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Prey Choice Order of *Crangon uritai* as a Predator for Juvenile *Pleuronectes yokohamae*

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Abstract: During the spring in the coastal waters of Hakodate Bay the shrimp *Crangon uritai* is the predominant predator on larval and juvenile marbled sole, *Pleuronectes yokohamae*. To investigate the prey preferences of *C. uritai*, *P. yokohamae* and two other prey species, a mysid *Nipponomysis* sp. and a gammarid *Haustorioides japonicus*, were used for predation experiments. Among the three prey organisms studied, *Nipponomysis* sp. was preyed on first, followed by *P. yokohamae*, and finally *H. japonicus*. Prey profitability did not differ between *P. yokohamae* and *Nipponomysis* sp., though *H. japonicus* was less profitable. *Nipponomysis* sp. was larger, more perceptible, and slower to escape than *P. yokohamae*. A relatively high abundance of mysid *Nipponomysis* sp. could restrict and reduce predation on *P. yokohamae* by *C. uritai*. Gammarid *H. japonicus* was able to escape relatively more easily, because its harder and slippery skin required more handling time than the other prey, possibly making it an undesirable food source for *C. uritai*. High perceptibility and low escape ability may be the most important factors affecting prey choice of *C. uritai*.

Key words: *Crangon uritai*; *Pleuronectes yokohamae*; Predator-prey interaction; Prey choice

Mortality during the early life stages of marine fishes is considered to be a major factor of inter-annual differences in recruitment. Various hypotheses concerning recruitment success or failure have been proposed, most of which involve larval starvation (Cushing and Dickson 1976; Cushing 1990), maternal effects (Kjesbu et al. 1996; Solemdal 1997) and predation (Hunter 1981; van der Veer 1985; Bailey and Houde 1989). Small changes in growth rate and duration of the larval stage can cause significant inter-annual fluctuations in recruitment, however predation is potentially more important than starvation as a final and direct regulator of recruitment under normal circumstances (Houde 1987).

Crangonid shrimp are the dominant mobile

epibenthic species in shallow sandy beaches of cool temperature seas (Price 1962; Tiews 1970), and one of the main predators of the larvae and juveniles of flatfish (Pihl and Rosenberg 1982; Gibson et al. 1993; Boddeke 1996; Attrill and Power 2000). In fact, predation alone by the shrimp *Crangon crangon* Linnaeus limits the year class strength of the plaice *Pleuronectes platessa* Linnaeus (van der Veer and Bergman 1987). The prey items of *C. crangon* are various small animals and algae (Amphipoda, Bivalvia, Crustacean Decapoda, fish larvae and juveniles, Isopoda, Mysidacea, Polychaeta, and green algae) (Price 1962; Kosaka 1970; Pihl and Rosenberg 1984; del Norte-Campos and Temming 1994). The shrimp *Crangon uritai* Hayashi and Kim feeds on mysids, gammarids, and larval and juvenile

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P. yokohamae (Nakaya et al. 2004). Although density-dependent predation by crangonid shrimps has been observed in the field (van der Veer and Bergman 1987; Oh et al. 2001; Nakaya et al. 2004), little attention has been given to the mechanisms of crangonid shrimp prey choice, such as the behavior, body shape, and escape ability of prey species. The role of prey escape ability and profitability on prey preference of crangonids is unclear. The recruitment of *P. yokohamae* would be seriously restricted by *C. uritai* predation. In order to estimate the shrimp predation impact in the field, it is necessary to clear the prey selectivity and feeding style of *C. uritai*. This study examined feeding and prey selectivity of *C. uritai*, and compared the vulnerability of three prey species: larval and juvenile marbled sole *P. yokohamae*, a mysid *Nipponomysis* sp. and a gammarid *Haustricides japonicus* Kamihira. As crangonid shrimp are nocturnal (*C. crangon*: Price 1962; Pihl and Rosenberg 1984; Ansell and Gibson 1993; del Norte-Campos and Temming 1994, *Crangon septemspinosa* Say: Wilcox and Jeffries 1974), we discussed predation behavior with respect to the following parameters as determined in a dark room (1) handling time (2) escape ability, and (3) perceptibility of prey species.

