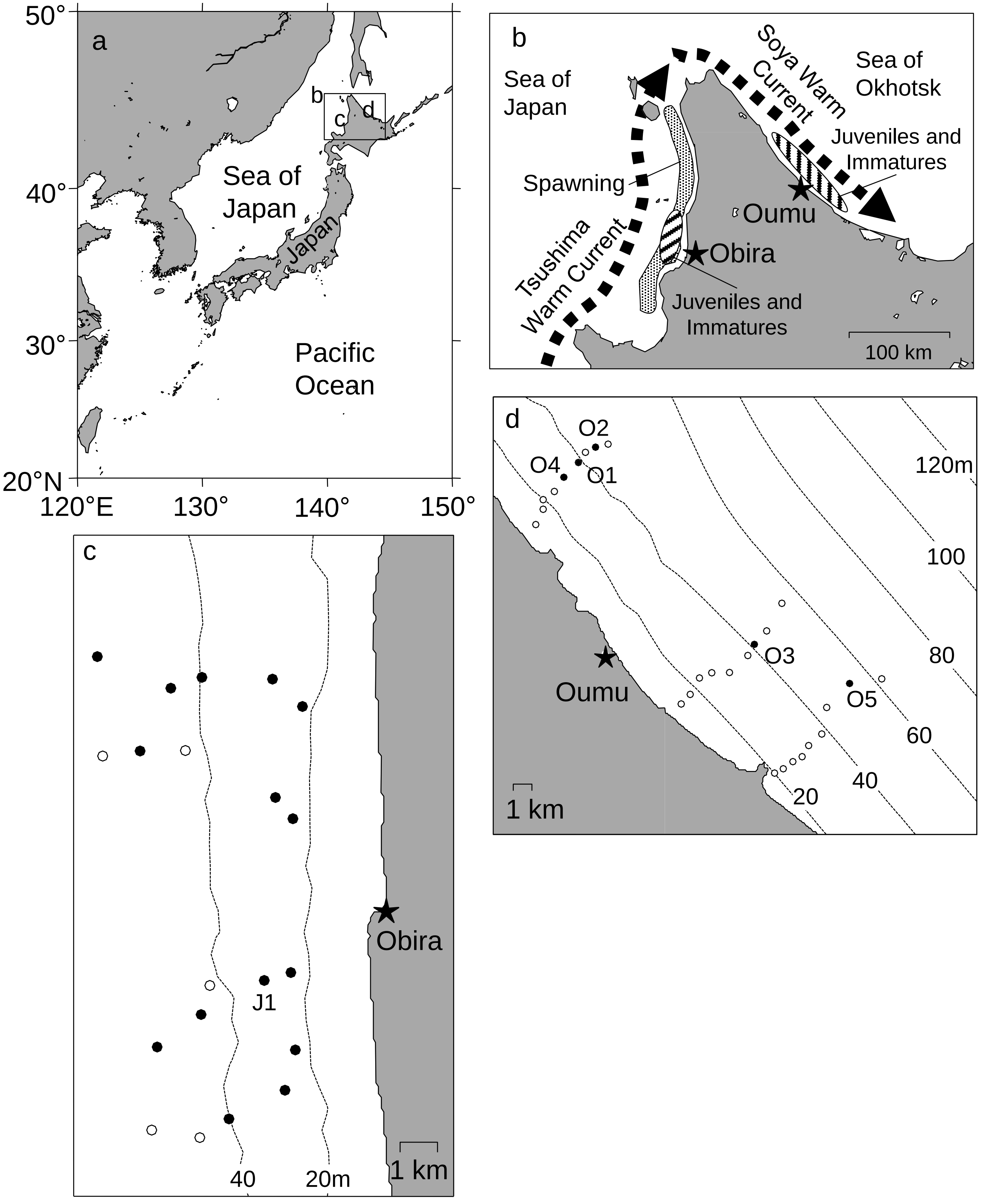
Fig. 2 Shapes of prey species and body sizes measured. Second largest lengths (SLLs) are indicated by abbreviations (underlined). SLLs of polychaetes are shown as *W* or *D* to indicate shapes of specific species

Fig. 3 Stomach contents of juveniles represented by *%IRI* for each sampling station or group, with bottom depth, median (range) of bottom temperature and area. Numerals above bars indicate numbers of juveniles examined

