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Spatial distribution and feeding habits of the shrimp *Crangon uritai*, as a predator on larval and juvenile marbled sole *Pleuronectes yokohamae*

Running title: Predation of marbled sole by crangon

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ABSTRACT: To examine predation on larval and juvenile *Pleuronectes yokohamae* by *Crangon uritai*, the spatial distribution and feeding habits of *C. uritai* were studied. *C. uritai* fed on various prey, including *P. yokohamae*. Density-dependent predation on juvenile *Crangon* spp., larval and juvenile gobiid fish *Chaenogobius heptacanthus*, mysids, and gammarids was observed. The abundance of alternative prey might therefore play an important role in reducing the pressure of predation on *P. yokohamae*. In each year, *C. uritai* migrated from depths of 10m in March to depths of 3m in May. There was a significant negative correlation between the weighted mean depth (WMD) of *C. uritai* and the weighted mean bottom water temperature (WMBWT). The migration was therefore delayed in the cold spring, during which *C. uritai* occupied depths of approximately 10m. In contrast, no significant correlation was found between the WMD of *P. yokohamae* and WMBWT. Settlement of *P. yokohamae* began at depths of 15m, mainly during early April. The spatial distributions of these two organisms show greater overlap during the cold spring, resulting in increased opportunities for predation.

KEY WORDS: **bottom water temperature, *Crangon uritai*, predation, *Pleuronectes yokohamae*, spatial distribution.**

INTRODUCTION

Year class strength is dependent on survival during the early life stages of fishes. Predation has been hypothesized as the major cause of mortality of 0-group flatfishes on nursery grounds,[1-3] where density-dependent mortality seems to occur soon after settlement with certain flatfishes.[4-7] Mortality of plaice *Pleuronectes platessa* (L.) juveniles in the Wadden Sea is due mainly to predation by the brown shrimp *Crangon crangon* L.[8] There are many previous reports about predation on newly-settled flatfishes by crangonid shrimp.[9-12] There have also been attempts to estimate predation by analyzing the diets of shrimp caught in the field.[13-16]

Some studies have examined the distribution of the shrimp *C. crangon*. *C. crangon* migrates seasonally,[17] and differences in water temperature affect its migration.[18] It is inferred that during these migrations predator (crangonids) – prey (larval and juvenile flatfish) distribution patterns change. However, there has been no study of the relationships between inter-annual difference in water temperature and predation opportunities.

Marbled sole *Pleuronectes yokohamae* Günther makes up most of the biomass of the demersal fish assemblage in Hakodate Bay (Fig. 1), and is caught commercially with bottom set nets and gill nets.[19] From March to April, pelagic larvae of *P. yokohamae* are mainly transported from the offshore spawning ground to the inshore nursery area by a northward-inshore compensatory drift in Hakodate Bay.[20] The pelagic larvae are widely distributed in waters, with depths of 5-20 m, but demersal larvae and juveniles are concentrated at 15 m depth, and drastic decrease for demersal larvae and juvenile *P. yokohamae* were observed at ≤ 10 m depths.[20] The mortality rate of plaice after settlement increased with the initial settlement density, and the predation from shrimp *C. crangon* caused the mortality.[16] So predation on the larvae and juveniles by crangonid shrimps could be one of the major causes of the decrease in demersal larvae and juvenile *P. yokohamae* densities in Hakodate Bay. This paper examines the role of *Crangon uritai* Hayashi and Kim as a predator on larval and juvenile *P. yokohamae*. We (1) analyzed the stomach contents of *C. uritai*, (2) clarified the spatial and temporal distribution of *C. uritai* in the nursery ground of *P. yokohamae*, and (3) described the spatial and temporal difference in the opportunities of the shrimp predation on *P. yokohamae*.

MATERIALS AND METHODS

As high abundances of larval *P. yokohamae* occur in Hakodate Bay in spring, samples were collected at five stations on a transect within this bay (at 3, 5, 10, 15, and 20 m depths) during April-May 1997, April-June 1998, and March-June 1999-2000 (Fig. 1). Sampling was carried out three times a month in March-April, and twice a month in May-June, of each year. Sampling times were during daytime (08:00-16:00), because large numbers of commercial set nets, gill nets, and pots were set up in this bay (≤ 15 m depths), making it dangerous to tow the sledge net on the bottom during nighttime. At each station, *C. uritai*, larval and juvenile *P. yokohamae*, and the other epibenthic organisms were collected in two tows with a sledge net (60 cm wide, 40 cm tall and 0.5 mm mesh) for 5 min at a towing speed of approximately 0.9 m/s. The positions where the sledge net was lowered and retrieved were determined by DGPS, and the towing distance was estimated from the distance between these two positions. Landing of the net on the sea bottom was verified by the vibration of the towing wire. All organisms were immediately boiled for a few seconds once on board to prevent the vomiting of stomach contents, and then fixed in a solution containing 10 % buffered formalin in sea water. On 8 June 1999, the abundance of *C. uritai* and *P. yokohamae* could not be estimated, because a large number of juvenile *Crangon* spp. clogged the mesh of the sledge net. In late March 2000, sampling could not be carried out because of the rough sea.

In the laboratory, all crangonid shrimps were counted, transferred into 70 % ethanol solution to prevent decalcification, and identified according to Hayashi and Kim.[21] Total length (TL) of *C. uritai* (from the posterior edge of the orbital to the end of the telson), was measured to the nearest 0.01 mm scale with an electric slide caliper. Under laboratory conditions, crangonid shrimps feed on flatfish juveniles that measure ≤ 50 % of their TLs.[8,9,22-24] As the size at settlement of *P. yokohamae* is about 8mm in body length,[25] the gastric contents of all *C. uritai* > 15 mm TL were examined. Fish larvae and juveniles in the gastric contents were identified to the lowest possible taxon, and the remaining food organisms were identified to family level where possible. Data on gastric contents were expressed as percent frequency of occurrence (F %: the percentage of *C. uritai* that preyed on a particular type of prey) and relative percent in F% (FO %: the F % of a particular prey type to the total F% of prey items; $FO\ \%_i = F\ \%_i \cdot 100 / \Sigma\ F\ \%$ for prey i). The number of stomachs of *C. uritai* used in this calculation included the number of empty stomachs. FO% was calculated for comparison of prey importance instead of numerical composition (N %), because small numbers of prey items were remained in the shrimp stomachs in general, however if large numbers of a particular small sized prey occurred, large N% of the small prey occupied the majority with bias.

