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Annual variation of potential predation impacts on larval and juvenile marbled sole *Pseudopleuronectes yokohamae* by sand shrimp *Crangon uritai* in Hakodate Bay, Hokkaido

Running title: Annual variation of shrimp predation

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ABSTRACT: An investigation was conducted to evaluate the annual variation in potential predation impact (PPI) on larval and juvenile *Pseudopleuronectes yokohamae* by *Crangon uritai* in Hakodate Bay using predator-prey size relationships. Laboratory experiments were designed to estimate the favorable prey size of *C. uritai* through back-calculation of body length (BL) of *P. yokohamae* from sagittal otolith diameter observed in the stomachs of *C. uritai*. The most favorable prey-predator size ratio (BL of *P. yokohamae* / Total length (TL) of *C. uritai*) class was 0.15–0.19, and ranged from 0.12–0.31. There was a significant positive correlation between the BL increase of *P. yokohamae* and the bottom water temperature in the field, such that BLs stagnated during the cold year of 1999 from April to June, and increased during the warm year of 2002. In contrast, no significant correlation was found between the TL increase of *C. uritai* and the bottom water temperature. Moreover, there were no significant differences in the mean TL of *C. uritai* between months (April–June) or years (1998–2002). Variation of PPI depended on the relationships between the growth rates of *P. yokohamae* and bottom water temperature. The warm year of 2002 therefore resulted in a period of higher potential predation impact ($PPI \geq 20$), being at least 20 days shorter than that of the cold year of 1999. These results suggest that increased bottom water temperature in the nursery area was one of the most important factors for cumulative predation loss.

KEY WORDS: *Crangon uritai*, prey-predator size, *Pseudopleuronectes yokohamae*, size selective predation

INTRODUCTION

Crangonid shrimp are recognized inhabitants of the sandy beach and are often predominant in cool temperature waters of the world's oceans. There are many reports concerning predation on newly settled flatfishes by these shrimp.¹⁻⁵ Year-class strength of plaice *Pleuronectes platessa* (L.) juveniles in the Wadden Sea is mainly caused by predation by the shrimp *Crangon crangon* (L.).¹ Research on the feeding ecology of crangonid shrimp has focused on daily food consumption,⁶ feeding rhythms^{7,8} and prey selectivity.⁹ Under laboratory conditions, crangonid shrimp feeds on flatfish juveniles that measure $\leq 50\%$ of the total length of the shrimp.^{1,10-13} Many studies have examined the shrimp predation loss, although it is difficult to assess mortality quantitatively because field observations of shrimp predation are rare. Therefore, an assessment is therefore required of the effects of a cumulative shrimp predation loss model is required. Burrow *et al.* discussed the pattern and rates of mortality in plaice predicted by a predation model in the field.¹⁴

The marbled sole *Pseudopleuronectes yokohamae* (Günther) makes up most of the biomass of the demersal fish assemblage in Hakodate Bay, and is caught commercially with bottom set nets and gill nets.¹⁵ From early March to the middle of April, demersal eggs are spawned and pelagic larvae of *P. yokohamae* are transported mainly from the offshore spawning ground (20–30 m depths at the bay mouth) to the inshore nursery area (mainly depths of 3–10 m from April to June).¹⁶ In the nursery area, *Crangon uritai* (Hayashi and Kim) is the dominant mobile epibenthic species in the shallow sandy beach, and shrimp predation has been observed.¹⁷ However, the annual variation of the predation impact on larval and juvenile marbled sole is unknown.

To estimate the marbled sole annual variation in cumulative shrimp predation loss, we investigated the preference size of prey flatfish by crangonid shrimp and used the preference prey-size distribution data in the field to estimate the potential predation period and potential predation impact for *P. yokohamae* by *C. uritai*. Our investigation involved two aspects: (i) the preference prey size of *C. uritai* was determined against a variable prey size at a given time, and (ii) the annual variation of potential predation impacts and their factors is discussed with prey-predator size distribution data collected in the field.

MATERIALS AND METHODS

Laboratory experiments

Crangon uritai were collected with a Hirota's sledge net (width: 60 cm; height: 40 cm; mesh size: 0.5 mm)¹⁸ from Hakodate Bay (depths of 3–10m in the flatfish nursery ground) during April–June of 2001. The shrimp were deprived of food for 2 days, including an acclimation time. Laboratory observations showed that optimal water temperature of larval and juvenile *P. yokohamae* for the maintenance of fish health (minimal asymptomatic infection, morphological abnormality and abnormal pigmentation) was $14.3 \pm 0.53^{\circ}\text{C}$.¹⁹ *Pseudopleuronectes yokohamae* were classified into two developmental stages, larva (stage I: the pupil of the left eye is on the top of the dorsal edge and the notochord reaches postflexion) and juvenile (stage J: the pupil of the left eye is beyond the dorsal edge), as defined by Minami.²⁰ Stage I and J individuals used in experiments were artificially incubated and reared at about 15°C since individuals of both stages were similar in body size. Total length (TL) of *C. uritai* (the posterior edge of the orbital to the end of the telson) and body length (BL) of

P. yokohamae were measured to the nearest 0.1 mm with a digital camera linked to monitors. In this study, BL is the general term for notochord length (NL: snout tip to notochord tip in pre-flexion larvae) and standard length (SL: snout tip to the posterior edge of the hypurals in post-flexion larvae or juvenile). The maximum diameters of *P. yokohamae* sagittal otoliths were measured with a microscope to the nearest 1 μm .

A factorial design experiment was conducted to estimate the prey-predator size range. Four marbled sole size class treatments (4.0–7.9, 8.0–11.9, 12.0–15.9 and 16.0–19.9 mm BL) were used in feeding tests with the predator *C. uritai* (19–50 mm TL). Six marbled sole were collected randomly in each size class (totaling 24 individuals) and given to a single individual of *C. uritai*. The diel motile activity of the similar crangonid shrimp *C. crangon* increased with higher water temperature (6–20°C) in laboratory observations.²¹ Feeding activity of *C. septemspinosa* increased with higher water temperature (5–15°C).²² The optimal water temperature of larval and juvenile *P. yokohamae* for the maintenance of fish health (minimal asymptomatic infection, morphological abnormality and abnormal pigmentation) was $14.3 \pm 0.53^\circ\text{C}$.¹⁹ In this study, the experiment was performed in tanks (40 cm×36 cm×15 cm depth) using filtered sea water at approximately 15°C. As crangonid shrimp are nocturnal feeders,^{7,8,23} all experiments were conducted under dark conditions. Two hours after the start of an experiment, all shrimp were immediately boiled for a few seconds to prevent vomiting of stomach contents, and then fixed in a 99.5% ethanol solution. Otoliths of larval and juvenile plaice are easier to observe than other body parts in the stomach.²⁴ Body lengths of the prey *P. yokohamae* were determined from the diameters of sagittal otoliths observed in the stomach of *C. uritai*, and a prey-predator size ratio was estimated. Additionally, in order to estimate the favorable prey-predator

size ratio (BL of *P. yokohamae* / TL of *C. uritai*) range accurately, the prey *P. yokohamae* were divided into of 0.05 (three individuals collected randomly in each of the six size ranges, totaling 18 individuals) and 18 *P. yokohamae* were given to a single individual of *C. uritai* (41 ± 0.4 mm TL).

