Nocturnal occurrence of the swimming crab *Ovalipes punctatus* in the swash zone of a sandy beach in northeastern Japan

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Swimming crabs belonging to the genus *Ovalipes* (Crustacea: Brachyura: Portunidae) are distributed worldwide along sandy coastlines of subtropical and temperate waters (Stephenson and Rees, 1968). They are extremely well adapted to life on sand, with their strong swimming and burrowing abilities (Brown and McLachlan, 1990). Crabs of this genus are voracious carnivores and significant predators of commercially important mollusks on sandy beaches (Du Preez, 1984; Brown and McLachlan, 1990). Recently, interest in their importance as a possible fisheries resource has increased (Sasaki and Kawasaki, 1980; Wear and Haddon, 1987).

Ovalipes punctatus (De Haan) is common in the coastal waters of Japan and China. It is found on sandy bottoms below the intertidal zone, but peak abundance is at 5–60 m. This species has an ontogenetic migration into deeper water (Kamei, 1976; Sasaki and Kawasaki, 1980). Sasaki and Kawasaki (1980) investigated the life history of *O. punctatus* in Sendai Bay (100 km south of the present study site), on the Pacific coast of northeastern Japan. Female crabs spawn from mid-September until mid-November in offshore water 40–60 m deep. The incubation period of the eggs is about 20 days. After a planktonic phase, the larvae settle on sandy bottoms in March and April. Settled crabs of both sexes grow to carapace widths (CW) of 50–65 mm in the first year. In the second year, females and males grow to 70–90 and 80–85 mm CW, respectively. The life span of this crab is 2 to 2.5 years. The minimum size at maturity is estimated to be 45–50 mm CW (Sasaki and Kawasaki, 1980), but the spawning population consists mainly of 2-year-old crabs of 75–80 mm CW. However, knowledge of the diet and feeding habits of this species has been extremely limited until now.

Ovalipes species, including *O. punctatus*, generally live below the intertidal zone. However, they are often found in the intertidal zone, especially at night (McLachlan et al., 1979; Brown and McLachlan, 1990). McLachlan et al. (1979) suggested that this occurrence is related to feeding, but details are still unknown. During the course of an ecological study of the sandy beach in Otsuchi Bay, we frequently found *O. punctatus* in the swash zone at night. This note examines the significance of the swash zone in the life history of the swimming crab *O. punctatus* in relation to feeding and molting.

Materials and methods

The study was conducted at Koshirahama Beach, in Otsuchi Bay, on the Pacific coast of northern Honshu, mainland Japan, in September of 1994 and August of 1995 (Table 1). The beach is about 120 m long, bounded on both ends by rocky shores, and is categorized as a "sheltered beach" according to McLachlan's (1980) rating scheme. Mean depth at 20, 50, and 100 m from the shoreline is 1.6, 3.5, and 5.5 m, respectively. The beach has a 1:13 (rise: run) slope and median particle diameter of the sediment is 260 µm. Other details of the study site are given in Takahashi and Kawaguchi (1995).

Crabs were sampled with a beach seine 1.1 m high by 8.3 m wide with 1.0-mm mesh. The net was hauled parallel to the shoreline at a depth of ca. 0–1 m. Samples were taken along the entire shoreline of Koshirahama Beach. All crabs were preserved in 10% formalin, and the carapace width (CW), sex, maturity and molt stage of each individual were recorded. The foregut was removed and stored in 70% ethanol for dietary analysis. Sexual maturity of *O. punctatus* was assigned by size classes as defined by Sasaki and Kawasaki (1980): juvenile (<30 mm CW), immature (31–50 mm CW), or adult (>51 mm CW). Molt stages were based on the criteria of Drach and Tchernigovtzeff (1967) and Norman and Jones (1992): 1) soft, no calcification of the new exoskeleton; 2) early papershell, thin, flexible exoskeleton, easily depressed when touched; 3) late papershell, hard exoskeleton except for the branchiostegite region which is compressible; 4) intermolt, completely hard exoskeleton; and 5) premolt, teeth on chelae well worn and having a less rounded appearance compared with those in earlier stages, complete exocuticle developed beneath the exoskeleton.

The diet of *O. punctatus* was analyzed by using the points method and the percentage occurrence method (Williams, 1981; Wear and Haddon, 1987). The points method assesses diet composition in terms of both foregut fullness and estimated volume of food in the foregut. First, the relative degree of foregut fullness of each crab was estimated visually by using six ordered classes (empty=class 0; trace=class 1; 25%=class 2; 50%=class 3; 75%=class 4; full=class 5). A visual assessment of fullness was possible because, except for the gastric mill, the foregut of *O. punctatus* is like a thin-walled translucent bag.

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Table 1

Details of the sampling dates and times (JST) and results in the swash zone of Koshirahama Beach, Otsuchi Bay.