Materials and Methods

For laboratory experiments, *C. uritai*, *H. japonicus* and *Nipponomysis* sp. were collected by sledge net (60 cm wide, 40 cm tall with a 0.5 mm mesh) at 1–5 m depths in Hakodate Bay. *P. yokohamae* were raised artificially for the experiment. Both stages of I (latest larval stage and eye migrating) and J (juvenile stage and eye migrated), being used for the experiment belonged to benthic habitat, and were so called juveniles in summary in this text. Both *Nipponomysis* sp. and *H. japonicus* are main prey items of *C. uritai* in the field (Nakaya et al. 2004). Over twenty individuals of each prey type were measured in length and weight. Total length (TL) or body length (BL) was measured to the nearest 0.01 mm with slide calipers, and their body weight in wet

Table 1. Mean prey sizes (with SD) of *P. yokohamae*, *Nipponomysis* sp., and *H. japonicus* used in predation experiments

	<i>P. yokohamae</i>	<i>Nipponomysis</i> sp.	<i>H. japonicus</i>
Body length (mm, $\pm$ SD)	8.7 $\pm$ 0.56	–	–
Total length (mm, $\pm$ SD)	–	13.0 $\pm$ 1.04	6.5 $\pm$ 0.39
Wet body weight (mg, $\pm$ SD)	10 $\pm$ 2.3	23 $\pm$ 4.8	9 $\pm$ 1.7
No.	22	22	22

weight (WW) was weighed to the nearest 1 mg. *Nipponomysis* sp. was larger than *P. yokohamae*, and *H. japonicus* was smaller than *P. yokohamae* (Table 1). Body sizes of prey items used in the experiment were largely the same as prey items found in Hakodate Bay. The experiments were performed at $18 \pm 0.5^\circ\text{C}$ (mean $\pm$ SD) in glass tanks (35 $\times$ 20 $\times$ 15 cm in length, breadth and height) filled with seawater. This experiment was done in 12 hours (maximum) because night-time was about 8.8–11.3 h in the field (N 41°46') from April to June. Predation experiments were carried out with sand on the bottom (3 cm depth, 1.0–0.5 mm diameter) of the experimental tank. Sand was collected from the coastal area of Hakodate Bay. Ten individuals of each *P. yokohamae*, *H. japonicus*, and *Nipponomysis* sp. were released into each experimental tank. The prey species were given 8 h to acclimatize in the experimental prey tank before the experiment. Five individuals of *C. uritai* (36 ± 2.4 mm TL) were removed from the main shrimp tank and placed in individual holding tanks for 24 hours. During this time the 5 shrimp were deprived of food to ensure they had empty stomachs (Gibson et al. 1995) prior to the experiment.

Predation rate with/without alternative prey

P. yokohamae was added to the prey tank either alone or with *H. japonicus* or *Nipponomysis* sp. Each combination was repeated 10 times. At 4, 8, and 12 h after the start of each experiment, the number of prey individuals in the tank was determined. At the end of each repetition all prey species in the water column and sediments were taken out and counted. A two-way ANOVA

was used to detect the effect of alternative prey presence and temporal change.

Prey features as a prey of C. uritai

Behavior and perceptibly of prey items were observed using an infra-red video camera (Panasonic WV-CD810, Matsushita Communications Industry, Inc.). Infra-red illumination does not frighten the prey or predator (Batty 1983). (1) Prey escape rate ($100 \times \text{escape individuals} / \text{attack times} (\%)$: about 50 attacks on each prey species) and, (2) handling time defined as the time required to pursue and ingest a prey item, and (3) escape distance and time as escape ability of prey species was also measured in a plastic tank ($35 \times 20 \times 10$ cm in length, breadth and height). These three prey species were not nocturnally active, but remained on the sand bottom frequently, and escape actions were only observed when the predator scraped the body of the prey individual. The tail of the prey was poked with a pin stick; the distance moved was measured with slide calipers and escape time was recorded. Analysis of variance (ANOVA) was used to compare the mean values. If the variances determined were heteroscedastic as shown by a $F_{\max}$ -test, the values were log transformed. Scheffe's test was used to compare multiple means of escape distance, handling time, and prey profitability. Analysis of covariance (ANCOVA) was used to compare the relationship between escape time and distance moved for each of the three prey species.