Field sampling

Pelagic larvae and settled individuals of *P. yokohamae* of the Kikonai Bay – Hakodate Bay population occurred mainly in Hakodate Bay. Over a wide area from Kikonai Bay to Hakodate Bay, yolk-sac and early yolk-absorbed larvae occurred mainly at the mouth of Hakodate Bay and in the inner part of the bay, respectively). A strong west-northwesterly wind blew frequently in March of each year. This wind would induce a southward-offshore drift of surface water and a northward inshore compensatory drift of deeper water in Hakodate Bay, and the river inflow had a lower influence on the bottom water salinity in this area (≥ 32.0 in all sampling).¹⁶ All samplings were performed at 3, 5, 10, 15 and 20 m depths in Hakodate Bay in the day (08:00–16:00 hours) approximately three times per month in March–April and twice per month in May–June during the period 1998–2002 (Table 1). *Crangon uritai*, and larval and juvenile *P. yokohamae* were collected with a sledge net (Hirota's sledge net: 60 cm wide, 40 cm tall and 0.5 mm mesh)¹⁸ for 5 minutes at a towing speed of approximately 0.9 m/s. The positions at which the sledge net was towed and retrieved were determined with a differential global positioning system (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.¹⁷ Catch efficiency (49.2%) of *C. uritai* was quoted using the mean levels of Yoshida *et al.*²⁴

Mean catch efficiencies of Hirota's sledge net with a distance wheel for *C. uritai* and *P. yokohamae* were obtained to estimate their accurate population densities on the assumption that the catch efficiency of the drop trap (a kind of box type quadrat and 0.5 m² sampling area detailed in Pihl and Rosenberg²⁵) was 100%. The drop trap was shown to be non-size selective and to have an efficiency close to 100% for the maximum mean size of the target species (*C. uritai*: 44.1–48.0 mm TL, *P. yokohamae*: 40.1–44.0 mm BL) in this investigation.²⁴ Bottom water temperature was measured with a CTD (conductivity temperature and depth profiler: SBE-19; Sea-Bird Electronics, Inc., Bellevue, WA, USA).

As the minimum size of *C. uritai* that feeds on *P. yokohamae* in the field is 19 mm TL,¹⁷ *C. uritai* larger than 19 mm TL were regarded as predators of larval and juvenile *P. yokohamae* and their size was measured to the nearest 0.1 mm with an electric slide caliper. Male and female *C. uritai* were distinguished on the basis of the difference in length of the endopods of the first pair of pleopods.²⁶ After the measurement, the gastric contents of all *C. uritai* \geq 19 mm TL were examined. The BLs of damaged *P. yokohamae* were restored using available formulae $BL(\text{mm}) = 10.7UJL(\text{mm}) + 0.58$ ($r^2 = 0.82$, $N = 22$, $P < 0.001$), where UJL is the upper jaw length.¹⁷ The BL increase per day for the population of larval and juvenile *P. yokohamae* was calculated using the mean BL difference divided by the days among each sampling.

To estimate the pre-shrimp predation risk density of pelagic larval *P. yokohamae*, planktonic sampling was carried out at five stations (3, 5, 10, 15 and 20 m depths) in Hakodate Bay three times a month during March–April from 1998 to 2002. Larvae of *P. yokohamae* were collected by oblique tows of a ring net (net opening diameter: 80 cm, mesh size: 0.33 mm). The ring net was retrieved obliquely from the bottom to the

surface at 0.9 m/s over 3 times at each sampling station (Table 1). The density of pelagic larvae was calculated from the mouth area of the ring net and filtration efficiency estimated using the ratio of the towing distance measured with a flow-meter (Cat. No. 5571-B; Rigo Co., Saitama, Japan) to the wire-out length. Density data in 1998–1999 were derived from Nakagami *et al.*¹⁶ The post-shrimp predation risk decreased the estimated density of juvenile *P. yokohamae* collected by the sledge net in July. Sampling methods and calculation of density estimations were the same in March to July.

Numerical value analysis

In order to calculate the size relationships between larval and juvenile *P. yokohamae* and *C. writai* on each sampling day, BL and TL measurements were made on 10 000 pairs chosen randomly from the available samples. This operation was repeated 100 times (Bootstrap method), and the mean value of the prey-predator size composition was estimated for each sampling day, using Excel software (Microsoft, Redmond, WA, USA). Relationships between the BL increase for *P. yokohamae* and the mean bottom water temperature among each sampling day were measured.

To estimate the shrimp predation intensity, potential predation impact (PPI) was calculated using laboratory observation data (the relationship between prey-predator size class and their predation probability) and field sampling data (the mean value of prey-predator size composition) in Hakodate Bay:

$$\text{PPI} = 100 \times \Sigma(a_i \times b_i / a_{\max}); (0 \leq \text{PPI} \leq 100)$$

where a_i is the predation probability in the i th prey-predator size class in the laboratory experiment ($0 \leq a_i \leq 1$), a_{\max} is the maximum predation probability in all prey-predator size ratios ($0 < a_{\max} \leq 1$), and b_i is the proportion of the prey-predator size ratio at each size class (i) in the field ($0 \leq b_i \leq 1$). A higher score indicates a higher potential predation impact. Moreover, Potential predation density (PPD) was calculated using PPI and predator shrimp density (inds/m²):

$$\text{PPD} = d_i \times \text{PPI}_i; (0 \leq \text{PPD})$$

where d_i is the predator shrimp density on each sampling day (i), and PPI_i is the PPI score on each sampling day (i). *Crangon uritai* is found at prey density exceeding 1.0 ind/m² for any prey item.¹⁷ However, the density of larval and juvenile *P. yokohamae* was lower than 1.0 ind/m² in the nursery area throughout the sampling period. In the present study, there was no consideration of the relationship between the density of larval and juvenile *P. yokohamae* and PPI score.