Body lengths (BL), or total lengths (TL), of undamaged prey items in the gastric contents were measured, and BLs or TLs of damaged specimens were estimated using the formulae in Table 1. The total number of prey items in the sample was counted at each station, and the densities (ind/m^2) of these prey organisms were calculated from the mouth width of the sledge net (0.6 m) to the towing distance. Categories of prey size were adopted to reflect observations of prey size in the gastric contents of *C. uritai*. Distribution overlap (Brey-Curtis overlap index: OI %) between *C. uritai* and *P. yokohamae* were calculated by sampling date as follows:

$$\text{OI } (\%) = 100 \ \{1\text{-}0.5 \ \Sigma \ |(c_i/\Sigma c_i)\text{-}(p_i/\Sigma p_i)|\}$$

where c_i (ind/100m^2) is the density of *C. uritai* at station i, and p_i (ind/100m^2) is the density of *P. yokohamae* at station i.

Weighted mean depths (WMD) of *C. uritai* and *P. yokohamae* were calculated as follows:

$$\text{WMD (m)} = \Sigma \ (d_i \cdot a_i) \ / \ \Sigma a_i,$$

where d_i (m) is the depth at station i, and a_i (ind/m^2) is the density at station i.[26] At each station water temperature on the sea bottom was measured with a CTD (Sea-Bird Electronics, Inc., SBE-19), or an STD (Alec Electronics Co. Ltd., AST-500). Weighted mean bottom water temperature (WMBWT) was calculated as follows:

$$\text{WMBWT (°C)} = \Sigma \ (t_i \cdot a_i) \ / \ \Sigma a_i$$

where t_i (ºC) is the bottom water temperature at station i and a_i (ind/m^2) is the density of *C. uritai* or *P. yokohamae* at station i.

RESULTS

Annual variation in bottom water temperature

Figure 2 shows seasonal changes in mean water temperatures on the sea bottom at 3, 5, and 10m depths of three stations. With the exception of a few days, bottom temperatures generally increased from late March to June. No data is available for late May, and early June of 1997, due to trouble of the STD. In 1999, lower bottom water temperatures were recorded from late March to the middle of April (0.8-1.4ºC lower than in 1997, 1.3-1.8ºC lower than in 1998, and 0.8-1.0ºC lower than in 2000), and from late May to early June (1.4-2.2ºC lower than in 1998, and 0.6-1.0ºC lower than in 2000).

Assemblage of crustacean decapods

Species composition of crustacean decapods collected with a sledge net at 3-20 m depth stations from March to June for the period 1999-2000 is shown in Table 2. The catches were dominated by *Crangon* (over 90 %), except for 9 March 1999 (71.8 %) and 18 March 1999 (87.6 %), and the other crustacean decapods occupied only a few catches through the sampling season in 1999-2000. Four crangonid shrimps were present: *Crangon dalli* Rathbun, *Crangon hakodatei* Rathbun, *Crangon amurensis* Brashnikov, and *C. uritai*. *C. dalli*, *C. hakodatei*, and *C. amurensis* were collected only at 15-20 m stations, and their densities were very low (all < 0.01 ind/m^2). In 1997 and 1998 we investigated species composition of Crangonidae only, and except for one individual of *C. dalli* collected at a depth of 20 m on 20 May 1998, samples were occupied exclusively by *C. uritai*.

State of the stomach contents of *C. uritai*

Feeding styles of crustacean decapods can be estimated from the morphology of the mouth organ.[27] *Crangon* spp. have low biting ability and swallow their prey; however they do possess a pair of ossicles in the stomach. We frequently found evidence of non-biting and swallowing of prey from the gastric contents of *C. uritai*, with some broken and unidentifiable pieces of prey also being observed. Therefore, bit off prey could not be enumerated by prey individual.

Predation on *P. yokohamae*

No larval or juvenile *P. yokohamae* was found in the gastric contents of the 145 individuals of *C. uritai* collected at the 15-20 m depth stations. Thirty three individuals of larval and juvenile *P. yokohamae* occurred in the diet of *C. uritai* collected at three stations of 3-10 m depths, and the minimum size of *C. uritai* that fed on *P. yokohamae* had a TL of 19 mm. The diet of *C. uritai* ≥ 19 mm TL is shown in Table 3. *P. yokohamae* consumed by *C. uritai* included preflexion larvae, flexion larvae, and juveniles, and their BLs ranged from 5.3 to 10.4 mm. Mean body length ratio (BL of *P. yokohamae* / TL of *C. uritai*) was 0.21 ± 0.07 (± standard deviation, N = 7, the range was 0.12-0.32), and this ration was estimated only from measurable or restorable BLs of *P. yokohamae*. Predation on *P. yokohamae* occurred between late March and mid April in 1999 (F % = 1.0-3.2), when water temperatures were lower than in other years, but did not occur in early and mid April 1997 and 1998, and between early March to mid April in 2000 (all F % = 0). Predation was observed on seven sampling days out of ten in 1999, but on fewer occasions in 1997 (two of five), in 1998 (two of seven), and in 2000 (two of nine). Predation was observed at 10m depths only during March - April of 1999, and at 5 m depths only in May in 1997 and 2000 (Table 4). Predation at the 3 m depth occurred from March to June, with predation in June occurring only at this depth.