Results

Prey choice order of C. uritai

Order of preference: *Nipponomysis* sp. > *P. yokohamae* > *H. japonicus* (Fig. 1). Within 4 hours after the introduction of five individuals of *C. uritai*, 2.3 of 10 individuals of *Nipponomysis* sp., 3.9 of 10 individuals of *P. yokohamae*, and 5.8 of 10 individuals of *H. japonicus* survived. This prey choice order was consistent as each experiment continued (8, 12 h). Of the three prey items, *Nipponomysis* sp. was the mostly preferred prey for *C. uritai*, and *H. japonicus*

was consumed least (Fig. 1: two-way ANOVA, prey types, $P < 0.001$, hours, $P = 0.12$, prey types $\times$ hours interaction, $P = 0.89$). Significant differences were found in all three pairs of prey items (Scheffe's test, all $P < 0.001$).

Without alternative prey, an average of 9.8 individuals of 10 *P. yokohamae* were consumed by 5 individuals of *C. uritai* within 4 h of the experiment (Fig. 2). All 10 individuals of *P. yokohamae* were the victims of predation within 4 h in eight cases out of ten. Remaining individuals of *P. yokohamae* differed significantly with the alternative-prey presence/absence (two-way ANOVA: $P < 0.001$), but not with respect to time ($P = 0.15$). An alternative prey $\times$ time interaction was not detected ($P = 0.23$), as both factors affected the remaining individuals equally.

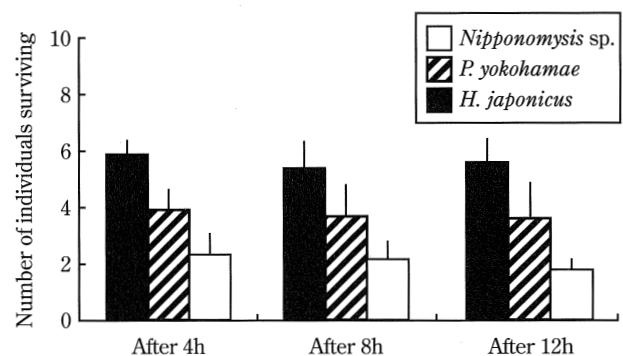


Fig. 1. Survival of individuals of three prey organisms (*P. yokohamae*, *Nipponomysis* sp., and *H. japonicus*) in predation experiments by *C. uritai*. Horizontal bars show standard deviations of mean values (at various times; $n = 10$).

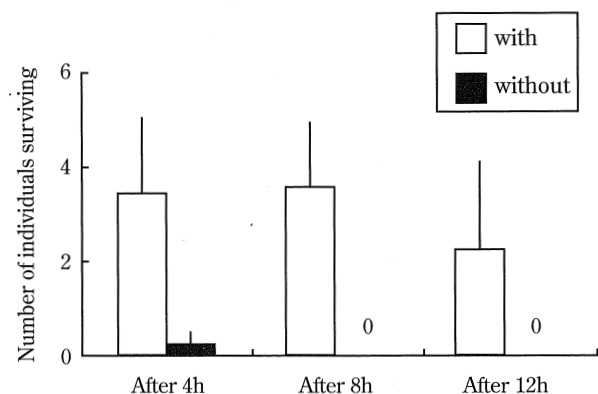


Fig. 2. The number of prey individuals remaining at various times after the start of predation experiments with and without alternative prey. Horizontal bars show the standard deviations (at various times; $n = 10$).

Predator-prey interactions

(1) Escape ability

No significant difference was found among the three slopes of the regression lines between escape time and escape distance (Fig. 3; ANCOVA, $P=0.10$). However, there was significant difference among the three intercepts ($P<0.001$; Table 2). According to these regression lines, the distances that would allow the species to escape within the first 0.1 sec were 5.2 cm for *P. yokohamae*, 3.9 cm for *Nipponomysis* sp., and 3.8 cm for *H. japonicus* (Table 2). Escape distance of *Nipponomysis* sp. (3.7 ± 1.10 cm) was significantly shorter than that of *P. yokohamae* (4.6 ± 1.08 cm; Scheffe's test: $P<0.01$) and *H. japonicus* (4.8 ± 1.38 cm; $P<0.001$; Fig. 4). Mean escape distance of