Statistical analysis

Two-way analysis of variance (ANOVA) was used to detect the shrimp TL frequency distributions and the density of *C. uritai* among months (April–June) and years (1998–2002). If there was a significant difference, Tukey's test was used for comparisons among months and between years. One-way ANOVA was used to detect otolith size difference among the left and right sides. If the variances determined were heteroscedastic as shown by an F_{\max} -test, the values were log transformed. Values were considered significant at the 5% level.

RESULTS

1 Laboratory experiment

Relationship between BL and sagittal otolith diameter of *Pseudopleuronectes yokohamae*

Measurements did not reveal differences between left and right side sagittal otolith diameter (one-way ANOVA, $P = 0.43$), so a mean value was used in later analysis. Relationships between BL of *P. yokohamae* and sagittal otolith diameter (Sod) were calculated as follows:

$$\text{BL (mm)} = 21.68 \times \text{Sod (mm)} + 2.26 \quad (r^2 = 0.97, N = 55, P < 0.001) \quad (1)$$

Prey-predator size ratio

Prey-predator size ratio was estimated using equation 1 (Fig. 1A). *Crangon uritai* fed on *P. yokohamae* within a 0.12–0.31 prey-predator size ratio. Moreover, six prey size class ratio treatments (0.05–0.09, 0.10–0.14, 0.15–0.19, 0.20–0.24, 0.25–0.29 and 0.30–0.34) were investigated with 41 ± 0.4 mm TL (Mean \pm standard deviation, SD) individuals of *C. uritai*. Three individuals of *P. yokohamae* were collected randomly in each of the six prey-predator size classes (totaling 18 individuals) and fed to a single individual of *C. uritai*. As a result, the most favorable prey-predator size ratio class was 0.15–0.19 (56.2% account for all), followed by 0.10–0.14 (27.2%), 0.20–0.24 (10.8%), 0.25–0.29 (5.6 %) and 0.30–0.34 (0.2%) (Fig. 1B).

2 Field observations

Bottom water temperature

Figure 2 shows seasonal changes in mean bottom water temperatures for different years. With the exception of 25 March 2002 (8.2°C), the bottom water temperatures were 6–7°C and generally increased in March. Conversely, from 18 to 29 March 1999, water temperatures sharply declined (7.4 to 6.0°C), and the lower temperature continued until the middle of April. On the other hand, from late March to June in 2002, the highest bottom water temperatures were recorded for the period 1998–2002. Throughout the sampling period in 1999, bottom water temperatures were 1.0–1.8°C lower than those recorded in 2002.

Prey-predator size ratio in the field

Prey-predator size ratio was estimated using back-calculated formulae for body size of *P. yokohamae* in the stomachs of *C. uritai*.¹⁷ The prey-predator size ratio varied from 0.11 to 0.32 for field-sampled data ($n = 7$). We used the prey-predator size ratio range observed in the laboratory (0.12–0.31) for the following analysis because the sampling size of field data was small.

Body length increase for *Pseudopleuronectes yokohamae*

Settlement stage individuals (stages E-J)²⁰ of *P. yokohamae* were not collected in March or on 25 May 2002. Therefore, Figure 3 therefore shows seasonal changes in BL of *P. yokohamae* collected with a sledge net from late March to late June. A small BL increase for *P. yokohamae* was recorded from April to June, but a large increase was detected after late May, except for the year 1999. On 8 June 1999, *P. yokohamae* was

not collected because many crustacean zoeae clogged the mesh of the sledge net.

There was a significant positive correlation between the BL increase of *P. yokohamae* and the mean bottom water temperature among each sampling day, except for early-late June in 1998 and 2002 ($r = 0.84$, $n = 29$, $P < 0.001$; Fig. 4). From early-late June in 1998 and 2002, the BL increase was low (0.13 and 0.11 mm/day, respectively), though the mean bottom water temperatures were high (14.8 and 15.1 °C, respectively).

Total length classification and population density of *Crangon uritai*

Mean TL for male and female individuals of *C. uritai* collected in the nursery ground of *P. yokohamae* did not differ significantly among months and years (two-way ANOVA without repetition for male: $P=0.08$, 0.19 , respectively, and female: $P=0.37$, 0.28 , respectively) (Fig. 5). The densities of *C. uritai* collected in the nursery ground between years were not significantly different (two-way ANOVA without repetition, $P=0.97$), although there were significant differences between months (two-way ANOVA without repetition, $P=0.01$). The density of *C. uritai* declined gradually with the advance of month (April: 1.0 ± 0.19 ind/m² (mean \pm SD); May: 0.7 ± 0.26 ind/m² and June: 0.3 ± 0.22 ind/m²).

Relationship between shrimp predation and density of larval and juvenile

P. yokohamae

Figure 6 shows the relationships between mean pre-shrimp predation density of pelagic-stage larvae of *P. yokohamae* collected with a plankton net during March–April. The occurrence of pelagic larvae fluctuated during March–April for each year.¹⁶ In 2002, the densities of pelagic larvae (collected during March–April) and settled

juveniles (collected in July) of *P. yokohamae* were the highest (16.2 ind/m² and 2.20 ind/100m², respectively). In 1999, although the density of pelagic larvae (collected during March–April) (11.0 ind/m²) was higher than the second period of 1998–2002, the density of settled juveniles was lower than the second period of 1998–2002 (0.10 ind/100m²). From March–April to July in 1999, the density (on the supposition that catch efficiency of a plankton net and a sledge net are 100%.) of *P. yokohamae* declined the most (ca. 0.01%) for the period 1998–2002. In 1998, 2000 and 2001, the density of pelagic larvae were lower than in 2002 and 1999 (3.6 ind/m², 0.2 ind/m² and 3.4 ind/m², respectively), and the density of settled juveniles were 0.28 ind/100m², 0.05 ind/100m² and 0.90 ind/100m², respectively.