Diet of *C. uritai*

C. uritai fed on various benthic crustaceans, and four taxonomic groups of fish larvae and juveniles: marbled sole *P. yokohamae*, osmerids *Hypomesus japonicus* (Brevoort) and *H. nipponensis* McAllister, a species of gobiid *Chaenogobius heptacanthus* (Hilgendorf), and pholidids *Pholis* spp. (Table 3). Gammarids were the most frequently consumed prey (mean F% = 14.5) during the sampling period, with ostracods being a common prey (mean F % = 6.9). In June of 1998-2000, the F% of juvenile *Crangon* spp. were high (min.-mean-max. F% = 8.2-27.6-50.0). The frequencies of occurrence of mysids, *C. heptacanthus* larvae and juveniles, pagurid zoeae and upogebiid zoeae were high in June.

Feeding style of *C. uritai*

The relationships between prey density and FO% of each prey item in the diet of *C. uritai* at 3-10 m depths are shown in Fig. 3. Density of each prey type is calculated using individuals that are smaller than the maximum size of individuals found in the gastric contents of *C. uritai*. *C. uritai* showed density-dependent predation on juvenile *Crangon* spp., larval and juvenile *C. heptacanthus*, mysids, and gammarids. However there was no evidence of density-dependent predation on larval and juvenile *P. yokohamae*.

Spatial overlap between predator *C. uritai* and prey *P. yokohamae*

The spatial distribution patterns of *C. uritai* ≥ 19 mm TL, and larval and juvenile *P. yokohamae* are shown in Fig. 4. Investigation of the relationships between weighted mean depth (WMD) of *C. uritai* or *P. yokohamae* and weighted mean bottom water temperature (WMBWT) only involved the data gathered when samples could be obtained from all stations (3-20 m depth stations). There was a significant negative correlation between the WMD of *C. uritai* and the WMBWT ($r = -0.68$, $N = 20$, $P < 0.01$, Fig. 5). In contrast, no significant correlation was found between the WMD of *P. yokohamae* and WMBWT ($N = 19$, $P > 0.05$). The peak abundance of *P. yokohamae* was recorded only at depths of 5-15 m, except for 20 m depths on 20 May 1998 and 8 June 2000（Fig. 4）. The WMDs of *P. yokohamae* were shallower than those of *C. uritai* during March, but deeper than those of *C. uritai* during April-May

(Fig. 4). In June, both *P. yokohamae* and *C. uritai* mainly distributed in the shallow depths (≤ 5 m depth). In the coldest year in early and mid April in 1999, the overlaps in distribution between *P. yokohamae* and *C. uritai* were relatively higher (26.4-56.2 %) than those in other years (1997, 1998, and 2000; 2.8-44.0 %), and the shrimp predation was only observed in 1999 during this period. However, the statistic comparison could not apply to compare with these OI% in early and mid April among years because of low sample sizes. There was not significant difference in OI% between predation days (median: 38.8 %) and non-predation days (34.4 %; *U*-test, $P = 0.64$) through the all sampling day (1997-2000).

Developmental stages of larval and juvenile *P. yokohamae* collected with a sledge net at depths of 3-20 m from March to June, were identified on each sampling day. Flexion larvae, which were mainly distributed on the sea bottom (Stage F[28]), were collected from early April, and only pre-flexion larvae were collected in March. Pre-flexion larvae were mainly distributed in mid-water layers, and were less abundant near the layers of the sea bottom.[20] Body length range of *P. yokohamae* in late June were 15.6-27.9 mm, 10.3-24.4 mm, 16.8-27.7 mm in 1998, 1999, and 2000, respectively.

DISCUSSION

Otoliths and crystalline lenses of the eyes of juvenile plaice *P. platessa*[8, 14-16] and juvenile stone flounder *P. bicololatus*[13] were evident in the contents of the digestive tract of crangonid shrimp. In this study, whole bodies of *P. yokohamae* were swallowed by *C. uritai*. Crangonid shrimp form the basis of size-dependent predation.[23, 29] *P. yokohamae* is more susceptible to the pressure of predation than other flatfishes because its settlement size is smaller than those of other species prone to predation by smaller sized shrimp. In the present study, the smallest *C. uritai* that preyed on *P. yokohamae* measured 19mm TL, while the smallest *C. crangon* that preyed on *P. platessa* in the field observation study was 30 mm TL.[8] This difference of the smallest predator size can be explained by the different settlement sizes of *P. yokohamae* (7-9 mm BL),[25] *P. platessa* (10-15 mm BL),[4] the Japanese flounder *P. olivaceus* (10-13 mm BL),[30] and the winter flounder *P. americanus* (10.1-14.5 mm SL).[9] In laboratory observations, van der Veer and Bergman,[8] Ansell et al.[14] and Wennhage and Pihl[16] pointed out that shrimp predation is density-dependent (functional response type III). In the present study, the same phenomenon was observed in the field. *C. uritai* fed opportunistically on juvenile *Crangon* spp., larval and juvenile *C. heptacanthus*, mysids, and gammarids (Fig. 3). However, mass predation on larval and juvenile *P. yokohamae* did not occur in day time, maybe due to a low abundance of fish. It is possible that dispersal recruitment of *P. yokohamae* prevents mass mortality due to predation by *C. uritai*. As *C. uritai* feeds on various prey items opportunistically in the laboratory (Nakaya et al., submitted), high predation pressure by *C. uritai* would not be concentrated only on *P. yokohamae*. Therefore the low density of larval and juvenile *P. yokohamae* in this nursery ground might not be due to the effects of heavy predation. High predation by *C. uritai* was found at prey concentration over 1.0 ind/m^2 for any prey type (Fig. 3). Among flatfishes, densities over 1.0 ind/m^2 were observed in the tidal gully of the Balgzand tidal flat area in the western Wadden Sea,[8] Torinoumi estuary in Sendai bay,[13] and at part of the shallow area of the Gullmars Fjord on the Swedish west coast.[10,16] In these environmental conditions, density-dependent predation would occur, and these abundance of newly settled flatfish would be regulated by crangonid shrimp predation. Therefore, an abundance of alternative prey (e.g. juvenile

Crangon spp., larval and juvenile *C. heptacanthus*, mysids, and gammarids) might play an important role in reducing the pressure of predation on *P. yokohamae*.

