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Nereidid Polychaetes as the Major Diet of Migratory Shorebirds on the Estuarine Tidal Flats at Fujimae-Higata in Japan

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The dietary items of five migratory shorebirds, Dunlin (*Calidris alpina*), Red-necked Stint (*C. ruficollis*), Grey Plover (*Pluvialis squatarola*), Whimbrel (*Numenius phaeopus*) and Black-headed Gull (*Larus ridibundus*), were examined by analyses of fecal droppings during the birds' migration or wintering and by surveys of macrobenthic fauna around their foraging sites on the tidal flats of Fujimae-higata, Nagoya, central Japan. Body parts of nereidid, capitellid, and spionid polychaetes and crustaceans were found in fecal droppings from all of these shorebirds. Two nereidid species (*Hediste diadroma* and *Neanthes succinea*) with relatively large body sizes seemed to be the majority dietary items. At one site, *H. diadroma* was dominant in terms of biomass (40–370 g/m^2) throughout year except, for less than 1 g/m^2 in March and May (within or just after reproduction of this species). Monthly changes in the occurrence of food items in fecal droppings of *C. alpina* were examined in 1999 and 2000. Most (85–100%) of the fecal droppings contained nereidid body parts, including *Hediste*-specific simple chaetae from November to April, whereas only 23% of the droppings contained them in May. Chaetae of capitellid or spionid polychaetes were frequently found from January to April (38–86% of droppings). Crustacean body parts, including amphipod appendages, were frequently found from March to May (86–100% of droppings). The relationship between foraging habits of the shorebirds and the life history of their major prey nereidid species is discussed.

Key words: dietary items, migratory shorebirds, fecal droppings, nereidid polychaetes, Dunlin

INTRODUCTION

Estuarine tidal flats in Japan and adjacent countries are important foraging places for many migratory shorebirds during the cold season (from autumn to spring), because these tidal flats are located along the East Asian-Australasian flyways of migratory birds (Akiyama, 1988; Hanawa and Takeishi, 2000; Sato and Koh, 2004). However, recent human impacts in Asian countries have caused severe loss or degradation of their habitats, endangering many bird species and their potential prey invertebrates (Wetlands International-Asia Pacific and International Waterfowl and Wetland Research Bureau-Japan Committee, 1996; Wada *et al*., 1996).

A stable food supply for shorebirds on tidal flats seems to be important to maintain their regular migration. Clarification of foraging habits (*e.g*., dietary items) of shorebirds is essential to knowing their carnivorous roles in the tidal flat ecosystem and to establish their effective conservation. Previous studies have revealed that macrobenthic invertebrates such as polychaetes, crustaceans, and mollusks constitute a major part of the diet of migratory shorebirds during the wintering period (see Akiyama, 1988). However, most such studies have been carried out in Europe, and little is known about the prey of shorebirds in Asian estuaries, though Nuka *et al*. (2005) revealed detailed foraging habits of the Sanderling (*Calidris alba*) in a Japanese sandy seashore. Although most previous studies on the prey items of shorebirds were carried out by analyses of stomach (gizzard) contents obtained from captured birds (Madon, 1935; Ehlert, 1964; Recher, 1966; Bengston and Svensson, 1968; Goss-Custard, 1969; Davidson, 1971; Kawaji and Shiraishi, 1979), there are other methods which do not require the killing of birds, *i.e*., watching the feeding behavior of representative individual birds through binoculars or telescope (*e.g*., Goss-Custard *et al*., 1977) and the analysis of regurgitated pellets (Worrall, 1984) or fecal droppings (Feare, 1966; Dit Durell and Kelly, 1990; Mouritsen, 1994; Akiyama, 2000; Nuka *et al*., 2005).

Fujimae-higata is 120-ha area of muddy tidal flats, located at the joined mouths of the Nikko-gawa and Shinkawa Rivers in the innermost part of Ise Bay, Nagoya, central Japan (Fig. 1). In a survey of major Japanese tidal flats from 1988 to 1996 (Japanese Association for Preservation of Birds, 1997), the second highest number of migrating or over-wintering waders (6,950 individuals) was recorded in the estuary that includes Fujimae-higata. In monthly counts

