Dietary preferences of the Japanese mitten crab *Eriocheir japonica* in a river and adjacent seacoast in north Kyushu, Japan

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Abstract: The diet of the Japanese mitten crab *Eriocheir japonica* was investigated by examining the stomach contents of middle- and large-sized crabs (carapace width >10 mm). Crabs were collected in the freshwater area (growth area), tidal river, and seacoast area (reproductive area) of the Saigo River, Fukuoka Prefecture, Japan. Analysis of the diet of *E. japonica* was carried out using the frequency of occurrence and percentage point methods. The stomach contents were classified into 4 large and 27 small categories. It was evident that *E. japonica* was an omnivore and a deposit feeder, mainly feeding on the detritus derived from vascular plants growing along the river channel. Filamentous algae *Cladophora* sp., aquatic insects (e.g., Chironomidae), sediments such as mud or sand, and artificial products such as plastic or yarn were often found, suggesting that *E. japonica* mainly feeds on detritus lying on the substrate without sorting well. Stomach contents of adult crabs in the tidal area exhibited higher frequency of animal materials (i.e., fish, gastropods, and crabs) than those of young and adult crabs in the freshwater area, suggesting that adult crabs in the tidal area eat more animal materials. Such an omnivorous feeding habit is similar to other related brachyuran crabs (grapsoidae) and may be one of the important factors which enables *E. japonica*’s wide distribution along the river and seacoast.

Key words: Dietary preferences, ecological niche, *Eriocheir japonica*, Japanese mitten crab

Introduction

The Japanese mitten crab *Eriocheir japonica* (de Haan) is a varunid crab distributed in Sakhalin, Maritime Province of Siberia, eastern Korea, the entire Japanese archipelago, and Taiwan (Miyake 1983). It is a catadromous species, migrating from the freshwater area of rivers to the sea for copulation and oviposition (Kobayashi 1999, Kobayashi & Matsuura 1991, 1995a, 1995b). This crab is an important fishery target in many Japanese rivers and its population has been exposed to strong fishing pressure (Kobayashi et al. 1997). This crab is a common large, benthic species, widely distributed from the upper reaches of rivers to tidal river and seacoast areas. Although many brachyuran crabs are distributed in the riverine and coastal environment in the temperate zone of Japan, there are no species distributed as widely as *E. japonica* (Kobayashi 2000). The reproductive area of *E. japonica* is the lower tidal river and adja-
tivity and strong adaptability to environment is common among congeneric species. The Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards, originally distributed in China and west Korea, has invaded and established in many European and North American countries (Peters & Panning 1933, Panning 1939, Nepszy & Leach 1973, Cohen & Carlton 1997, Clark et al. 1998, U. S. National Management Plan 2003). Impact on the ecological systems in the invaded countries has been elucidated by the research on feeding habit of this species. Feeding habits are considered to be an important factor for the success of invasion and establishment in new countries (Rudnick & Resh 2005). A similar tendency may be applicable to *E. japonica*. Currently *E. japonica* has been found in the Columbia River, USA as an alien species (Jensen & Armstrong 2004). However, feeding habit of *E. japonica* and its ecological niche in natural conditions have still remained unclear.

Analysis of stomach content has been used as a representative method for investigation of the diet of brachyuran crabs (Bernardez et al. 2000, Cannicci et al. 1996, Chen et al. 2004, Vannini et al. 1989, Williams 1981). The present paper analyzes the stomach contents of *E. japonica* gathered from a small river and adjacent seacoast in the temperate zone of Japan and compares the frequency of each food item between collection sites (growth area and reproductive area), body sizes (middle and large size), and seasons to elucidate changes in the diet. The food preference of *E. japonica* is compared with those of related species and cohabiting species, and its ecological niche is discussed to explain the wide distribution of this species in the river and marine environment.