Most *C. uritai* were collected at ≤ 10 m depths through the sampling period in Hakodate Bay (Fig. 4), but they tend to migrate to 3 m depths with increasing water temperature. Gibson et al.[31] observed the seasonal movement of predator-prey *C. crangon* - *P. platessa*, and they indicated that *C. crangon* migrated to onshore areas with temperature increases, as observed in this study with *C. uritai*. Crangonid species release zoeae in the onshore area, and the timing of this release is regulated by temperature.[18,32,33] On the other hand, demersal larvae of *P. yokohamae* were mainly collected at 10-15 m depths in April-May, and their abundance was low at ≤ 5 m depths[20] where *C. uritai* was concentrated during warm years. Water temperature influenced the migration of *C. uritai*, but did not seem to restrict the distribution of larval and juvenile *P. yokohamae* (Fig. 5), so that opportunities for predation would be influenced by water temperature year by year. In the case of *C. crangon* and *P. platessa*, *P. platessa* settled at ≤ 1.5 m depths, and warm temperatures in winter increased the spatial overlap in the Wadden Sea.[8] In contrast, in the present study, low water temperature likely increased the opportunity for predation because of the difference in settlement depths between *P. platessa* and *P. yokohamae*.

C. uritai were distributed at 3-5 m depths after early April in warm years (1997, 1998, and 2000), and *P. yokohamae* were distributed deeper than those of *C. uritai* (Fig. 4). During the cold year in particular late march to middle April 1999, *C. uritai* stayed at 10 m depth (near the main settling ground of *P. yokohamae*),[21] and the shrimp predation was observed. Therefore the shrimp predation of *P. yokohamae* was likely related to predator-prey overlaps. Through the sampling days in 1997-2000, there was not significant difference about OI% between predation days and non-predation days, however these OI% were inclusive of the sampling days when the predation risk would be low. For example only pre-flexion larvae of *P. yokohamae* were collected in March; they were pelagic and occurred in mid-water layers and near the sea bottom. Although four individuals of pre-flexion larvae were victims of predation in March 1999 (Table 4), most larvae in the mid-water layer would not be prone to predation by the epibenthic predator *C. uritai*. In addition, large number of *P. yokohamae* grew larger-sized in warm June, these juveniles might not be victims. So, high predation risk would occur under the high overlap situation between these two organisms when settled individuals of *P. yokohamae* were collected mainly after early April essentially.

Wennhage and Pihl[16] observe relatively higher shrimp predation (F% = 6.0) on newly settled plaice from an area with a high density of newly settled plaice (13.3ind/m^2) from a Swedish fjord. Though we could not observe such high density areas in this study through the sampling season, the frequency of occurrence was about 1.5 % of *P. yokohamae* in the stomachs of *C. uritai* over the four years (33 out of 2263 individuals in stomachs of *C. uritai*, maximum F % by sampling day was 6.5 %). Daily food consumption for *C. crangon* has been estimated as 12 % of body weight in western Sweden[34] and 16 % of body weight under 18.5°C in northern Wadden Sea.[35] Digestion speed is fast, and it can be observed only after 2.5-3 hours, shrimp predation could not be detected for about 4 hours at 18°C conditions.[8] As the residence time of *P. yokohamae* in the stomach of *C. uritai* is very short, there could be a high predation pressure despite the relatively low F % in the field. Therefore the shrimp predation may be one of the important mortality factors for settled *P. yokohamae*. It is difficult to assess the mortality quantitatively because field observations of the occurrence of shrimp predation are rare. The use of mt-DNA for the analysis of stomach contents will be one of the important methods for the detection of predation by crangonids.[36]

Although the diel feeding cycle of *C. uritai* is not known, similar crangonid shrimps are nocturnal feeders (*C. crangon*,[34,35] *C. affinis*[13,37]). In the present study, diurnal samplings were carried out and prey items were found in stomachs of *C. uritai*. This indicated that *C. uritai* would feed on *P. yokohamae* at night and during daytime. Further investigations are needed on the effect of diel changes on the food intake by predatory shrimp for estimate the predation impact.

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Table 1 Back-calculate formulae for whole body sizes of prey items in stomachs of *C. uritai*. Each formula was estimated by the least square method from specimens collected with a sledge net in Hakodate Bay

Modification Formula	*n*	r^2	*P*-value
Pleuronectes yokohamae			
BL (mm) = 10.7 UJL (mm) + 0.58	22	0.82	< 0.001
Crangon spp. juveniles			
TL (mm) = 4.06 CL (mm) + 0.63	22	0.80	< 0.001
Gammarids			
TL (mm) = 1.27 BD (mm) + 3.35	22	0.82	< 0.001
Chaenogobius heptacanthus			
TL (mm) = 3.89 HL (mm) + 0.76	22	0.99	< 0.001
Mysids			
TL (mm) = 3.20 CL (mm) + 0.30	22	0.96	< 0.001

*BL (body length), UJL (upper jaw length), TL (total length), CL (carapace length), BD (body depth), and HL (head length).

Table 2 Species composition by individual (%) of crustacean decapods (≥ 19 mm in total length in shrimp and carapace width in crab) collected with the sledge net at 3-20 m stations in 1999-2000