3 Estimation of Potential Predation Impact (PPI) and Potential Predation Density (PPD)

At each sampling, prey-predator size distributions (BL of *P. yokohamae* / TL of *C. uritai*) were estimated using collected samples in the field and combined randomly with their BL and TL (Bootstrap method) (Fig. 7). Further, PPI was calculated with the overlaps of their prey-predator size distributions in the field and favorable prey-predator size ratios of laboratory observations on each sampling day (Fig. 8A). PPI scores in March were zero, with the exception of those recorded for 25 March 2002 (22.1). Periods with tentative PPI scores exceeding 20 totaled approximately 50 days (at least from early April to late May) in 1999. In 2002, the same period totaled approximately 30 days (from late March to late April). In 1998, although the sampling started on 7 April, high PPI periods continued in early-middle May and totaled at least 35 days. Similar periods in 2000 (no data in March) and 2001 (no data in April) could not be

estimated. The end of high PPI periods ($PPI \geq 20$) followed the early in 2002, and PPI scores in early and late May were already low (6.2 and 0.6, respectively). Conversely, the PPI scores in early and late May of 1999 were higher than for other years (23.7 and 26.8, respectively), and the score was higher in late June of 1999 (1.8) than in other years (0–0.4).

Figure 8B shows the seasonal change of PPD scores. Values were lowest in early and late May of 2002 (PPD = 2.2 and 0.2, respectively), and highest for the same periods of 1999 (PPD = 24.9 and 15.0, respectively).

DISCUSSION

Prey–predator size ratios estimated under laboratory conditions revealed that crangonid shrimp feed on flatfish juveniles that measure $\leq 50\%$ of crangonid TL.^{1,10–13} In this study, predation by shrimp on *P. yokohamae* was tested in free prey–predator size ratio class treatments. Thus, the most favorable prey–predator size class ratio was estimated as 0.15–0.19, with a range of 0.12–0.31.

In field observations, although shrimp predation began in late March of 2002 and was earlier than the start observed in other years, high temperatures continued throughout the predation periods. The warmer year of 2002 resulted in periods of high potential predation impact ($PPI \geq 20$) that were estimated to be at least 20 days shorter than corresponding periods of the coldest year of 1999 (Fig. 8A). Conversely, PPI values in 1999 were high almost throughout the predation periods, and PPI estimated for the middle of May was much higher (PPI = 26.8) than that of other years. PPD scores for early and late May of 2002 were low (2.2 and 0.2, respectively), while scores in 1999 were higher (24.9 and 15.0, respectively) (Fig. 8B). PPD scores changed to resemble

PPI scores. Low and variable trawl efficiencies were recorded, but the trawls were not size-selective within the size range of individuals captured.^{24,27} This study investigated the preference size ratio of prey flatfish by crangonid shrimp and used the preference prey-size ratio distribution data in the field to estimate the potential predation period and potential predation impact for *P. yokohamae* by *C. uritai*. The juvenile density (collected with a sledge net) in July of 1999 during postpredation periods declined by approximately 0.01% of the larval density (collected with a plankton net) in prepredation periods of March–April. These scores were the lowest for 1998–2002. As the larval densities of March–April were different in each year, it is not easy to compare directly with their survival rate in each year. In 1998, 2000, and 2001, larval densities were relatively low, and the survival rate of juveniles in July was overestimated (0.08%, 0.22%, and 0.27%, respectively). This tendency applies to the coldest year in 1999 and low survival rate in July would be expected. However, the rate was remarkable low (0.01%). Conversely, in the warm year of 2002, the higher survival rate in July (0.14%) appeared in spite of the highest density of larvae in March–April. Therefore, it is suggested that in the cold year the survival rate would be low, and high in the warm year. The cold spring was not only associated with a great overlap of spatial distributions of prey and predators,¹⁷ but delayed the BL increase of *P. yokohamae* (Fig. 3), and the higher PPI and PPD periods were extended. In general, higher water temperature results in higher growth rate of fish larvae and juveniles.^{28,29} Growth speed of larval and juvenile *P. yokohamae* increased with higher water temperature (10–18°C) under laboratory conditions.¹⁹ However, our field observations indicated that the BL increase of the population declined above 14°C (during June of 1999 and 2002, Fig. 4). Relationships between growth rate and water temperature differ greatly according to

feeding level.³⁰ Lower growth periods over a short time soon after settlement have been recorded for flatfishes.³¹ In the present study, most suffer from shrimp predation soon after settlement, and the predation risks for *P. yokohamae* were temperature dependent ($\leq 14^{\circ}\text{C}$ in the field).

From 2001–2003, although the ambient densities of copepod nauplii were high in 2001 and 2003 and low in 2002, BL increase of *P. yokohamae* in 2002 was highest among the three years. These results suggest that the prey density could not be affected more by the bottom water temperature (Joh M, unpubl. data, 2005). However, as the settlement stage of *P. yokohamae* feeds on various prey items including benthic prey,²⁰ further investigation is needed to clarify the relationships between food condition and growth.

In the field, there was a significant positive correlation between the BL increase of *P. yokohamae* and the increase in bottom water temperature (Fig. 4). In contrast, no significant correlation was found between the TL increase of *C. uritai* and the bottom water temperature, and there were no significant differences in the TL increase of *C. uritai* between months (April–June) or years (1998–2002) (Fig. 5). This stable mean TL of *C. uritai* results because almost all of the large-sized individuals brood eggs from April to June (Nakaya M, unpubl. data, 2005), and therefore, these individuals could not molt.

The density of *C. uritai* declined gradually from April to June. In this period, although the large sized individuals (female population) declined, individuals < 19 mm TL (male) would molt and become potential predators on larval and juvenile *P. yokohamae*. Therefore, there would be no difference in mean TL of male individuals between months (April–June) or years (1998–2002).

Diel motile activity of crangonid shrimp increased with higher water temperature (6–20°C) under laboratory conditions (*C. crangon*³² and *C. septemspinosa*⁶). Motile activity of *C. septemspinosa* at 16°C was approximately three times higher during the day and 12.5 times higher at night, relative to the activity exhibited at 10°C.⁶ Further, shrimp gross caloric intake increased by 79% as temperature increased from 10–16°C.³³ In Hakodate Bay, the density of *C. uritai* in early predation periods was approximately three times higher than in late predation periods, and the opportunity to the shrimp for predation on *P. yokohamae* must be higher. Conversely, the caloric energy intake for each predator shrimp during early predation periods may be lower than late predation periods because of the differences in bottom water temperatures (early predation periods 7–9°C, late predation periods 13–15°C). In this experiment, no data were gathered to evaluate the relationship between the activity of *C. uritai* and water temperature. Further investigation will be required to clarify this aspect of *C. uritai* biology.

In this study, we discussed the annual variation of potential shrimp predation periods. Slight differences of growth rate have a significant effect on survival during early life history (growth–predation hypothesis).^{34–36} Future investigations are needed to test the size preference of *C. uritai* and the growth–predation hypothesis by elucidating the individual growth history of *P. yokohamae* using otolith daily increments.