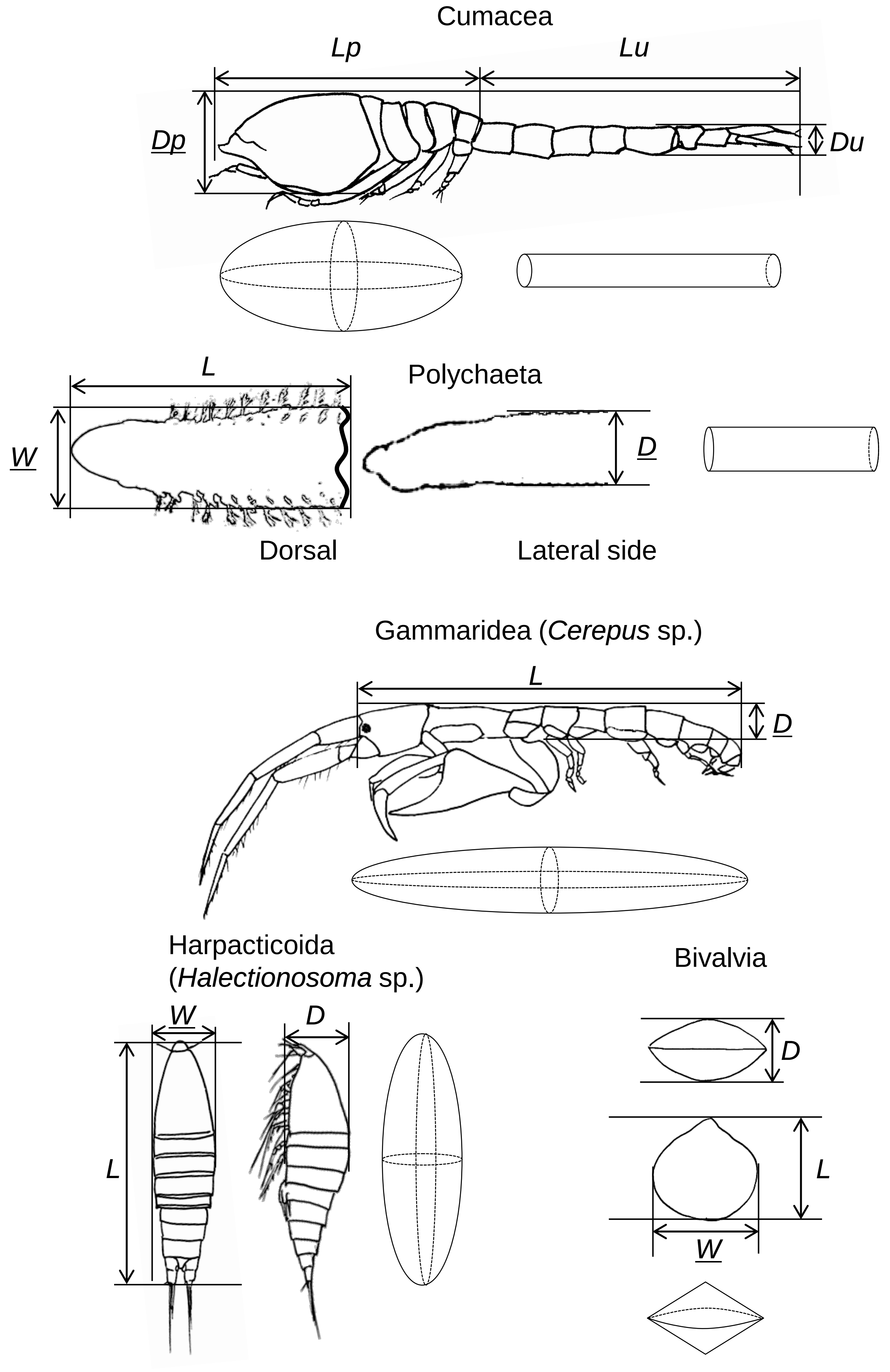
Fig. 4 Plot of juvenile standard length (SL; mm) and second-largest length (μm) of four major prey items (gammarids, harpacticoid copepods, polychaetes and bivalves)

Fig. 5 Box plots of food-item numbers per juvenile stomach (individual juvenile^{-1}; **a**), prey volume per juvenile stomach (mm^3 juvenile^{-1}; **b**), and Fulton's condition factor *K* of juveniles by sampling station or group and area (**c**). Numerals above boxes indicate number of juveniles examined