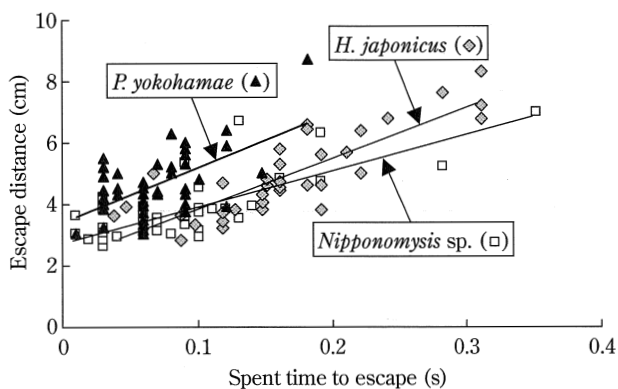


Fig. 3. Relationships between spent time to escape and escape distance for each prey species in the laboratory. Regression lines of *P. yokohamae*: $y = 18.3x + 3.4$, $r^2 = 0.35$, $n = 43$, $P < 0.001$, *H. japonicus*: $y = 16.6x + 2.2$, $r^2 = 0.72$, $n = 45$, $P < 0.001$, and *Nipponomysis* sp.: $y = 11.9x + 2.7$, $r^2 = 0.59$, $n = 45$, $P < 0.001$.

P. yokohamae did not differ significantly from that of *H. japonicus* (Scheffe's test: $P > 0.05$). Escape rate was estimated from number of prey individuals sacrificed per total number of attacks on an infra-red video camera. Escape rates for *P. yokohamae*, *Nipponomysis* sp. and *H. japonicus* were 55%, 38% and 80% respectively, with significant differences being found for all three pairs of prey items ($G_{adj} = 21.7$, $P < 0.001$).

(2) Handling time

C. uritai cannot prey on more than one individual at a time because it must occupy its time pursuing and biting a single prey individual. Mean handling times were 78 sec for *Nipponomysis* sp., 16 sec for *P. yokohamae* and 184 sec for *H. japonicus*. Significant

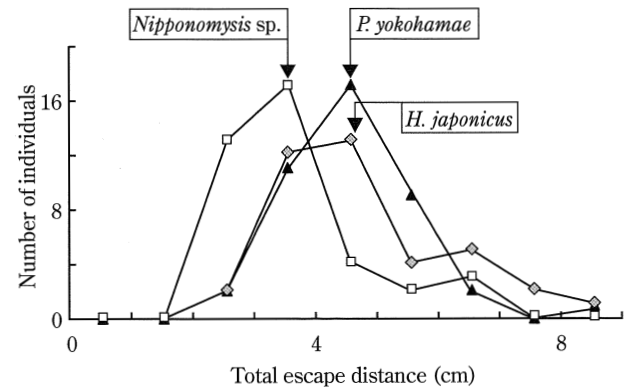


Fig. 4. Frequency distribution of escape distance for each prey animals (*P. yokohamae*, *Nipponomysis* sp., and *H. japonicus*) following a reaction. Escape reactions were elicited by poking the tails of prey individuals with a pin stick. Each location of the arrow shows the mean escape distance.

Table 2. Escape ability, handling time, and profitability for three prey types used in the experiments

	<i>P. yokohamae</i>	<i>Nipponomysis</i> sp.	<i>H. japonicus</i>	Statistical significance
Initial escape distance (cm at first 0.1 sec)	5.2	3.9	3.8	Not tested
Escape distance (cm, $\pm$ SD)	4.6 ± 1.08	3.7 ± 1.10	4.8 ± 1.38	* $P < 0.001$
Sample size	43	45	45	
Escape rate (%)	55	38	80	# $P < 0.001$
Sample size	42	63	58	
Handling time (s, $\pm$ SD)	16 ± 9.7	78 ± 48.4	184 ± 121.5	* $P < 0.001$
Sample size	33	32	33	
Profitability (mg/s, $\pm$ SD)	0.4 ± 0.29	0.5 ± 0.29	0.1 ± 0.12	* $P < 0.001$
Sample size	23	21	20	

* One-way ANOVA, # G-test.

differences were found in all three pairs of prey items (Fig. 5, Table 2; Scheffe's test: all $P < 0.001$). *C. uritai* mainly swallowed *P. yokohamae* (96%: 23 cases out of 24) and *Nipponomysis* sp. (80%: 16/20), and rarely bit off portions of the prey item. In contrast, *C. uritai* occasionally swallowed *H. japonicus* (29%: 6/21), but preferred to bite off portions of the prey item (71%: 15/21).