1999	Family	Species	9 Mar	18 Mar	29 Mar	11 Apr	17 Apr	29 Apr	8 May	23 May	8 June	21 June
	Crangonidae	*Crangon uritai*	61.5	86.4	91.5	80.6	87.9	98.4	99.0	98.9	nd	99.5
		C. amurensis	10.3	1.2	6.0	4.7	3.2	0	0.4	0.6	nd	0
		C. hakodatei	0	0	2.0	7.0	6.8	1.4	0.3	0.4	nd	0
		C. dalli	0	0	0	0.3	0	0	0	0	nd	0
	Pagridae	*Pagurus ochotensis*	17.1	2.5	0	0	0.4	0	0	0	nd	0
		P. pectinatus	11.1	0	0	0	0	0	0	0	nd	0
	Atelecyclidae	*Telmessus acutidens*	0	1.2	0.6	6.0	1.4	0	0	0	nd	0.5
	Idoteidae	*Synidotea laevidorsalis*	0	3.7	0	1.0	0	0	0.3	0	nd	0
		Idotea ochotensis	0	1.2	0	0.3	0	0	0	0	nd	0
		Cleantiella isopus	0	0	0	0.3	0	0	0	0	nd	0
	Hippolytidae	*Heptacarpus geniculatus*	0	3.7	0	0	0	0	0	0	nd	0
		Heptacarpus sp.	0	0	0	0	0	0.2	0	0.2	nd	0
	Upogebiidae	*Upogebia major*	0	0	0	0	0.4	0	0	0	nd	0
		No. of samples	117	81	352	386	281	644	717	535	nd	221

2000	Family	Species	1 Mar	14 Mar		3 Apr	17 Apr	30 Apr	9 May	24 May	8 June	21 June
	Crangonidae	*Crangon uritai*	73.1	77.3		79.1	99.7	86.2	88.4	90.0	93.5	95.6
		C. amurensis	16.6	17.0		20.4	0.3	13.5	7.6	0.6	6.5	2.2
		C. hakodatei	0.4	0		7.0	0	0	0	0	0	0
		C. dalli	0	0		0	0	0	0	0	0	0
	Pagridae	*Pagurus ochotensis*	2.4	0.4		0	0	0	0.8	9.4	0	0
		P. pectinatus	0	0		0	0	0.3	0.4	0	0	0
	Atelecyclidae	*Telmessus acutidens*	2.4	0.4		0	0	0	0.8	0	0	2.2
	Idoteidae	*Synidotea laevidorsalis*	0	0		0	0	0	0	0	0	0
		Idotea ochotensis	0	0		0	0	0	0	0	0	0
		Cleantiella isopus	0	0		0	0	0	0	0	0	0
	Hippolytidae	*Heptacarpus geniculatus*	4.3	5.2		0.3	0	0	0	0	0	0
		Heptacarpus sp.	0.8	0		0	0	0	0	0	0	0
	Upogebiidae	*Upogebia major*	0	0		0.3	0	0	2.0	0	0	0
		No. of samples	253	481		397	315	326	249	160	46	91

Table 3-1 Percent frequency of occurrence (F%) in stomachs of *C. uritai* ≥ 19mmTL collected at 3-10m depth stations in 1997-2000

	1997				
Food item	11 Apr.	18 Apr.	29 Apr.	7 May	22 May
PISCES larvae and juveniles					
Pleuronectes yokohamae	0	0	0	5.7	2.4
Hypomesus spp.	0	0	0	0	0
Pholis spp.	0	0	0	1.4	0
Chaenogobius heptacanthus	0	0	0	0	0
BIVALVIA	0	0	0.9	0.7	0.8
Mesogastropoda	0	0	1.9	0	0
POLYCHAETA	1.4	2.0	3.7	6.4	0
Crangon spp. juveniles	1.4	0	0	2.9	2.4
Hippolytidae juveniles	0	0	0	0	0
Mysidacea	1.4	2.0	0	0	3.3
Gammaridea	25.4	0	7.4	14.3	20.3
Isopoda	1.4	8.2	16.7	0	1.6
Ostracoda	5.6	2.0	0.9	4.3	4.9
Calanoida	1.4	4.1	6.5	0.7	0.8
Harpacticoida	4.2	0	0	2.9	0.8
Crangon spp. eggs	0	0	0	0.7	4.9
Brachyura foot	0	0	5.6	0.7	4.9
Cumacea	1.4	0	0	0.7	0
Pycnogonida	0	0	2.8	0.7	0
Brachyura zoea	0	0	0.9	0	0.8
Pagridae zoea	0	0	0	0.7	0.8
Upogebiidae zoea	0	0	0	0.7	0
Unidentified food	8.5	18.4	7.4	14.3	4.1
Empty stomachs (%)	40.8	29.7	28.0	22.1	25.2
No. of stomachs analysed	71	49	108	140	123

Table 3-2 Cont.

	1998						
Food item	7 Apr.	17 Apr.	28 Apr.	6 May	20 May	9 June	24 June
PISCES larvae and juveniles							
Pleuronectes yokohamae	0	0	2.2	0	0	5.0	0
Hypomesus spp.	0	0	0	0	0	0	0
Pholis spp.	0	0	0	0	0	0	11.8
Chaenogobius heptacanthus	0	0	0	0	1.4	2.5	8.8
BIVALVIA	9.6	7.0	4.5	3.8	5.5	2.5	2.9
Mesogastropoda	0	1.8	0	0	0	0	0
POLYCHAETA	5.5	7.0	3.4	5.1	4.1	7.5	2.9
Crangon spp. juveniles	2.7	0	5.6	12.7	11.0	20.0	47.1
Hippolytidae juveniles	0	0	0	1.3	2.7	0	0
Mysidacea	4.1	0	0	1.3	5.5	10.0	5.9
Gammaridae	8.2	17.5	5.6	20.3	5.5	2.5	5.9
Isopoda	1.4	3.5	1.1	1.3	0	0	2.9
Ostracoda	9.6	12.3	15.7	17.7	8.2	7.5	0
Calanoida	0	0	0	6.3	21.9	0	0
Harpacticoida	1.4	0	0	0	4.1	2.5	0
Crangon spp. eggs	4.1	0	3.4	0	1.4	0	2.9
Brachyura foot	2.7	0	1.1	0	0	0	0
Cumacea	0	0	0	0	0	0	0
Pycnogonida	0	0	0	0	0	0	0
Brachyura zoea	0	0	0	0	1.4	0	0
Pagridae zoea	0	0	0	0	0	0	0
Upogebiidae zoea	0	0	0	0	0	0	0
Unidentified food	23.3	17.5	22.5	11.4	19.2	17.5	17.6
Empty stomachs (%)	39.0	29.7	25.7	19.4	20.3	22.6	11.8
No. of stomachs analysed	73	57	89	79	73	40	34

Table 3-3 Cont.