Fig. 6 Plot of Fulton's condition factor *K* and Warwick and Clarke's diversity index with taxonomic distance Δ^*. Open characters: 2010, solid characters: 2011



Kobayashi *et al*. Fig. 1 (8.5 cm width)



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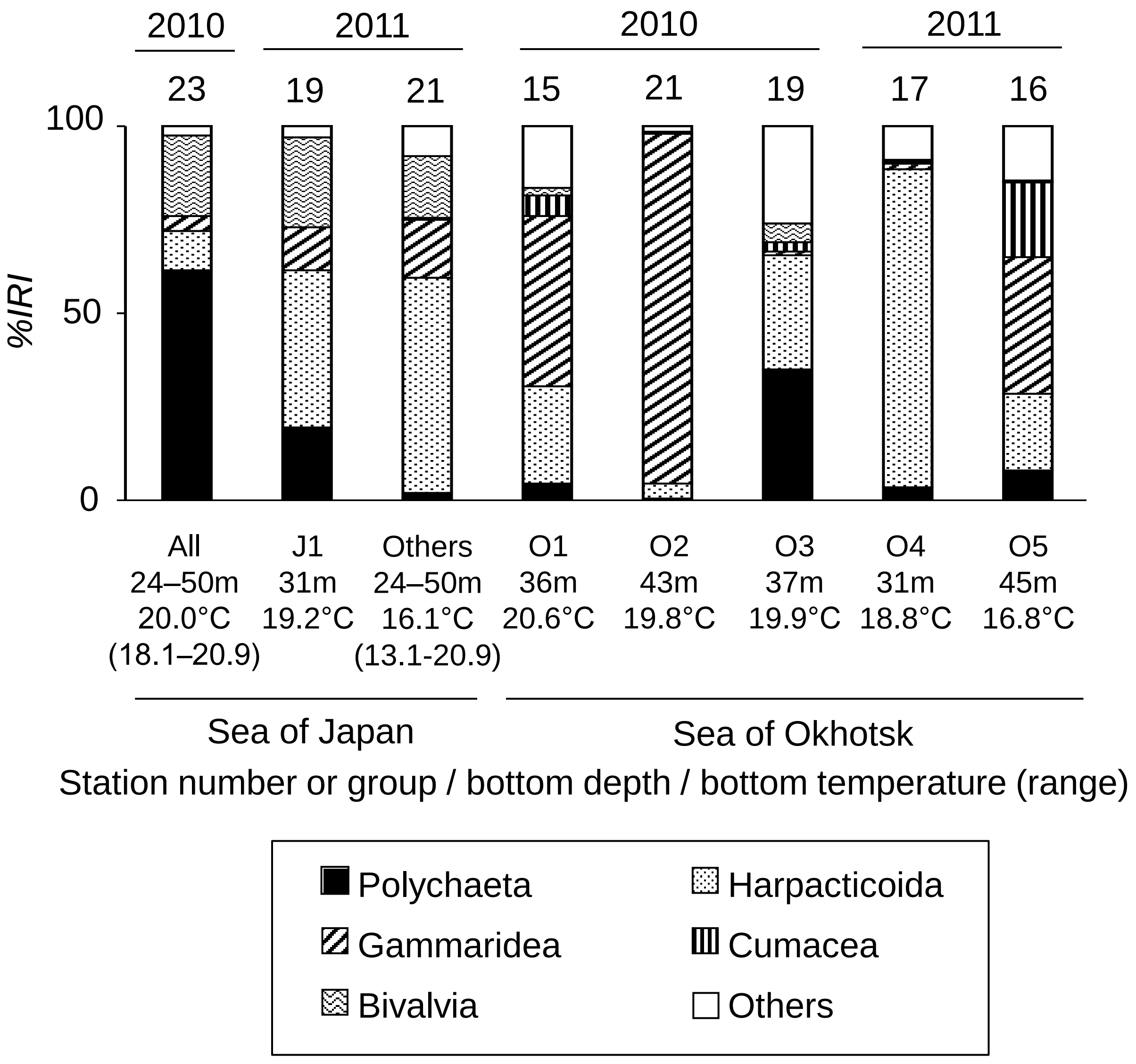