**Materials and Methods**

**Collection site**

The collection site was selected in the lower region (from the river mouth to about 2 km upstream) of the Saigo River and adjacent sea coast, in Fukutsu City, Fukuoka Prefecture, Japan (33°46′N, 130°30′E, Fig. 1). Preliminary surveys in this river suggested that *Eriocheir japonica* was not as abundant in the upper region as in the lower region, so collections were made only in the lower region. The sampling area was established as follows (Fig. 1). Area I consists of three sites: Site 1, intertidal and shallow subtidal zones of the seacoast near the river mouth; Site 2, the lower tidal river area near the river mouth; Site 3, middle tidal river area. Thus Area I is lower than the middle tidal river area of the Saigo River is considered to be of the weakly mixed type (Okuda 1996), and a salt wedge invades the tidal river area, reaching the weir during high water of the spring tide. At Site 4, freshwater always flows except for a short time (<1 h) during the flood tide. Sea weeds derived from the seacoast were often supplied by high tide in the lower part of Area II.

There is a sparse growth of riparian vegetation along the channel in the banks, but trees including deciduous broad-leaf trees which supply dead leaves and branches to the river are growing outside the channel walls in the tidal river area (Site 3–4). In the freshwater area (Site 5–7), riparian vegetation grows densely along the channel in the banks and supplies a large amount of detritus derived from dead leaves, stems and roots to the channel. Detritus often deposits on the riverbed of pools in the river. In the submerged area, filamentous green algae attached to the rocks or concrete substrate and submerged vascular plants grow in the pool area. Within the study site, organically polluted water always flows into the main stream of Saigo River through its tributaries from the surrounding residences and paddy fields. For the species of vegetation, see Table 1.

Cohabiting animals with *E. japonica* were categorized into three types: salt water (including brackish and sea) animals, diadromous animals and freshwater animals (Table 1). The salt water animals were found within the four sites downstream from Site 4. Diadromous animals were collected in the sites including tidal area and freshwater area. Freshwater animals usually occurred within three sites upstream from Site 5, and occasionally occurred in Site 4 (Kobayashi 1998). Among grapsoid crabs, three varunid

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**Fig. 1.** Map of the Saigo River and location of the collection sites.
species (*Hemigrapsus penicillatus* (de Haan), *Hemigrapsus sanguineus* (de Haan) and *Gaetice depressus* (de Haan)) were abundantly collected in Area I all year round. As for other grapsoid species, migratory varunid crab *Varuna litterata* (Fabricius) and terrestrial sesarmid crabs *Sesarmops intermedium* (de Haan) and *Chiromantes dehaani* (H. Milne Edwards) occurred mainly in Area II (Kobayashi 1998).

The water temperature at site 4 varied from 8.2°C (January) to 30.0°C (August) during the sampling period. It was lower than 10.0°C from December to February (Kobayashi 1998).

Area I (especially site 1 and 2) is the reproductive area of *E. japonica* where adult crabs exhibit mating, spawning eggs and hatching from September to June (Kobayashi 2003). Area II is the growth area of *E. japonica* where young crabs grow after the settlement of megalopa. Exuviae of *E. japonica* were often collected on the riverbed except during the winter season (Kobayashi 2003). Megalopa larvae of *E. japonica* settle on the lower limit of this area (Site 4) and metamorphose to crab stage in late autumn and early summer. Young crabs grow larger and migrate upstream to the upper freshwater area. They attain maturity from August to December in the freshwater area and migrate downstream to the lower tidal area (Kobayashi 1998, 2003).