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Fig. 1 (a) Relationship between total length of predator *Crangon uritai* and body length of prey *Pseudopleuronectes yokohamae* ($n = 20$) for predation (□) and non-predation (○) individuals. (b) Predator-prey size ratio distribution derived from laboratory observations ($n = 22$).

Fig. 2 Annual variation of mean water temperatures on the sea bottom in nursery areas (3–10 m depths) in Hakodate Bay from March to June for 1998 (■), 1999 (○), 2000 (◊), 2001 (×), and 2002 (●).

Fig. 3 Mean body length of *Pseudopleuronectes yokohamae* from April to June for 1998 (■), 1999 (○), 2000 (◊), 2001 (×), and 2002 (●) on each sampling day. Vertical bars indicate standard deviations.

Fig. 4 Relationship between the body length increase of *Pseudopleuronectes yokohamae* (mm/day) and mean bottom water temperature (°C).

Fig. 5 Mean total length of *Crangon uritai* from April to June on each sampling day for 1998 (■), 1999 (○), 2000 (◊), 2001 (×), and 2002 (●) for (A) females, and (B) males. Vertical bars indicate standard deviations.

Fig. 6 Relationship between mean larval density of *Pseudopleuronectes yokohamae* collected with a plankton net during March–April and mean juvenile density of *Pseudopleuronectes yokohamae* collected with a sledge net in July. Numbers above each solid circle indicate sampling year.

Fig. 7 Predator–prey size ratio distribution estimated from bootstrap simulation used with field-collected size distribution data and size ratio data.

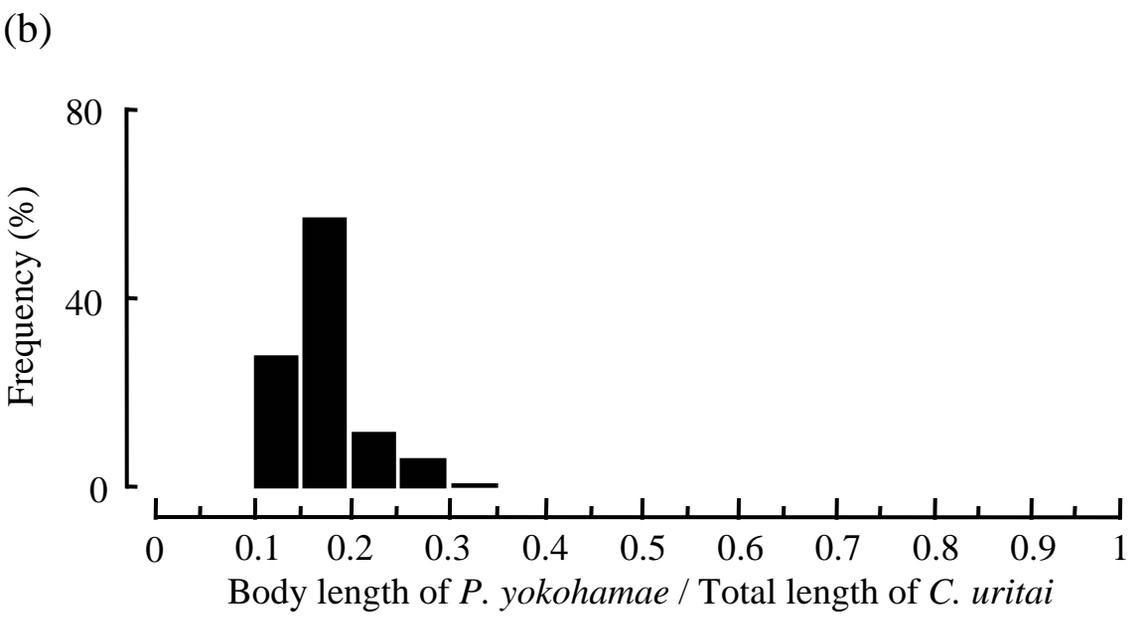
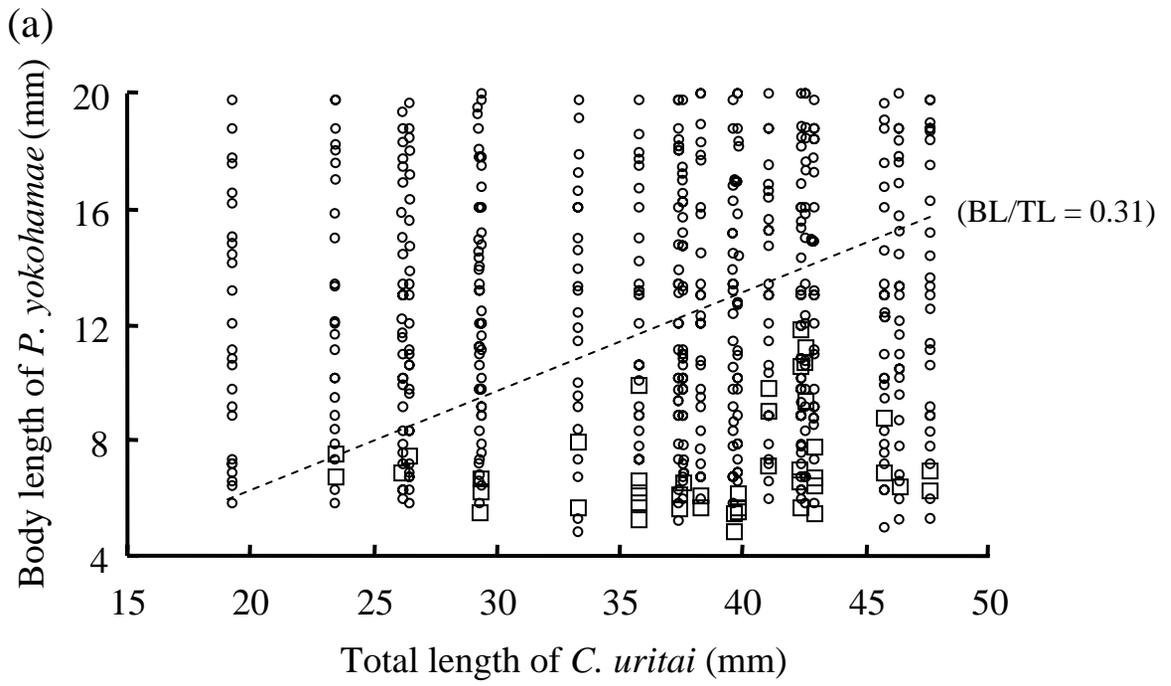
Fig. 8 Seasonal change of (A) potential predation impacts (PPI), and (B) potential predation density of *Crangon uritai* (PPD) based on the favorable size ratio between