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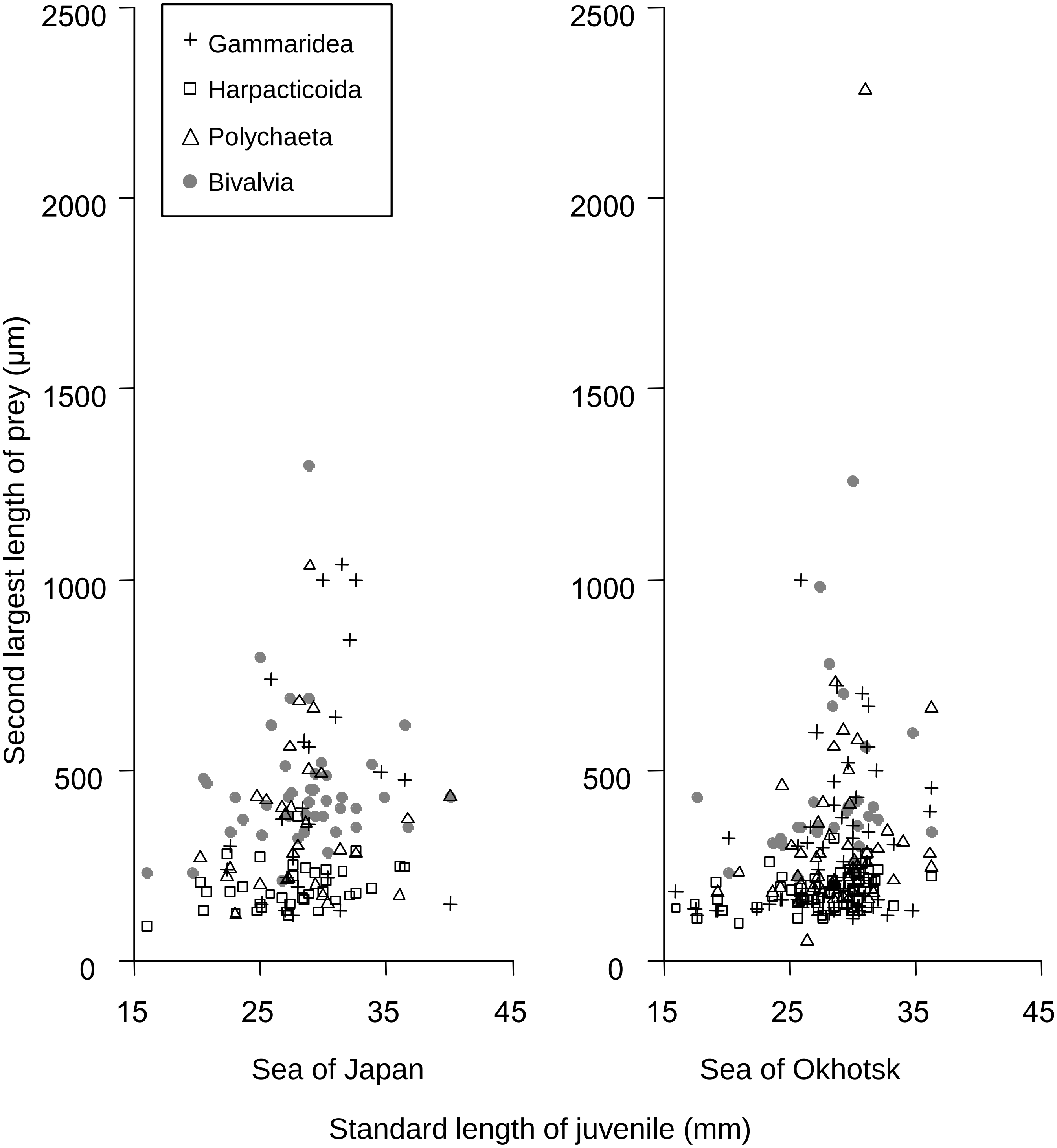