### Table 1. Representative species distributed in the collection sites.

| Deciduous broad-leaf tree | Magnoliophyta Magnoliopsida | Cinnamomum camphora (Linnaeus) |
|---------------------------|-----------------------------|--------------------------------|
| Riparian vegetation | Magnoliophyta Monocotyledoneae | Phragmites australis Trinius ex Steudel / Phragmites japonica Steudel / Typha angustifolia Linnaeus |
| Freshwater filamentous algae | Magnoliophyta Chlorophyta | Persicaria thunbergii (Siebold & Zuccarini) |
| Submerged vascular plant | Magnoliophyta Monocotyledoneae | Cladophora sp. |
| Sea weeds | Magnoliophyta Chlorophyta | Egeria densa (Planch) |
| Sheathed bacteria | Protobacteria | Ulva pertusa Kjellman |
| Saltwater animals | Arthropoda Crustacea | Balanus albiocostatus Pilsbry |
| | Decapoda | Gaetice depressus (de Haan) / Hemigrapsus sanguineus (de Haan) / Hemigrapsus penicillatus (de Haan) |
| | Mollusca Gastropoda | Monodonta labio form confusa Tapprone-Canefri / Chrolostonia lischkai (Tapprone-Canefri) / Thais (Reishia) clavigera (Kuster) / Nodilittorina radiata (Eyoud & Souleyet) / Collisella dorsuosa (Gould) / Patelloida saccharina form lanx (Reeve) |
| | Bivalvia | Mytilus galloprovincialis Lamark / Crassostrea gigas (Thunberg) |
| | Cnidaria Anthozoa | Anthopleura japonica Verri |
| | Annelida Polychaeta | Hestites sp. |
| | Vertebrata Pisces | Takifuga niphobles Jordan & Snyder / Acanthogobius flavimanus (Temminck & Schlegel) |
| | [Diadromous animals] | Arthropoda Crustacea | Macrobrachium formosense Bate / Caridina leucosticta Stimpson / Chiromantes dehaani (H. Milne Edwards) / Sesarmops intermedium (de Haan) / Clithon retropicatus (Martens) / Anguilla japonica Temminck & Schlegel / Mugil cephalus Linnaeus / Rhinogobius sp. CB / Rhinogobius giurinus (Rutter) |
| | Vertebrata Pisces | Procambarus clarkii (Girard) / Chironomidae spp. / Baetis sp. / Anax parthenope julius Brauer |
| | [Freshwater animals] | Arthropoda Insecta | Procambimus clarkii (Girard) / Chironomidae spp. / Baetis sp. / Anax parthenope julius Brauer |
| | Decapoda | Semisulcospira libertina (Gould) / Carassius auratus langsdorffii Temminck & Schlegel / Cyprinus carpio Linnaeus / Zacco platypus (Temminck & Schlegel) |
| | Mollusca Gastropoda | Rana catesbeiana Shaw |
Sampling

Hand or net sampling of *E. japonica* was conducted mainly during the ebb tide at daytime from December, 1996 to April, 1997 in Area I, and once a month from May, 1996 to April, 1997 in Area II. Crabs were killed by cutting the nerve system just after collection and fixed in 10% formaline within 2 hours after collection in the laboratory. Maximum carapace width (CW) of crabs was measured to the nearest 0.1 mm. They were sexed according to the shape of the abdomen. Female crabs were categorized into juveniles and adults, based on the morphological difference of the abdominal segments (Kobayashi & Matsuura 1992). Because it was not easy to dissect the crabs of CW <10 mm, only crabs of 10 mm ≤ CW were used for analysis in the present data. Crabs collected in Area II were categorized into middle size (10 mm ≤ CW ≤ 35 mm) and large size (35 mm ≤ CW) based on the size of emergence of adult crabs; adult crabs participating in reproduction emerge mostly in 35 mm ≤ CW (Kobayashi & Matsuura 1992). Their stomach was removed to examine the contents under a binocular microscope.

Quantitative analysis of the diet of *E. japonica* was carried out using the frequency of occurrence and percentage point methods. Each method describes different aspects of the relative importance of food items and the scores given by each were highly correlated for most types of food. Feeding preference of crabs can be directly reflected in the point method, but not so much in the occurrence method. However, the point method is generally unsuitable for foods consisting of high proportion of soft tissue, whereas the occurrence method is appropriate for most foods (Williams 1981).

The frequency of occurrence method was calculated for each food item by dividing the number of crabs with stomachs containing the specific food item by the total number of crabs in the sample:

\[ \% \text{frequency of occurrence for } i \text{th food} = \frac{A_i}{n} \times 100 \]

where \( A_i \) is the number of crabs with stomachs containing the food item \( i \), and \( n \) is the number of crabs analyzed in the sample.