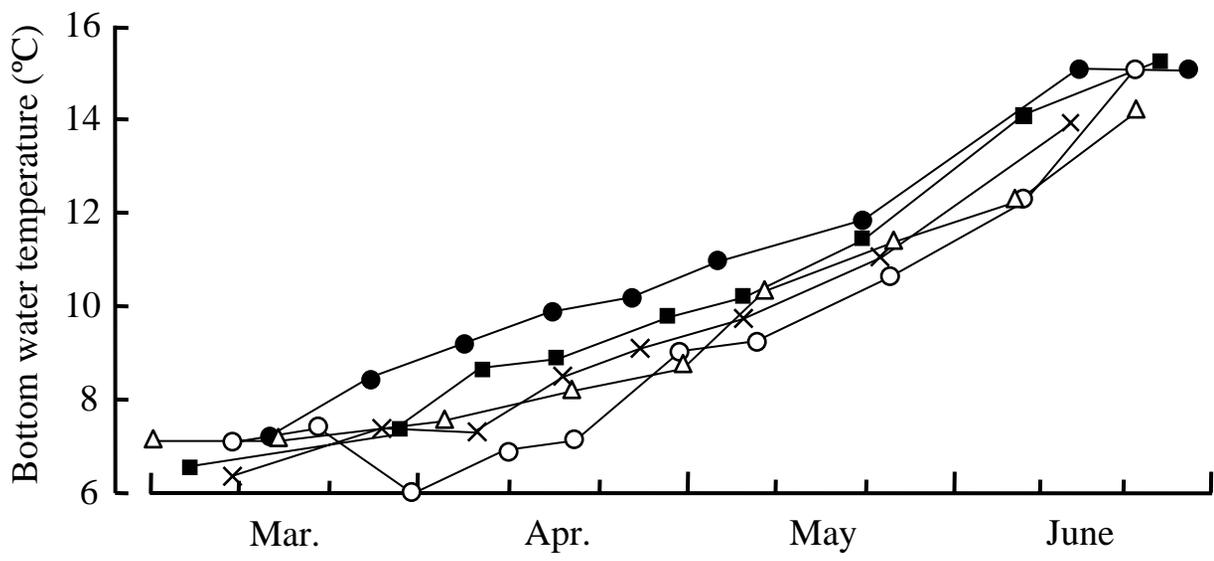
larval and juvenile *Pseudopleuronectes yokohamae* and *Crangon uritai*, for 1998 (■), 1999 (○), 2000 (◊), 2001 (×), and 2002 (●). The dotted horizontal line in (A) shows tentative PPI score = 20.

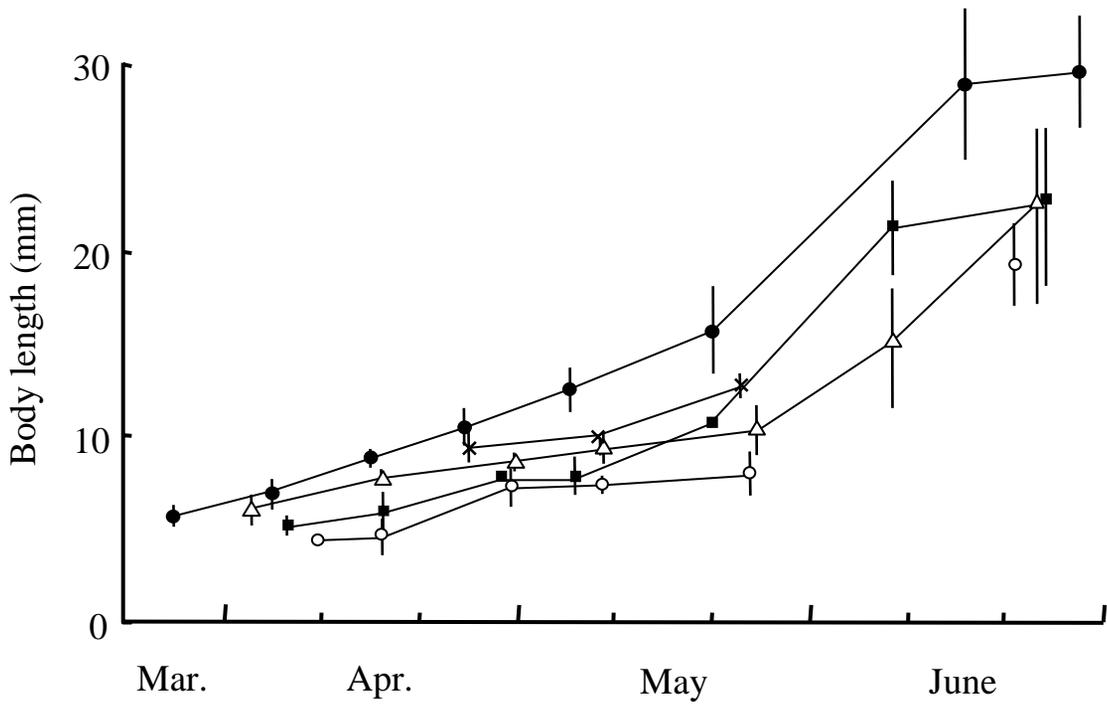
Table. 1 Number of sampling stations and gear in Hakodate Bay from March to July in 1998-2002.