	1999									
Food item	9 Mar.	18 Mar.	29 Mar.	11 Apr.	17 Apr.	29 Apr.	8 May	23 May	8 June	21 June
PISCES larvae and juveniles										
Pleuronectes yokohamae	1.4	3.7	1.0	3.2	1.4	0	0	0	5.6	6.5
Hypomesus spp.	0	0	0	0	0	1.1	1	0	2.8	0
Pholis spp.	0	0	0	1.1	0	0	0	0	5.6	1.3
Chaenogobius heptacanthus	0	0	0	0	0	1.1	0	0	19.4	3
BIVALVIA	6.9	9.3	7.0	4.2	2.8	4.3	3.1	1.3	0	3
Mesogastropoda	0	0	0	1.1	2.8	1.1	1	0	0	0
POLYCHAETA	2.8	0	4.0	7.4	2.8	4.3	1	0	0	1.3
Crangon spp. juvenile	0	0	0	0	1.4	2.1	4.1	3.8	50.0	23.4
Hippolytidae juvemile	0	0	0	1.1	1.4	1.1	0	1.3	5.6	2.6
Mysidacea	0	0	1.0	0	4.2	1.1	6.1	0	0	35.1
Gammaridea	8.3	20.4	27.0	13.7	12.7	27.7	26.5	20.0	5.6	4
Isopoda	1.4	0	4.0	0	1.4	2.1	2	0	0	1.3
Ostracoda	9.7	11.1	9.0	5.3	11.3	4.3	4.1	7.5	11.1	5.2
Calanoida	0	3.7	0	0	0	0	0	1.3	11.1	0
Harpacticoida	0	1.9	0	0	0	0	0	0	0	0
Crangon spp. eggs	0	0	0	1.1	2.8	2.1	2	0	0	1.3
Brachyura foot	0	0	1.0	1.1	2.8	0	0	5	0	0
Cumacea	0	0	0	0	0	0	0	0	0	0
Pycnogonida	0	0	1.0	0	0	0	0	0	0	0
Brachyura zoea	0	0	0	0	0	0	0	0	2.8	0
Pagridae zoea	0	0	0	0	0	0	0	1.3	27.8	0
Upogebiidae zoea	0	0	0	0	1.4	0	0	1.3	41.7	0
Unidentified food	16.9	7.4	8.0	23.2	14.1	11.7	11.2	7.5	0	5.2
Empty stomachs (%)	43.1	44.4	20.0	31.7	30.8	28.7	35.4	40.0	11.1	14.9
No. of stomachs analysed	72	54	100	95	71	94	98	80	36	77

Table 3-4 Cont.

	2000								
Food item	1 Mar.	14 Mar.	3 Apr.	17 Apr.	30 Apr.	9 May	24 May	8 June	21 June
PISCES larvae and juveniles									
Pleuronectes yokohamae	0	0	0	0	2.0	0	3.8	0	0
Hypomesus spp.	0	0	0	0	0	0	0	0	0
Pholis spp.	0	0	0	0	0	3.8	0	0	0
Chaenogobius heptacanthus	0	0	0	0	0	0	3.8	27.9	63.0
BIVALVIA	1.5	2.9	0	3.2	8.0	1.9	7.7	1.6	5.6
Mesogastropoda	0	0	1.4	0	0	1.9	0	0	0
POLYCHAETA	0	0	1.4	0	2.0	5.7	0	0	0
Crangon spp. juvenile	0	0	0	0	0	3.8	9.6	8.2	16.7
Hippolytidae juvemile	0	0	0	0	0	0	1.9	4.9	0
Mysidacea	1.5	0	1.4	3.2	0	1.9	0	8.2	0
Gammaridea	16.7	11.8	19.7	11.1	23.0	11.3	1.9	4.9	3.7
Isopoda	0	0	0	0	2.0	0	1.9	0	0
Ostracoda	3.0	5.9	0	4.8	5.0	7.5	9.6	1.6	1.9
Calanoida	0	0	0	0	0	0	0	0	0
Harpacticoida	0	0	0	0	0	0	0	0	0
Crangon spp. eggs	0	0	0	0	2.0	0	0	0	0
Brachyura foot	0	1.5	0	0	2.0	1.9	0	0	0
Cumacea	0	0	0	0	0	0	0	0	0
Pycnogonida	0	0	1.4	0	0	0	0	0	0
Brachyura zoea	0	0	0	0	0	0	0	1.6	0
Pagridae zoea	0	0	0	0	0	0	0	6.6	0
Upogebiidae zoea	0	0	0	0	0	0	0	1.6	3.7
Unidentified food	19.7	26.5	16.9	17.5	31.0	26.4	21.2	23.0	7.4
Empty stomachs (%)	57.5	51.4	59.1	57.1	27.4	35.8	38.5	41.0	33.3
No. of stomachs analysed	66	68	71	63	62	53	52	61	54

Table 4 Number of *C. uritai* feeding on *P. yokohamae* by depth, month, and year

		Depth (m)		
	Year	10	5	3
Mar.	1999	3	0	1
	2000	0	0	0
Apr.	1997	0	0	0
	1998	0	0	2
	1999	3	0	1
	2000	0	0	1
May	1997	0	8	3
	1998	0	0	0
	1999	0	0	0
	2000	0	1	1
June	1998	0	0	2
	1999	0	0	7
	2000	0	0	0
Total		6	9	18
No. of stomachs analysed		530	717	1016