Date	Day or night	Sampling time (h)	No. of crabs collected
22 Aug 1995	Day	8:02	3
25 Aug 1995	Day	13:12	2
30 Aug 1995	Day	13:15	3
12 Sept 1994	Night	20:54	30
25 Aug 1995	Night	21:06	23
30 Aug 1995	Night	20:48	35

Food items were identified to the lowest possible taxon under a binocular dissecting microscope. The relative contribution of each prey category to the total volume of the foregut contents was assessed subjectively in the following way: a category representing 95–100% of the total contents was awarded 100 points; 65–95%, 75 points; 35–65%, 50 points; 5–35%, 25 points; 5% or less, 2.5 points; empty, 0 points. The points that each prey category received were weighted by multiplying by a factor that depended on the degree of foregut fullness, i.e. full = 1, 75% = 0.75, 50% = 0.5, 25% = 0.25 and trace = 0.02 (Wear and Haddon, 1987). The maximum and minimum weighted points possible for a single category in a single foregut were 100 (100 · 1.0) and 0.05 (2.5 · 0.02), respectively. The following percentages were calculated for each prey category (Williams, 1981):

$$\text{Percentage points for } i\text{th prey} = \left(\sum_{j=1}^{n} a_{ij} \Big/ A \right) 100; \text{ and}$$

$$\text{Percentage occurrence for } i\text{th prey} = (b_i/N)100,$$

where a_{ij} = the number of points for prey item i in the foregut of the jth crab;
A = the total points for all the crabs and all the prey items in all the foreguts examined;
N = the number of crabs examined with food in the foregut; and
b_i = the number of crabs with foreguts containing prey category i.

Results

Diel change in the swash zone occurrence pattern

A total of 96 crabs (41 males, 55 females), ranging from 12 to 80 mm CW, were collected from the swash zone of Koshirahama Beach (Fig. 1). No ovigerous females were collected.

Almost all specimens were collected at night (88 individuals, 92% of the total catch) and only 8 crabs were collected during the day (Fig. 1). Juvenile (35) and immature (39) crabs dominated the nocturnal catches, accounting for 40% and 44% of the total nocturnal catch, respectively (Table 2). Fourteen adult crabs were also caught at night, constituting 16% of the nocturnal samples (Table 2). Daytime catches consisted of 1 immature and 7 juvenile crabs (Table 2). On average, crabs caught at night (36 mm CW) were significantly larger than crabs caught during the day (25 mm CW) (P<0.01; t-test).

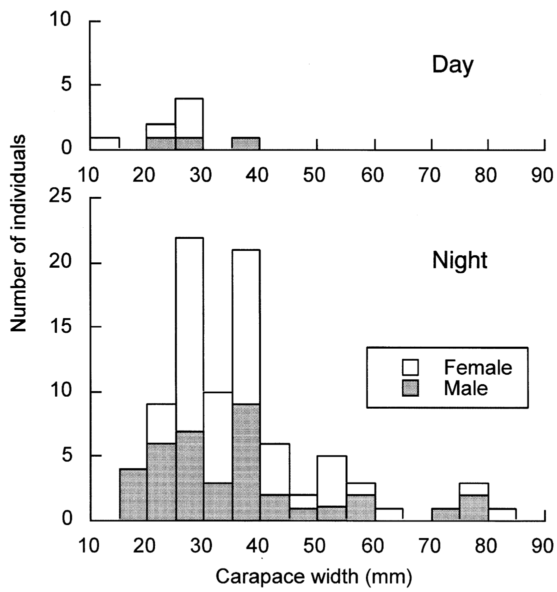

Figure 1

Histograms of carapace width for the swimming crab *Ovalipes punctatus* found in the swash zone of Koshirahama Beach, Otsuchi Bay, during the day and at night. All the specimens were collected in September 1994 or August 1995.

All crabs were in the intermolt or the papershell stages (early and late papershell); no soft-shelled and premolt crabs were collected. During the daytime, 7 out of 8 crabs were in the papershell stages and only one individual was classified as intermolt (Table 2). At night, 5 juvenile and 5 immature papershell crabs were collected, accounting for 14% and 13% of the total catch for each category, respectively (Table 2). Of the adults collected at night, 9 were in the papershell stages, accounting for 64% of the total adult crabs taken.

Feeding activity and diet composition

Because feeding habits of early and late papershell crabs are not different from those of intermolt stages in portunid crabs (Norman and Jones, 1992), analysis for foregut fullness and diet was conducted by pooling all molt stages. The percent frequency of each class of foregut fullness is shown separately for day and night in Figure 2. Although the daytime sample was small, 50% of the crabs had empty foreguts (Fig. 2), but at night over 70% of the

Table 2

Ovalipes punctatus caught in the swash zone of Koshirahama Beach, Otsuchi Bay, during the summers of 1994 and 1995. The numbers of each developmental stage and of papershell crabs caught during the day and at night are shown. No softshell and premolt crabs were collected.