(3) Profitability

Profitability of a prey item can be defined as the prey value divided by its own handling time. The larger the index, the more profitable the prey. When encounter rates are equal between two different prey types, a prey organism ought to be chosen with respect to this index. We defined profitability as the prey body weight in wet weight (measured in living at each prey individuals before measurement the handling time) divided by handling time for each prey species. Indices for *Nipponomysis* sp. (0.5 ± 0.29 mg/s), and *P. yokohamae* (0.4 ± 0.29 mg/s) were significantly higher than that for *H. japonicus* (Table 2, 0.1 ± 0.12 mg/s; Scheffe's test: $P < 0.01$ and $P < 0.001$, respectively). Indices between *P. yokohamae* and *Nipponomysis* sp. did not differ significantly (Scheffe's test: $P = 0.20$).

(4) Behavior

In predation experiment, the behavioral differences among prey types were observed.

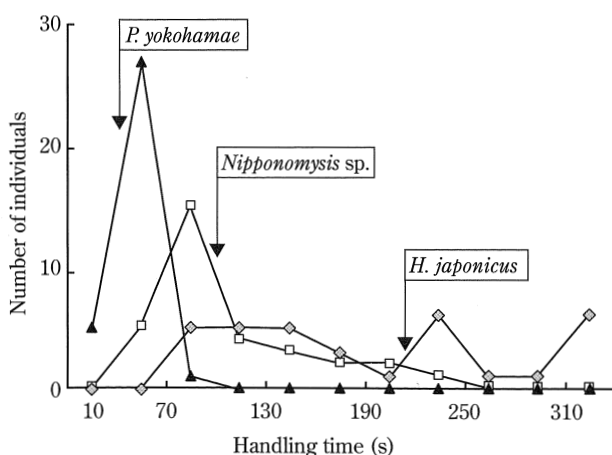


Fig. 5. Frequency distribution of handling time for each prey species of *C. uritai*. Handling time defined as the time required to pursue and ingest a prey item. Each location of the arrow shows the mean handling time.

All *P. yokohamae* remained close to the bottom of the water tank, without shrimp predation attack. *H. japonicus* moved from the bottom to the surface, but remained predominantly on the bottom. On the other hand, *Nipponomysis* sp. fidgeted about, hovering just above the bottom or moving elsewhere.

Discussion

Crangonid shrimp have a density-dependent predation pattern (van der Veer and Bergman 1987; Oh et al. 2001), and choose the most abundant prey items from various food sources in the environment (Nakaya et al. 2004). Prey density is one of the most important factors affecting prey choice in *C. uritai*, because the encounter rate between prey and predator often changes. Prey selection of animals is decided by many factors, including prey perceptibility, prey escape ability, handling time, prey volume and caloric value, nutrition, defense, probability of successful capture, preference, past memories of prey, and the predator's physical condition. In the rearing tanks, prey choice order of *C. uritai* followed feeding behavior theory (Stephens and Krebs 1986), and the ideal prey was noticeable, possessed low escape ability, and imparted a high profitability. As prey choice order in this study was investigated in darkness, *C. uritai* found prey items without employing its sense of sight.

Nipponomysis sp. displayed a more fidgety behavior and demonstrated a lower escape ability than *P. yokohamae*, but both possessed a similar profitability (Table 2, Figs. 2–4). Prey perceptibility and escape ability may be a more important factors for prey selection than profitability for *C. uritai*. Artificially raised *P. yokohamae* was used in this study. Wild flatfish were less susceptible to predation than hatchery-reared ones, owing to difference of behavioral pattern and high escape ability (Yamashita et al. 1993; Kellison et al. 2000). So, *Nipponomysis* sp. may be more selective prey of *C. uritai* than *P. yokohamae* in the field.