The percentage points for each food item were calculated by summing the weighted points for each item and dividing it by the total number of points for all crabs and all food items in the sample.

\[ \text{Percentage points for } i \text{th food} = 100 \times \sum_{j=1}^{m} \frac{B_{ij}}{\sum_{j=1}^{m} \sum_{j=1}^{n} B_{ij}} \]

where \( B_{ij} \) is the number of points of food item \( i \) in the stomach of the \( j \)th crab, and \( n \) is the number of crabs analyzed in the sample and \( m \) is the number of food items. The number of points for each food category of each crab was calculated by multiplying the relative contribution to the stomach contents (point a) by a value dependent on the degree of stomach fullness (value b) (Table 2).

The cumulative number of different food taxa found in the stomach, the frequency of occurrence, and the percentage points were then calculated as crabs were added, one at a time, to a sample. Sand and unidentified materials were also considered as stomach content categories.

### Results

**Carapace width (CW)**

Crabs collected in Area I from December, 1996 to April, 1997 ranged in size from 32.1 to 62.7 mm CW for males and from 36.9 to 62.7 mm CW for females. All females were adult. In Area II, the maximum size collected from May, 1996 to April, 1997 was 57.7 mm CW for males and 71.0 mm CW for females. Size composition changed seasonally: proportion of large-size crabs (35 mm ≤ CW) was low in May–June, 1996 (male 14.7%, female 5.6%) and March–April, 1997 (male 7.7%, female 0%). Growth of juveniles and process of attaining maturity (puberty molt) were exhibited from May to October, 1996. Adult females occurred from September, 1996 to February, 1997 (Fig. 2).

**Stomach contents**

A total of 97 male and 96 female specimens of *Eriocheir japonica* were collected in Area I, of which 96 males (99.0%) and 91 females (94.8%) had food contents for analysis. In Area II, a total of 404 male and 357 female specimens of *E. japonica* were collected of which 318 male (78.7%), and 288 females (80.7%) had food contents for analysis.

Stomach contents were classified into 4 large categories

| Table 2. Calculation method of the number of points for each category: A, relationships between relative contribution to the stomach contents and point a; B, relationships between degree of stomach fullness and value b. Point for each food category = point a × value b. The maximum points possible for a single category in a single stomach is 100 (100 × 1.0); the minimum weighted points possible is 0.05 (2.5 × 0.02). |
|---------------------------------|-------------------------------|-----------------------------|
| **A.** Relative contribution to the stomach contents | point a | 95–100% | 100 |
| | 65–95% | 75 |
| | 35–65% | 50 |
| | 5–35% | 25 |
| | ≤5% | 2.5 |
| | empty | 0 |
| **B.** Degree of stomach fullness | value b | full | 1.00 |
| | 75% | 0.75 |
| | 50% | 0.50 |
| | 25% | 0.25 |
| | trace | 0.02 |
(I–IV) and 27 small categories (1–27, Table 3) including both plant and animal material, as well as sediment and anthropogenic refuse. Every item was fragmented or digested in the stomach.

I. Plant tissue: This included materials from tissues of vascular plants, moss and algae growing around the sampling site. Leaf or stem of grass (1) and leaf of broadleaf tree (2) were of a brown color including a small amount of charred black color changed from green color of live condition.

II. Animal tissue: This included materials from tissues of animals living around the sampling site. Species of brachyura (12 & 13) were identified from their setae and pattern of spots on the exoskeleton. Exoskeleton of brachyura was without soft tissue in most cases. Particles of soft tissue and soft shell derived from a post-molt crab occurred in only one case of *E. japonica*.