Day or night	Developmental stage of crabs (CW)	Total number of crabs collected	Number of papershell crabs: Early papershell	Late papershell
Day	Juvenile (12–30 mm)	7	6	—
	Immature (31–50 mm)	1	1	—
	Adult (51–80 mm)	—	—	—
Night	Juvenile (12–30 mm)	35	4	1
	Immature (31–50 mm)	39	4	1
	Adult (51–80 mm)	14	3	6

Table 3

Percentage occurrence, points, and percentage points for the 12 categories of foregut content in 69 *Ovalipes punctatus* from Koshirahama Beach, Otsuchi Bay. The points express the dietary contribution in terms of foregut fullness and estimated volume of food items in the foregut (see text). Sand was excluded from the calculation of the percentage points.

Food item	Percentage occurrence	Points	Percentage points
Crustaceans			
Haustorioides japonicus	59	1437.5	26.1
Archaeomysis kokuboi	54	1287.5	23.4
Excirolana chiltoni	30	528.7	9.6
Crangon sp.	14	540.0	9.8
Crustacean fragments	42	1115.6	20.3
Other crustaceans	4	62.5	1.1
Mollusks			
Bivalves	6	41.3	0.7
Gastropods	1	25.0	0.5
Fishes			
Unidentified fish	3	5.0	0.1
Other items			
Unidentified organic matter	19	456.3	8.3
Algae	3	3.8	0.1
Sand	94	970.6	—

foreguts examined were more than half full (classes 3–5) and 7% had empty foreguts, which suggests that the crabs fed actively in the swash zone at night (Fig. 2).

When describing the diet of portunid crabs, Williams (1981) recommended including only individuals with foreguts more than 50% full (i.e. classes 3–5). Applying this criterion, we found 69 crabs (39 females, 30 males) for the diet analysis, 66 of which were collected at night. Because there was no significant difference in the diets by sex (chi-square test, $P>0.5$), the male and female data were combined. Forguts contained 11 prey categories plus sand; percent frequency of occurrence, total points, and the relative proportions of the diet components in terms of points are listed in Table 3. Although sand is not considered a part of the diet, it contributed more than 14% to the total points of the foregut contents.

Small crustaceans were frequent and predominant in the foreguts of *O. punctatus* (Table 3). The sand-burrowing amphipod *Haustorioides japonicus* was the most frequent prey, contributing 26.1% of the total points. Second most frequent prey was the sand-burrowing mysid *Archaeomysis kokuboi* (23.3% of the total points), followed by the sand-burrowing isopod *Excirolana chiltoni* (9.6%) and sand shrimps *Crangon* sp. (9.8%). Fragments that probably came from these crustaceans produced 20.3% of the total points (Table 3). The results show 90.2% of the total diet volume of *O. punctatus* consisted of crustacean prey. Mollusks and fish were not important in the diet (1.3% collectively).

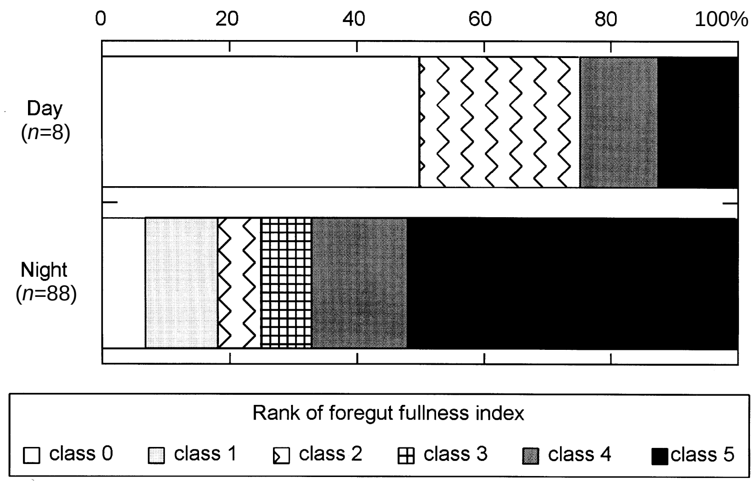

Figure 2

Difference in the foregut fullness index of the swimming crab *Ovalipes punctatus* in the swash zone of Koshirahama Beach, Otsuchi Bay between day and night. Class 0 = empty foregut, class 1 = trace items in foregut, class 2 = foregut 25% full, class 3 = 50% full , class 4 = 75% full, class 5 = full.