C. uritai displayed two feeding techniques: swallowing whole and biting off. The biting off

feeding technique requires more handling time than the swallowing whole feeding technique. Crangonid shrimps bite off *P. platessa* (van der Veer and Bergman 1987), and *Paralichthys olivaceus* Temminck et Schlegel juveniles (Seikai et al. 1993), but *C. uritai* often swallow whole bodies of *P. yokohamae* (Nakaya et al. 2004). This difference can be explained by the settlement size of *P. yokohamae* (7–9 mm BL: Minami 1981; Table 1) which was smaller than that of *P. platessa* (10–15 mm BL: Zijlstra et al. 1982), *P. olivaceus* (10–13 mm BL: Minami 1982) and *Pleuronectes americanus* (Walbaum) (10.1–14.5 mm in standard length: Witting and Able 1995). *P. yokohamae* juveniles were therefore more profitable prey items than other larger-size flatfishes that were bitten by crangonid shrimps.

The characteristics of the different kinds of prey species, such as body texture, firmness and shape, had a great effect on handling time and gastric evacuation (Webb 1986; Hoyle and Keast 1986). With respect to evacuation time, there are some reports that crustaceans such as mysids and euphausiids are easier to digest than fish juveniles and mollusks (Koshiishi et al. 1982; MacDonald et al. 1982; Yoshida et al. 1993; Andersen 1998, 1999; Temming and Herrmann 2001). In the present study, *Nipponomysis* sp. did not have a significantly higher profitability than *P. yokohamae*; however, the possibility of a higher profitability of *Nipponomysis* sp. relative to *P. yokohamae* may exist when considering evacuation time. A relatively high abundance of *Nipponomysis* sp. would restrict and reduce the effects of predation on *P. yokohamae* by *C. uritai* in the field. As individuals of *H. japonicus* displayed a relatively higher escape ability (Table 2) and possessed a harder and slipperier skin, *C. uritai* needed a longer handling time than that needed to handle other prey items. We conclude that *H. japonicus* may be an undesirable food source for *C. uritai*. But the density of gammarids as *H. japonicus* in sandy area is usually high (e.g. in Hakodate Bay: Nakaya et al. 2004). The gammarids are therefore a main source of food for *C. uritai*. For example, in

Hakodate Bay, gammarids are 13 (mean value, maximum 57) times as abundant as Mysids, and 191 (mean value, maximum 295) times as abundant as *P. yokohamae* (Nakaya et al. unpublished). Calorimetric contents of each prey type were not measured in this study. Inclusive energy of mysid is 4.1 kJ/g wet weight (WW) (Tyler 1973) and 3.1–4.0 kJ/gWW (Kooka et al. 2002). Fish larvae and juvenile are as the follows: *Pleuronectes* sub adult 4.4–4.7 kJ/gWW (Paul et al. 1995), greenback flounder juvenile 4.5–4.6 kJ/gWW (Verbeeten et al. 1999), and gammarid are 3.5 kJ/gWW (Percy and Fife 1981). Though the energy content of fish larvae and juveniles is slightly higher than that of other prey types, there is no substantial difference in energy content among the three prey types studied. Further investigations have clarified, the relationship between mysid density and shrimp predation for *P. yokohamae* in the field. The existence of alternative prey (e.g. mysids) would restrict and reduce the effects of predation on any other commercial flatfishes by crangonid shrimps.

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マコガレイ稚魚の捕食者としてのエビジャコの餌選択機構

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餌種の特徴の違いとエビジャコの餌選択の関係を知らるために、捕食実験を行った。実験はエビジャコ5個体に対して、マコガレイ稚魚とその他エビジャコの主要な餌であるアミ類の1種 *Nipponomysis* sp.とヨコエビ類の1種ナミノリソコエビを、それぞれ10個体ずつ同時に与えて行った。捕食結果、マコガレイ稚魚はエビジャコにとって処理に時間を要しない餌であるが、底面から離れることがほとんどないため発見されにくく、逃避能力も高いため、*Nipponomysis* sp.よりも捕食されにくい餌であった。ナミノリソコエビはマコガレイ稚魚に比べて小型であるが、捕獲してから処理に時間を要するため、最も捕食されにくい餌であった。このことからマコガレイ稚魚よりも相対的に目立ちやすく、逃避能力が低く、かつ処理に時間を要しない餌（アミ類）の存在は、エビジャコによるマコガレイ稚魚の被食頻度を低下させていると考えられた。