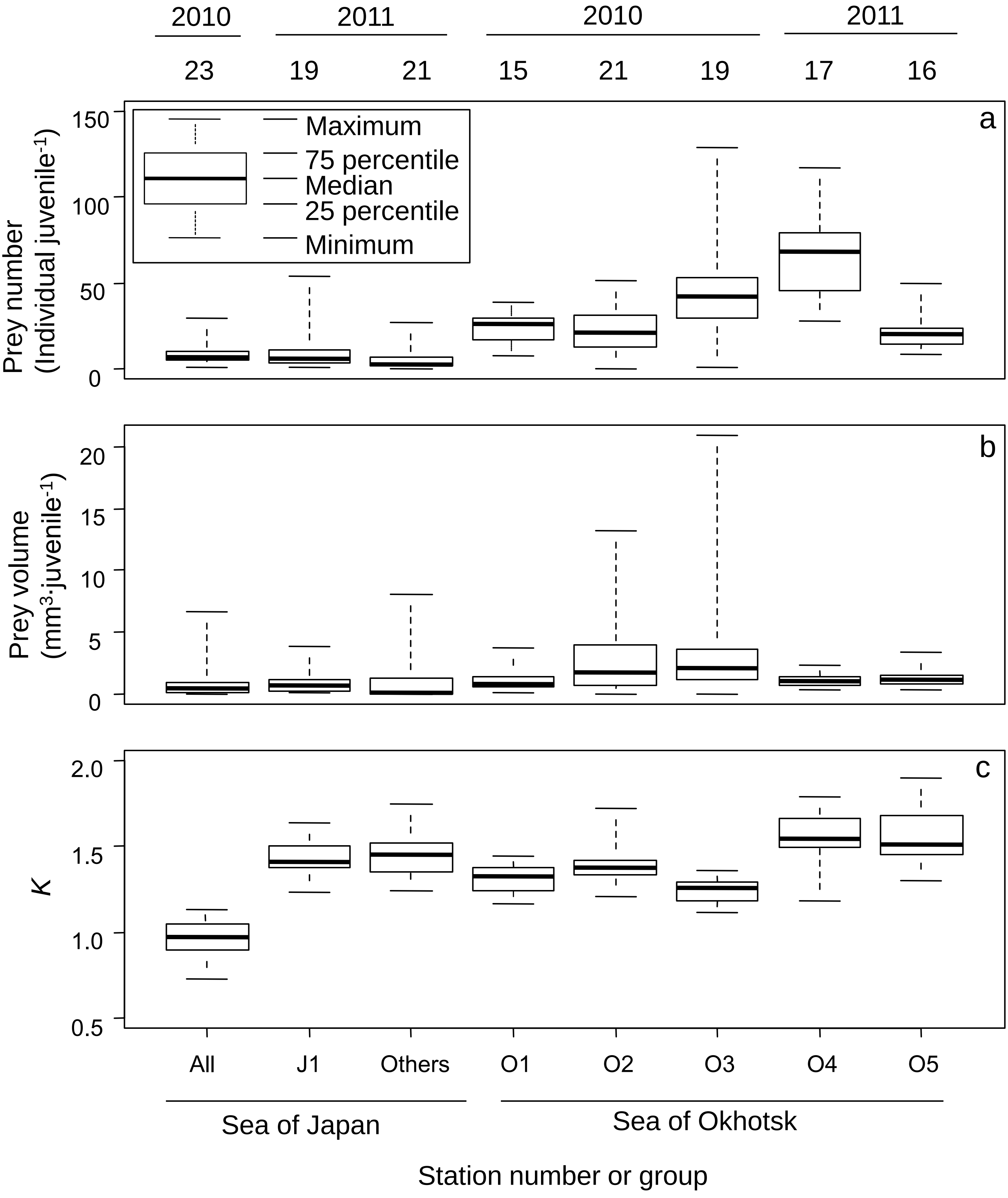
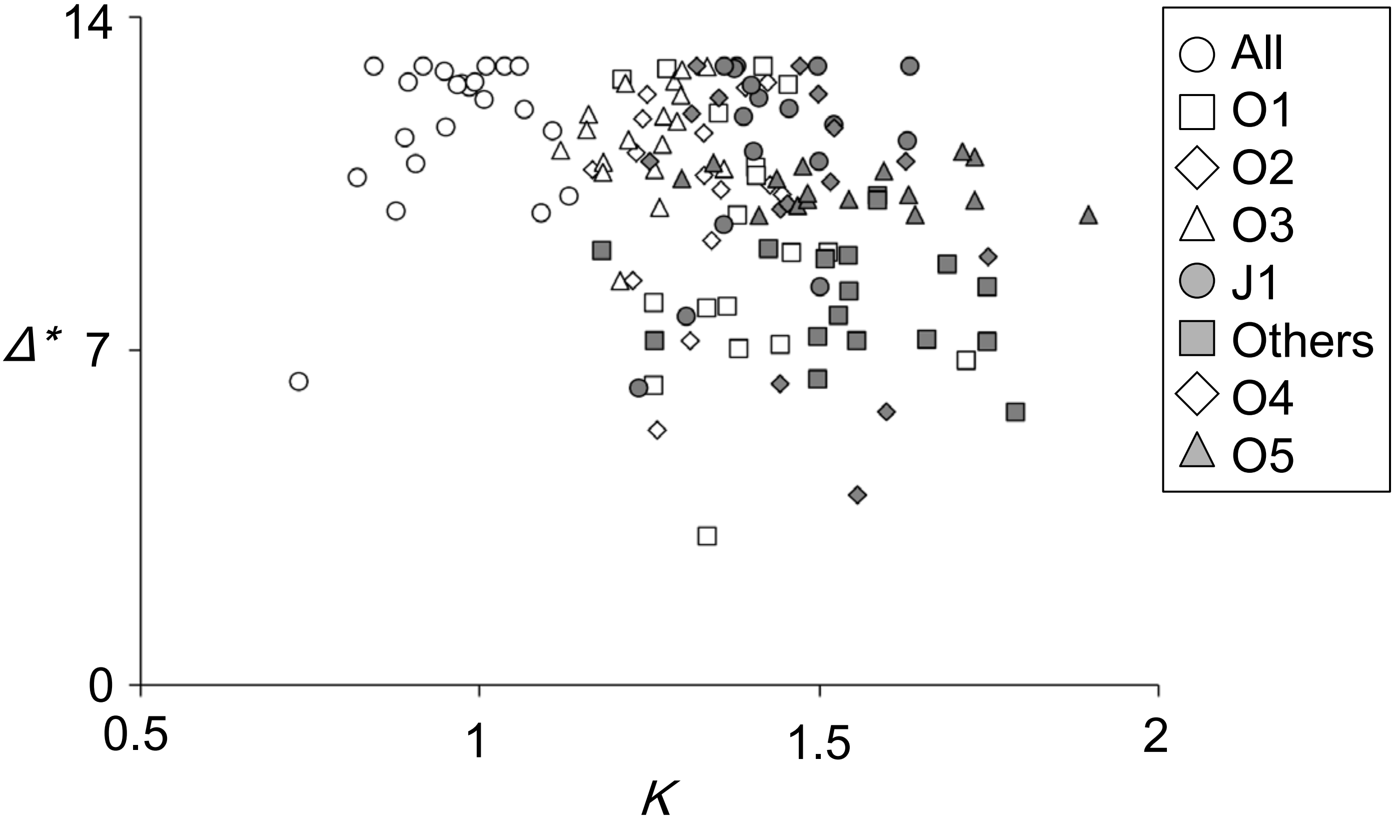