Discussion

Ovalipes punctatus occurred nocturnally in the swash zone of Koshirahama Beach, Otsuchi Bay. The nocturnal occurrence in the swash zone for congeners such as *O. trimaculatus* from South Africa (reported as *O. punctatus*, see Schoeman and Cockcroft, 1993) is often observed elsewhere (McLachlan et al., 1979; Brown and McLachlan, 1990). McLachlan et al. (1979) suggested that occurrence in the swash zone is related to feeding. Generally, *Ovalipes* species are active nocturnally (Caine, 1974; Du Preez, 1983). Our observations of foregut fullness and abundance support these findings. Furthermore, because peracarid crustaceans that live close to the sandy shoreline dominated the foregut contents (Kamihira, 1979; Takahashi and Kawaguchi, 1995; authors' pers. obs.), we concluded that part of the crab population migrates from deeper waters into the swash zone at night to exploit the crustacean fauna of sandy beaches.

Feeding in the swash zone is advantageous for the crabs because important prey, such as the amphipod *H. japonicus*, the mysid *A. kokuboi*, and the isopod *E. chiltoni*, are abundant in the swash zone of Koshirahama Beach. These species are considerably more abundant near the shoreline than other macrobenthic organisms that live in the offshore area (authors' pers. obs.). The peracarids, especially mysids and isopods, burrow into the sand during daytime, then emerge into water column in the swash zone at night (Takahashi and Kawaguchi, 1997; authors' pers. obs.) which makes them more vulnerable to predation by *O. punctatus* and fishes (Takahashi et al., 1999). The predominance of peracarid crustaceans in the foreguts of the crabs suggests that *O. punctatus* capture the peracarids effectively in the swash zone of Koshirahama Beach at night.

Species of *Ovalipes* are known as opportunistic, broad-spectrum predators. They are extremely versatile, feeding on both less active prey, such as mollusks, and on mobile animals, such as amphipods, mysids, isopods, and fish (Caine, 1974; Haefner, 1985; Wear and Haddon, 1987; Ropes, 1989; Stehlik, 1993).

The swash zone also serves as a refuge from predation. Species of *Ovalipes* (including congeneric species) are occasionally found in the guts of fish and decapod crustaceans (McDermott, 1983; Du Preez and McLachlan, 1984; Mitchell, 1984; Wear and Haddon, 1987; Stehlik, 1993). Cannibalism is a major cause of mortality in many portunid crabs during their early life stages; the importance of refuges has been emphasized as a factor regulating crab recruitment in natural populations (Hines and Ruiz, 1995). In estuarine ecosystems, habitats with structural complexity, i.e. seagrass beds, mussel beds, filamentous algae, are effective as refuges for juvenile crabs, whereas risk of predation is higher in open sand, the main habitat of *Ovalipes* (Wilson et al., 1987; Ryer et al., 1997, Moksnes et al., 1998). In sand habitat, small *Ovalipes* burrow deep by using reverse gill current to hide from predators during the day (Barshaw and Able, 1990).

Nocturnal emergence of *Ovalipes* makes them more vulnerable to cannibalism. In the swash zone of Koshirahama Beach at night, almost all the *O. punctatus* were juvenile and immature crabs. This finding suggests that small individuals avoid the deeper zone, where the risk of cannibalism is high. For blue crabs, *Callinectes sapidus*, shallow water areas function as refuges from predation when habitats have little structural complexity (Dittel et al., 1995; Hines and Ruiz, 1995). The swash zone is probably difficult for larger predators to penetrate and they risk being stranded. In addition, birds that exploit the swash zone are less active at night (Brown and McLachlan, 1990).

Softshell and premolt crabs were not collected in the swash zone; it appears that this zone may not be a molting ground owing to its dynamic characteristics. However, most diurnal and adult crabs in the samples were papershell crabs, which are also vulnerable to predation; the swash zone, therefore, may be important as a refuge for postmolt crabs.

In our study, juvenile and immature crabs dominated the population of *O. punctatus* in the swash zone during late summer. From the size of the crabs, these were first-year crabs born in the previous winter or spring, and therefore their occurrence in the swash zone may be limited to the summer and fall, when these juvenile and immature crabs appear (Sasaki and Kawasaki, 1980). A similar seasonal occurrence of juvenile *O. ocellatus* from July to October on exposed sandy beaches of the mid-Atlantic Coast of the United States has been reported in an inshore area (McDermott, 1983). The occurrence and behavior of *O. punctatus* in the swash zone suggest that this habitat is important as a feeding ground and a refuge from predation. Intertidal sand-burrowing peracarids, the major diet items of *O. punctatus*, also consume particulate organic matter and organisms in the swash zone (Kamihira, 1992; Takahashi and Kawaguchi, 1998). Thus by feeding in the swash zone, young *O. punctatus* transport some of the secondary production from the swash zone to the offshore area through their ontogenetic migration into deeper water.

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