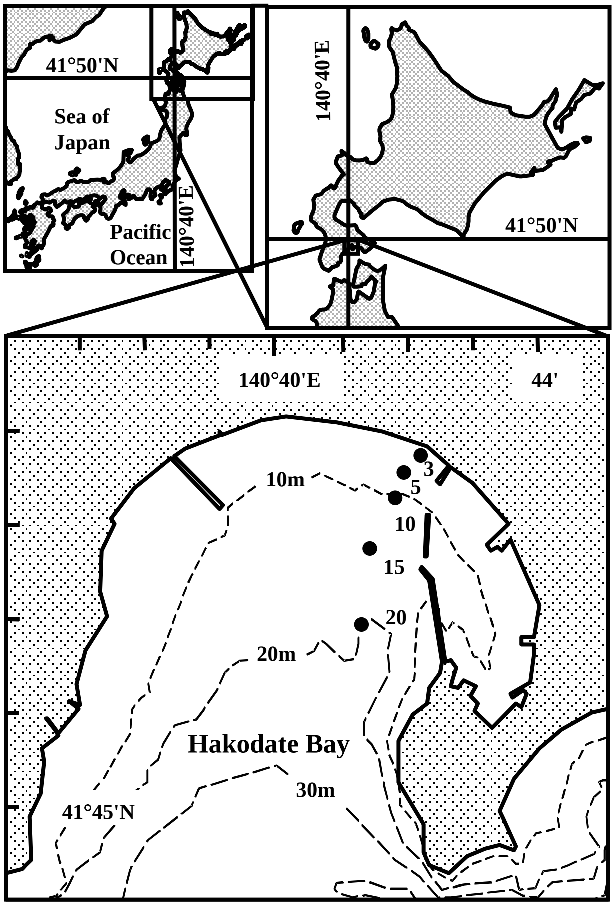

Fig. 1. Location of sampling stations in Hakodate Bay. Numerals show the station depth in meters. Dashed lines show isobaths.

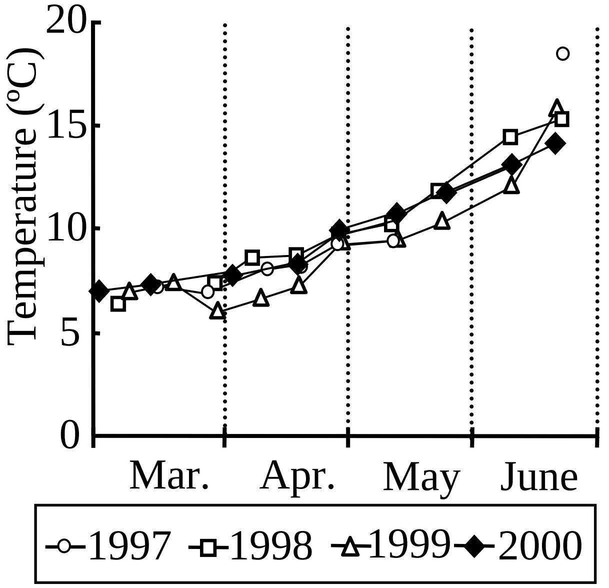

Fig. 2 Annual variation of mean water temperature on the sea bottom at three sampling stations (3-10 m depth) in Hakodate Bay from March to June in 1997-2000.

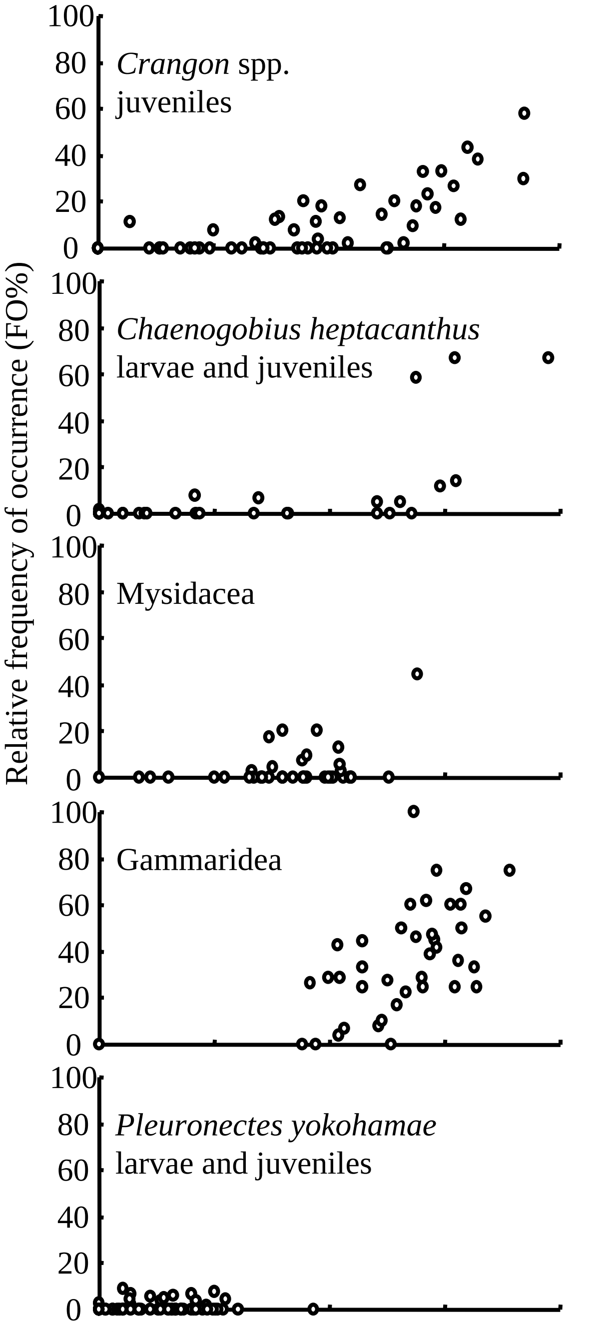

Fig. 3 Relationships between the abundance and relative frequency of occurrence (FO%) of five prey items in the gastric contents of *C. uritai*. Abundance data of larval and juvenile *P. yokohamae* were quoted from Nakagami et al.[20] Body size ranges available by *C. uritai* are as follows; *Crangon* spp. juveniles (TL: 2.9-8.5 mm), gammarids (1.1-10.5 mm), larvae and juveniles of a gobiid *Chenogobius heptacanthus* (4.6-12.3 mm), and mysids (2.3-16.8 mm).