III. Sediment was particles of sediment materials.

IV. Others included mainly artificial materials from debris of waste dumped to the collection site.

Food preference in 4 categories

Data obtained in the large categories of plant tissue, animal tissue, sediment and other for each sex and size in 2 areas are shown in Table 4. Both sexes of *E. japonica* predominantly ate plants in Area I (84.4% and 67.0% in frequency of occurrence and 53.1% and 53.4% in percentage point, respectively) and Area II (middle size, 92.1% and 88.7% in frequency occurrence and 78.5% and 79.1% in percentage point; large size, 90.1% and 84.9% in frequency occurrence and 64.3% and 69.3% percentage point, respectively). The frequency of plant tissues decreased as the life stage of crabs proceeds in both sexes. As for animal tissues, frequency was relatively high in Area I (54.2% and 53.8% in frequency of occurrence and 33.0% and 35.6% in percentage point, respectively) but low in Area II (middle size, 22.0% and 17.9% in frequency occurrence and 3.9% and 6.5% in percentage point; large size, 27.5% and 21.5% in frequency occurrence and 6.5% and 6.4% percentage point, respectively). The frequency of animal tissues increased as the life stage proceeded in both sexes.

Food preference was statistically compared using the frequencies of occurrence in the 4 food categories between 2 groups (male and female) in Area I, between 4 groups (middle-sized male, large-sized male, middle size female and large size female) in Area II, and between 2 groups of the same size and sexes in 2 areas (male in Area I and large male in Area II, and female in Area I and large female in Area II). Between sexes, there was no significant difference between the occurrence of plant and animal tissues (male, df=3, χ² = 2.947, p = 0.466; female, df=3, χ² = 2.715, p = 0.466). In Area II, however, significant differences were present between sizes of both sexes (male, df=3, χ² = 18.959, p = 0.003; female, df=3, χ² = 23.382, p<0.0001) with occurrences of animal tissue and other materials being slightly greater for large-sized crabs than small-sized crabs in both sexes. Significant differences were also detected between areas for both sexes (male, df=3, χ² = 8.473, p = 0.040; female, df=3, χ² = 15.446, p = 0.0015).

Therefore, sexual difference in food preference was not detected for the crabs collected within an area, but crabs changed food preference slightly as they grew, and changed after reaching the tidal area; preference of plant tissues decreased and that of animal tissues increased in the later life stages in both sexes.

Food preference in 27 items

Figure 3 shows the total frequency distribution of 27 food items (see Small category in Table 3) from December, 1996 to April, 1997 in Area I. In the occurrence method, sand was predominant (65.9 and 69.8%). Other dominant items in occurrence were leaf or stem of grass (45.1 and 59.4%), other crustacea (30.2 and 31.9%), yarn (23.1 and 44.8%), unidentified animal tissue (16.5 and 21.9%), wood or bamboo (13.2 and 20.8%), sea weed (8.8 and 10.4%),...
Table 3. List of the stomach contents of *Eriocheir japonica* collected in the lower freshwater area of the Saigo River and adjacent sea.

| Large category | Small category | Detail |
|----------------|----------------|--------|
| I. Plant tissue | 1. leaf or stem of grass | mainly leaf or stem of grass of monocotyledonae plants |
| | 2. leaf of broadleaf tree | |
| | 3. root of vascular plant | |
| | 4. wood or bamboo | lignified tissue of vascular plants |
| | 5. pollen | indgested small granules (200–300 μm) |
| | 6. freshwater submerged plant | leaves of submerged vascular plant *Egeria densa* |
| | 7. freshwater filamentous algae | filamentatous cells of *Cladophora* sp. |
| | 8. moss | thallus of *Bryopsis* sp. |
| | 9. sea weed | tissue of foliose green algae *Ulva* sp. |
| II. Animal tissue | 10. terrestrial insect | fragmented exoskeleton of small Coleoptera adults and Diptera adults |
| | 11. aquatic insect | fragmented exoskeleton or exuvia of Diptera larvae (Chironomidae), Trichoptera larvae (Hydropsychidae) and Coleoptera larvae (Dytiscidae) |
| | 12. *Eriocheir japonica* | fragmented exoskeleton or exuvia of *Eriocheir japonica* |
| | 13. other brachyura | fragmented exoskeleton or exuvia of *Hemigrapsus sanguineus*, *Hemigrapsus penicilatus*, etc. |
| | 14. Pisces | tissue with fins, scales and bones |
| | 15. Mollusca | tissue with pieces of shell and radula |
| | 16. Annelida | tissue with setae and segments of oligochaete or polychaete |
| | 17. Sponge | |
| | 18. unidentified animal materials | |
| III. Sediment | 19. mud | clastics of nearly <62.5 μm |
| | 20. sand | clastics of nearly 2 mm–62.5 μm |
| IV. Others | 21. plastic | thin films of polyethylene with white or black color, and fragment of nylon resin |
| | 22. rubber | particles of rubber band |
| | 23. yarn | wool, cotton and synthetic fiber derived from clothes, gunny bags and fishing nets |
| | 24. gum | |
| | 25. metal | small particles of aluminium or steel |
| | 26. human hair | |
| | 27. feather | |