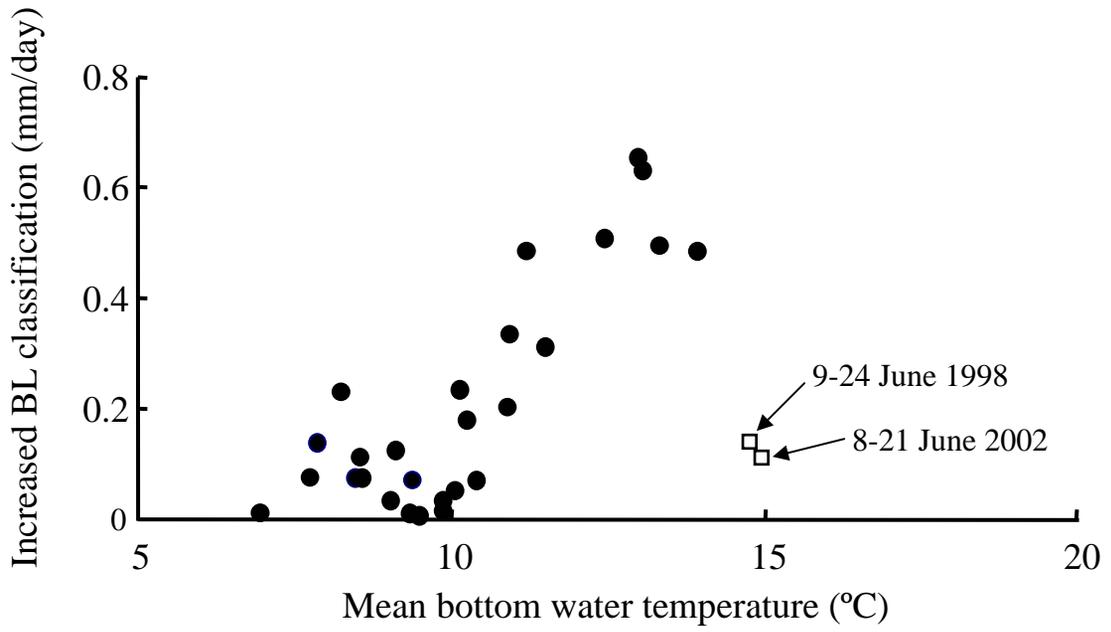
Year	Month	Day	Gear	No. of stations	No. of cast
1998	Mar.	4	P	5	15
		27	P	5	15
	Apr.	7	P, S	5	15, 10
		17	P, S	5	15, 10
		28	P, S	5	15, 16
	May	6	P, S	5	15, 20
		20	P, S	5	15, 20
	June	9	S	3	18
		24	S	3	18
	July	10	S	3	18
1999	Mar.	9	P, S	5, 3	15, 6
		18	P, S	5, 3	15, 6
		29	P, S	5	15, 10
	Apr.	10	P, S	5	15, 10
		17	P, S	5	15, 10
		29	P, S	5	15, 14
	May	8	P, S	5	15, 14
		23	P, S	5	15, 20
	June	9	S	3	12
		21	S	3	12
July	5	S	3	14	
2000	Mar.	1	P, S	5	15, 10
		14	P, S	5	15, 10
	Apr.	3	P, S	5	15, 10
		17	P, S	5, 4	15, 12
	May	30	P, S	5, 4	15, 14
		9	P, S	4, 3	12, 12
	June	24	P, S	4	12, 13
		8	S	3	10
	July	21	S	3	12
		10	S	3	18
2001	Mar.	9	P, S	5	15, 10
		26	P, S	5	15, 10
	Apr.	6	P, S	5	15, 14
		16	P, S	5	15, 14
		25	P, S	5	15, 14
	May	8	P, S	4	13, 12
		23	P, S	4	4, 18
	June	13	S	3	18
		July	10	S	3
	2002	Mar.	13	P, S	5
25			P, S	5	15, 10
Apr.		5	P, S	5	15, 14
		15	P, S	5	15, 14
		24	P, S	5	15, 18
May		6	P, S	4	15, 16
		20	P, S	4	12, 18
June		17	S	3	12
		28	S	3	12
July		26	S	3	15

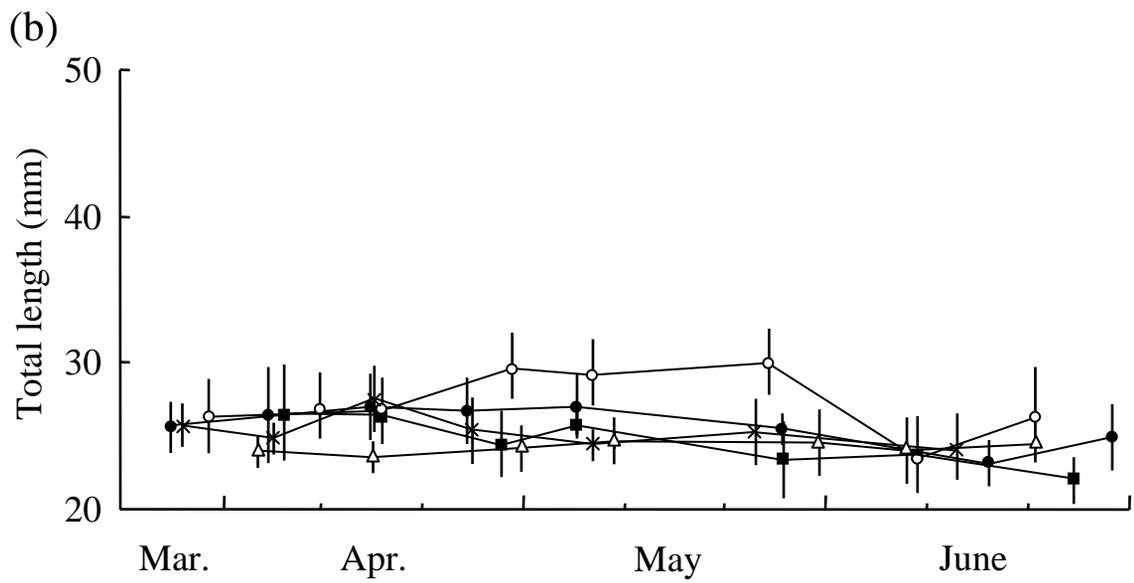
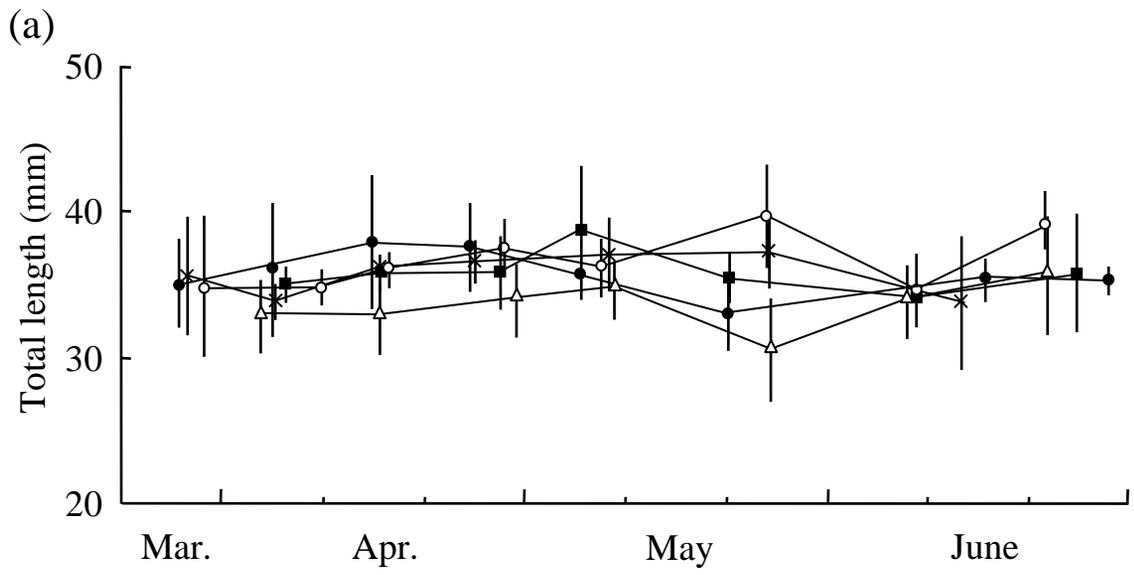
P, plankton net; S, sledge net.