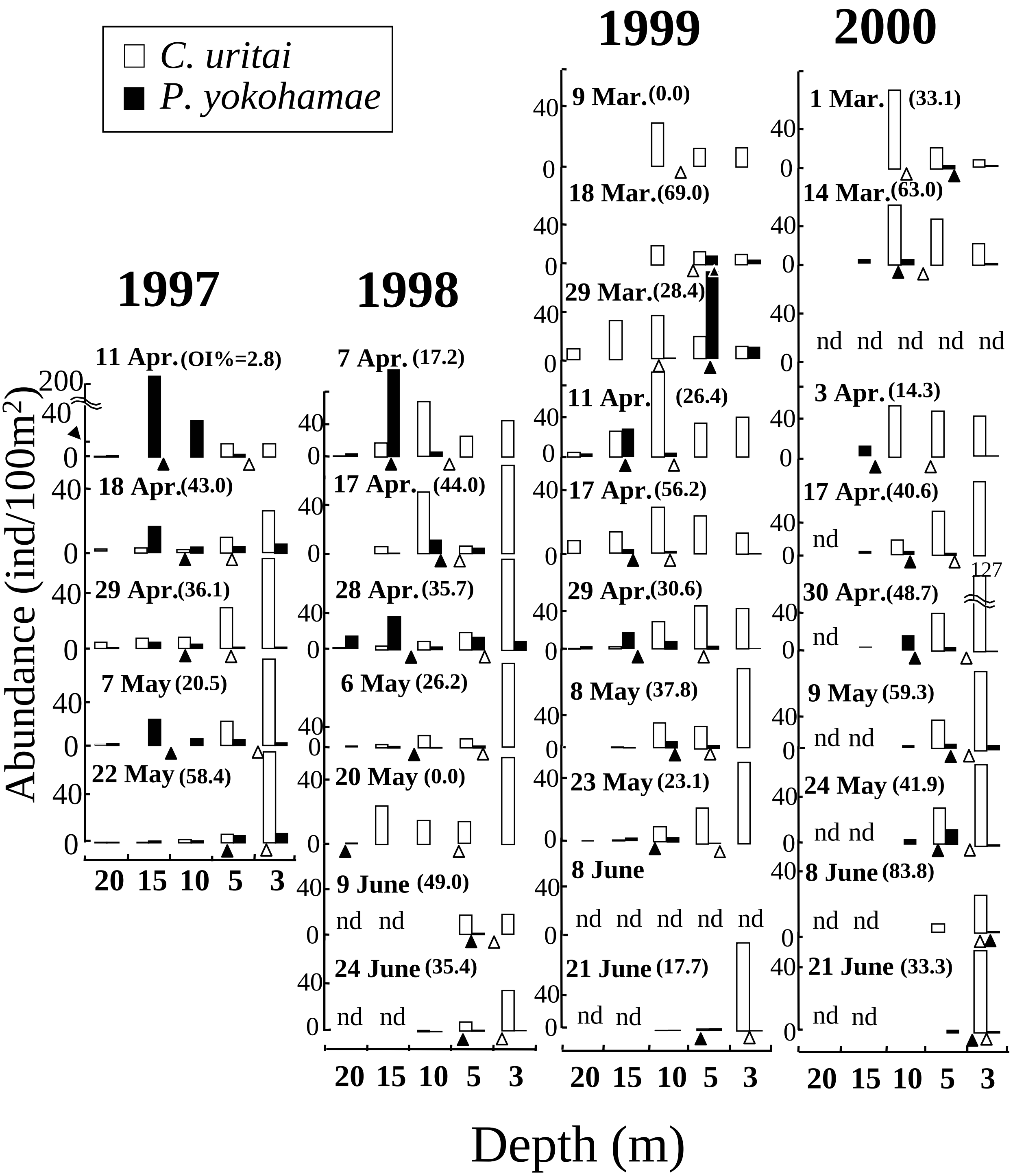

Fig. 4 Spatial distribution of *C. uritai* (≥ 19mm TL, open bar), and larval and juvenile *P. yokohamae* (solid bar) in Hakodate Bay for the period 1997–2000. Samples were collected on the sea bottom along a transect on two hauls using a sledge net. The bottom rows of open triangles and solid triangles show weighted mean depths of *C. uritai* and *P. yokohamae*, respectively. Numerals in parentheses show the Brey-Curtis overlap index % (OI%) between *C. uritai* and *P. yokohamae*. nd: no data.

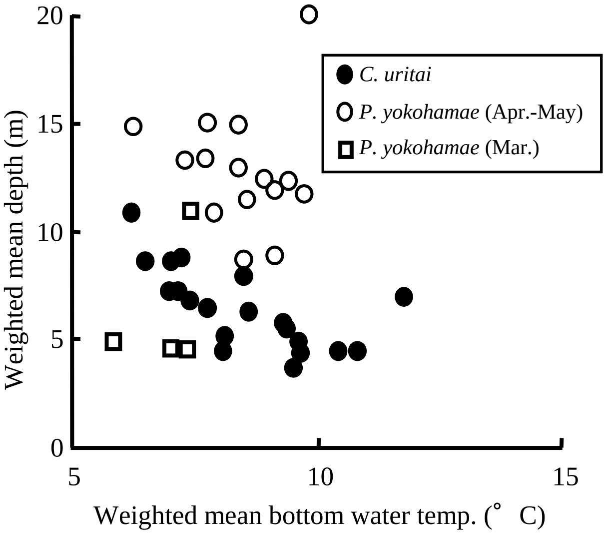

Fig 5 Relationship between weighted mean bottom water temperature (WMBWT) and weighted mean depths (WMD) of *C. uritai* and *P. yokohamae*. WMD of *C. uritai* was significantly correlated with WMBWT ($r = -0.68$, $N = 20$, $P<0.01$), but WMD of *P. yokohamae* showed no such correlation ($N = 19$, $P > 0.05$).