Fig. 3. Frequencies of stomach contents of *Eriocheir japonica* in 27 food item categories for each sex in Area I. For the categories of food item, see Table 3.
plastics (8.8 and 9.4%), and pisces (5.5 and 6.3%). Meanwhile, the predominant item in the point method was leaf or stem of grass (29.8 and 30.5%). Other dominant items in point were wood or bamboo (11.5 and 18.0%), other crustacea (12.2 and 15.3%), unidentified animal tissue (10.9 and 11.2%), pisces (5.3 and 7.9%), leaf of broadleaf tree (8.8 and 4.2%), and sand (4.0 and 5.9%).

The total frequency distribution of 27 items within a year in Area II is shown in Fig. 4. Among 27 items, leaf or stem of grass was predominant in both sizes and sexes, and in both methods (74.2–81.0% in occurrence and 52.5–69.5% in point). In the occurrence method, other dominant items were sand (35.4–47.5%), mud (26.9–38.6%), filamentous algae (15.9–19.4%), yarn (7.2–19.4%), aquatic insects (6.5–12.3%), plastic (2.6–12.9%), wood or bamboo (2.6–11.8), terrestrial insects (5.6–7.0%), Eriocheir japonica (1.5–8.9%) and unidentified animal tissue (2.2–6.5%). While in the point method, other dominant items were filamentous algae (6.4–10.5%), mud (9.6–16.3%), sand (6.2–7.0%), wood or bamboo (1.8–5.1), Eriocheir japonica (1.1–3.0%), plastic (0.9–2.9%) and yarn (0.6–2.9%).

Seasonal variation of stomach contents in 27 food items in Area II is shown in Fig. 6. A similar tendency was recorded in all seasons. Leaf or stem of grass was mostly predominant both in occurrence and point (63.2–86.2% occurrence and 36.7–74.7% point), and sand and mud were found in high occurrence (27.4–47.9% occurrence and 23.9–69.9% point). Occurrence and point of animal tissue were very low in all seasons. But in January and February, 1997, the tendency was slightly different. Point of leaf or stem of grass was the lowest of all seasons (36.7%). Occurrence and point of filamentous algae was lowest (4.2% and

| Food category | Plant tissue | Animal tissue | Sediment | Others | Total |
|---------------|--------------|---------------|----------|--------|-------|
| Total         |              |               |          |        |       |
| Plant tissue  |              |               |          |        |       |
| Animal tissue |              |               |          |        |       |
| Sediment      |              |               |          |        |       |
| Others        |              |               |          |        |       |

**Table 4.** Frequency (%) of occurrence and point in 4 food categories in both sexes of Eriocheir japonica collected in Area I and Area II. Number in parenthesis indicates the number of occurrence or point in each food taxa.
Discussion