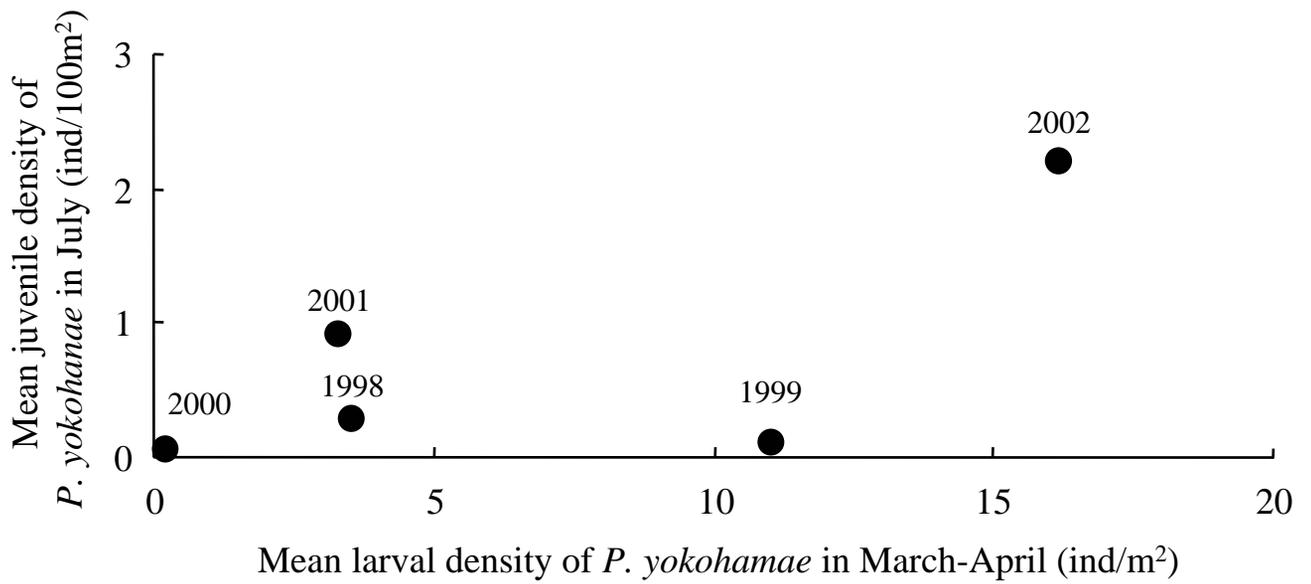




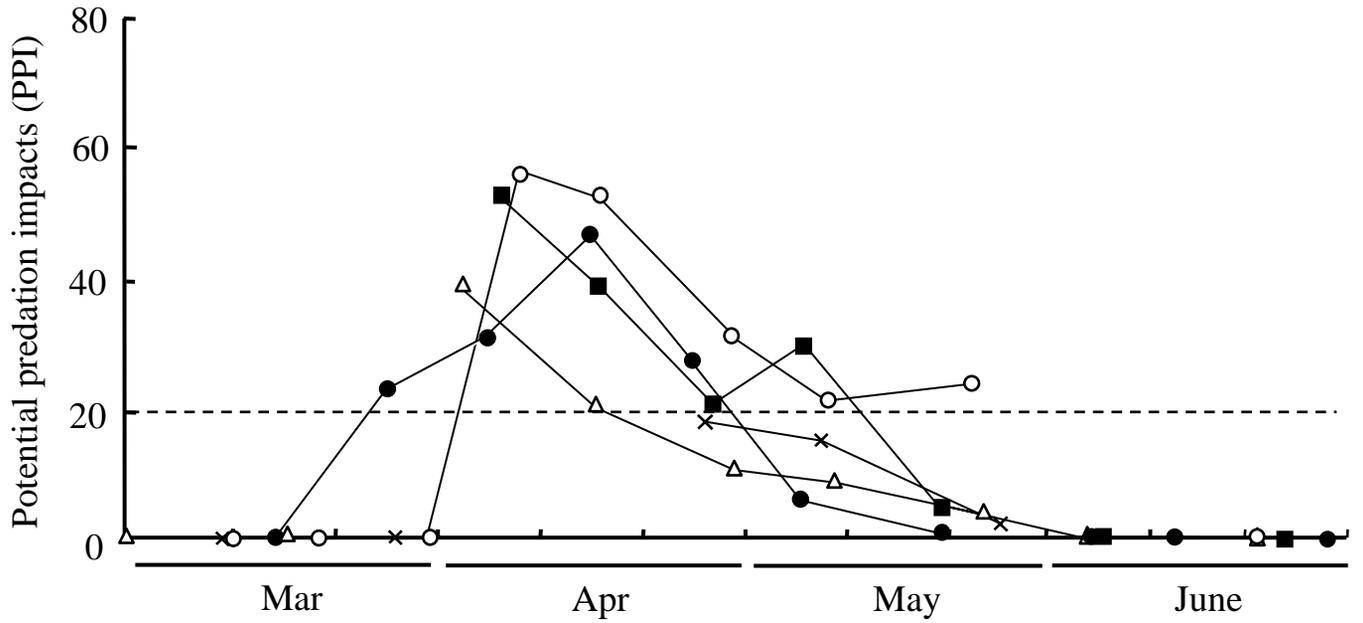








(a)



(b)