Kobayashi *et al.* Fig. 4 (8.5 cm width)



Kobayashi *et al*. Fig. 5 (8.5 cm width)



Kobayashi *et al*. Fig. 6 (8.5 cm width)

Table 1. Collection records of *Pseudopleuronectes herzensteini* in the two seas around northern Hokkaido

Area	Time	Date	Number of sampling sta.	Bottom depth (m)		Bottom temperature (°C)		Number of juvenile collected	SL (mm)*
				All sta.*	Juvenile collected*	All sta.*	Juvenile collected*		
Sea of Japan	05:58–12:34	Aug. 18, 2010	15	39 (24–50)	39 (24–48)	20.0 (12.5–22.0)	20.1 (12.8–22.0)	25	27.0 (16.0–40.1)
Sea of Japan	06:03–13:33	Aug. 17–18, 2011	20	39 (24–50)	31 (24–48)	14.9 (12.7–20.9)	17.1 (13.1–20.9)	61	28.8 (19.4–36.4)
Sea of Okhotsk	06:00–14:00	Aug. 25–26, 2010	27	30 (8–50)	30 (8–50)	20.0 (18.0–20.9)	20.0 (18.0–20.9)	260	28.3 (15.8–38.2)
Sea of Okhotsk	06:00–14:00	Aug. 24–25, 2011	27	30 (8–50)	31 (8–50)	18.8 (14.3–20.2)	18.8 (14.3–20.2)	298	29.2 (20.4–39.5)

*: median (range)

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