Feeding preference of *Eriocheir japonica*

Stomach contents showed that *Eriocheir japonica* was an omnivore and deposit feeder in the Saigo River, mainly feeding on the detritus derived from vascular plants, both in Area I (reproductive area in tidal river and seacoast area) and Area II (growth area in lower freshwater area). In most cases, stomachs were filled with a large amount of decomposing tissues of vascular plants. Most of them seemed to be derived from riparian plants such as *Phragmites communis*, *Phragmites japonica*, *Typha angustifolia*, *Persicaria thunbergii*, etc., growing along the river channel. As for submerged plants, filamentous algae *Cladophora* sp. was found at a comparatively high frequency (15.9–19.4% in frequency occurrence method vs 6.4–10.5% for percentage point method) in the freshwater area, but freshwater submerged vascular plants such as *Egeria densa* were found at low frequencies. In the tidal area, seaweeds such as the foliose green alga, *Ulva* sp., which are abundantly drifting or growing on rocks in site 1, occurred at low frequencies compared to its abundance. The riparian vegetation always supplies a large amount of detritus into the river, as coarse particle organic matter (CPOM) not only to the freshwater area, but also to the tidal river and adjacent seacoast area. Crabs can easily consume such detritus lying on the river bottom. Riparian vegetation in the riverine environment may therefore play an important role in sustaining the population of *E. japonica*. In Area I, wood or bamboo (lignified tissues) accounted for high frequency in the food contents relative to Area II. This result may reflect the degree of decomposition of detritus in each environment. Abundant soft tissues before decomposition are supplied from riparian plants in the freshwater area (Area II), but decomposition...
of soft tissues proceeds and tissues of woody plants composed of persistent fiber remained around the rivermouth (Area I).

Within Area II (growth area/upper tidal river—freshwater area), the frequency of animal materials was very low for both scoring methods in all seasons. Soft animal tissue is easily digestible and the actual frequency of consumption of these items may not be reflected well in the percentage point method, although the frequency of occurrence method also indicated that active predation on living animals was rare in the freshwater area. However, high points suggested that the predominant item found in stomachs with greater fullness was mostly leaves or stems of vascular plants. Fragments of exoskeleton of *E. japonica* occurred in stomach contents, but muscle and other inner parts were rarely attached to them. Exuviae of *E. japonica* are often found on the riverbed except during winter (Kobayashi 2003) and crabs can easily pick up and nibble at them. Thus, *E. japonica* may be a scavenger rather than a cannibal. Insects were found infrequently and were mostly fragmented exoskeleton or exuviae. Unidentified animal tissues may be derived from pisces or mollusca, but those frequencies were very low. Sediment components (sand and mud) were found at high frequency, suggesting that crabs must swallow sediment components without sorting well in order to remove food within the sediment. Artificial products such as plastics (mainly film of polyethylene) and yarns were often found in the stomach contents. Fragments of these materials were frequently found on the riverbed of the Saigo River and the beach of Genkai-nada, because this river flows through a residential area of Fukutsu City where garbage is often dumped (personal observation). Thus it appears that *E. japonica* is an omnivorous scavenger that feeds on detritus lying on the substrate without examining well in natural conditions, and specification of feeding with good discrimination prior to ingestion has not been evolved.

In winter (January and February, 1997), the stomach contents of *E. japonica* in freshwater area differed slightly from those in other seasons: the frequency of leaf or stem of grass and filamentous algae decreased and that of mud increased (Fig. 5). This may be partly caused by the change of vegetation in winter. Plants growing along the channel in the study site died down and the biomass of riparian vegetation decreased drastically. Thus the supply of detritus with nutrients may have decreased. Additionally, filamentous algae attached to submerged stones became mostly extinct and the sheathed bacteria, *Sphaerotilus* sp. grew and covered a large part of the substratum. Lower temperatures result in decreased consumption and locomotion (Kobayashi & Matsuura 1991), and crabs tend to eat sediments rather than other foods that require foraging.

Frequency of animal tissue in stomach contents was greater in Area I (reproductive area in tidal river and sea coast area) than in Area II (growth area in upper tidal river to freshwater area), suggesting that adult crabs in the reproductive area tend to eat more animal materials compared to juveniles and adults distributed in the growth area. At first, this may be caused by the abundance of benthic animals in the seacoast. Many marine benthic animals and fishes inhabit the boulder and rocky shore of the river mouth and seacoast. There are also many carcasses of marine animals derived from the offshore area and river animals from the upstream area of the river; these are washed ashore on the beach. In contrast there are fewer benthic animals living in the freshwater area of the Saigo River because of seasonal fluctuation of the flow rate and reduced oxygen with eutrophication. Secondly, feeding preferences of *Eriocheir japonica* may change as crabs grow and attain maturity.
Adult crabs may prefer animal materials more than juveniles. Results of surveys using baited traps (crab basket) support this: collected crabs are limited to larger size (25mm CW<) regardless of the mesh size all the year round (Kobayashi & Matsuura 1991). Therefore, in the freshwater area E. japonica eat mainly plant material with low calories, but crabs grow rapidly in spring and summer. As crabs grow larger they change food preference and eat more animal materials with high calories and nutritional quality. After reaching the tidal area, adult crabs continue to eat animal materials more frequently, but growth is sacrificed for reproduction.

Ecological niche of Eriocheir japonica

The present results suggest that the omnivorous and opportunistic feeding habit of this species is not a limiting factor for its wide distribution in the natural environment (Kobayashi 2000). Detritus derived from riparian vegetation (such as Phragmites communis, Phragmites japonica) densely grown along the channel and terrestrial vegetation (such as broad-leaf trees providing abundant dead leaves and branches in the autumn) are available as food for E. japonica. Even on the concrete channel wall, filamentous algae attached to the substratum are available as food. Furthermore, not only the products within the river channel (autochthonous materials) but also allochthonous materials, including terrestrial organic materials flowing into rivers, are available in the natural environment.

The Chinese mitten crab E. sinensis is also an omnivore biased to herbivore and detrital feeding, and its feeding habit is similar to that found for E. japonica. The dominant stomach contents of E. sinensis are vascular plants, algae, fish, oligochaeta, aquatic insects and crustaceans including prawns and amphipoda. Detritus derived from vascular plants occupies a high proportion of the stomach contents. Food preference changes as the crabs grow larger and the adult crabs tend to prefer animal materials, such as insects, fish and crustaceans. Herbivorous feeding of E. sinensis can affect aquatic plant communities and decrease macrophyte biomass, when population density is high (Jin et al. 2001, Jin et al. 2001, Jin et al. 2003, Panning 1939, Rudnick & Resh 2005). The feeding habit is not specialized and is an important factor for the success of invasion and establishment in new environments. It has been reported that many grapsoid crabs are also herbivores or omnivores in wetland ecosystems (Buck et al. 2003, Frantini et al. 2000, Kennish 1997, Ölafsson et al. 2002, Puccio 2006, Skilleter & Anderson 1986, Smith et al. 1989; for a review, Wolcott & O’Connor 1992) and facilitate the circulation of organic matter and energy flow in the tropical and temperate area (Camilleri 1989, Emmerson & McGwynne 1992, Leighton & Lopez 1977, Werry & Lee 2005). The omnivorous and detrital feeding habit common among the grapsoid species along with its wide salinity tolerance and migratory abilities (Kobayashi 2003) are also important factors for E. japonica to maintain populations in a wide range of environments.

Furthermore, scarcity of competitive species may be one of the important factors for the widespread distribution of this species. Component species greatly varied in each environment and potential competitors such as amphidromous prawns, the red swamp crawfish and grapsoid crabs are often found in the same habitat as E. japonica (Table 1). However, they may differ from E. japonica in microhabitat preference, food preference, behavior, and body size. Alternatively, available food resources may be abundant for omnivorous species in the environment. Consequently, they seem to have little impact on the distribution pattern and the completion of life cycle of E. japonica (Kobayashi & Matsuura 1994). Information on niche overlap among such species is needed for a better understanding of the ecological niche and distribution of E. japonica.

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