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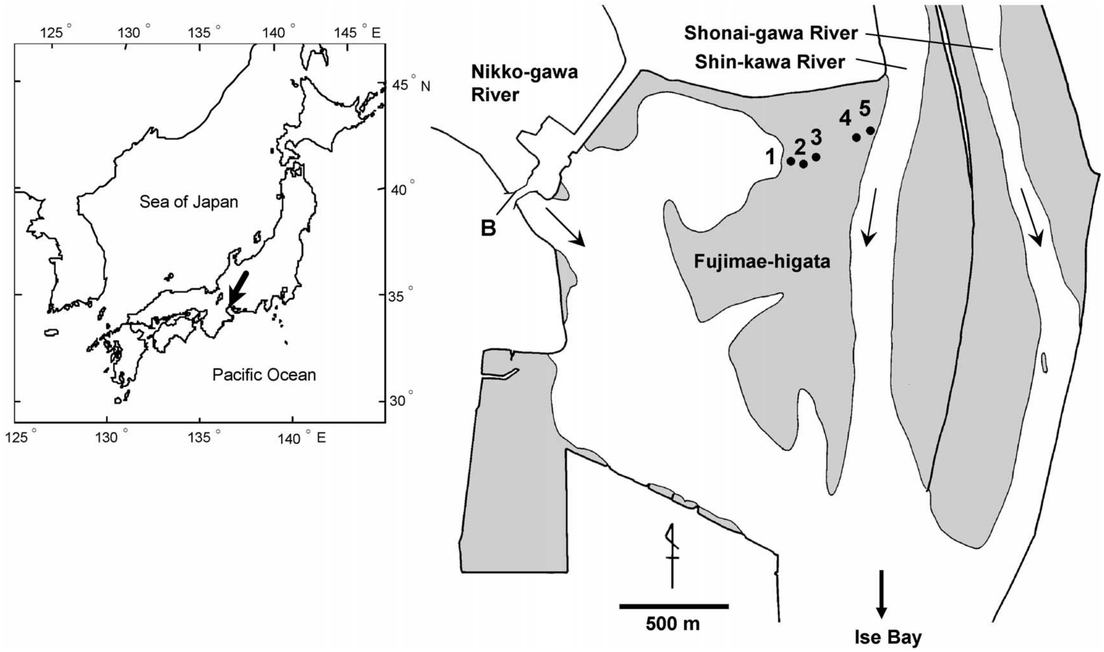
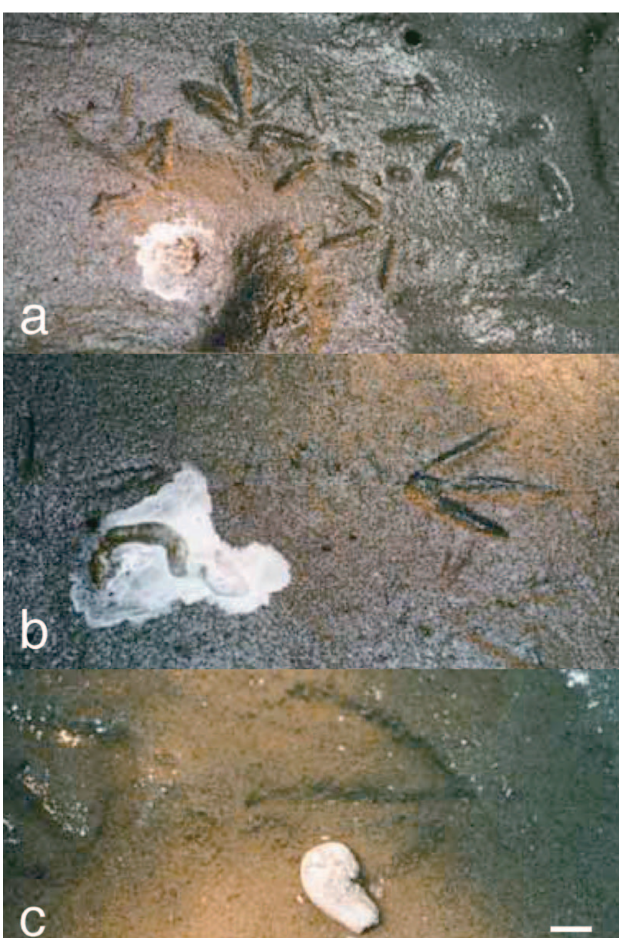


Fig. 1. Maps showing the location of the study area in Japan (left) and the locations of the collecting stations (right). Stations 1 to 5 were on the tidal flats of Fujimae-higata, located at the joined mouths of the Nikko-gawa and Shin-kawa Rivers in the innermost part of Ise Bay, central Japan. Gray areas indicate tidal flats appearing at mean low water level on spring tides. Arrows indicate river flows into Ise Bay. B, Nikko-gawa-ohhashi Bridge.



from April 1999 to March 2000 at Fujimae-higata, more than 500 Dunlin (*Calidris alpina*) and more than 50 Black-headed gulls (*Larus ridibundus*) were observed continuously from January to May and September to May, respectively (Nagoya City, 2001).

The Dunlin is the most common wader species wintering in Japanese estuaries. Total numbers of wintering individuals of *C. alpina* counted in 90–97 major habitats in Japan ranged from 29,000 to 37,000 between 1999 and 2002, constituting 63 to 67% of the whole wader populations (World Wide Fund for Nature Japan, 2003).

The present study was conducted to describe the dietary items of the Dunlin and four other common species of estuarine shorebirds by monthly analyses of their fecal droppings and surveys of the macrobenthic fauna around a foraging site in Fujimae-higata throughout the wintering period.

MATERIALS AND METHODS

Analyses of fecal droppings

In the eastern part of Fujimae-higata (around stations 1–5 in Fig. 1) where high foraging activity of shorebirds had been observed, fecal droppings of five species of shorebirds were collected from the surface of exposed tidal flats around the lowest one of two low tides in months during two wintering periods. The lowest tides occur at night in winter (from November to February) and in the day in spring (from March to May). Wintering shorebirds usually

Fig. 2. Fecal droppings and the footprints of shorebirds on the tidal flats of Fujimae-higata. **(a)** Dunlin (*Calidris alpina*) on 18 January 1999. **(b)** Grey Plover (*Pluvialis squatarola*) on 18 January 1999. **(c)** Black-headed Gull (*Larus ridibundus*) on 18 January 1999. Scale, 1 cm.

feed regularly by day and night (Mouritsen, 1994). Prior to each sampling, locations of foraging populations of each species on the tidal flats were determined with binoculars from the edge of land, and then visited for sampling. Bird species could be identified even at night, because Fujimae-higata is continuously lighted by illumination from surrounding factories working at night. We sampled only droppings for which correct identification was ensured by examination of the size and shape of footprints around the droppings (Fig. 2). Footprints of the Dunlin (*Calidris alpina*; length of middle finger around 2.5 cm) were smaller than those of the Grey Plover (*Pluvialis squatarola*; around 3.5 cm) and Black-headed Gull (*Larus ridibundus*; around 5.5 cm).

During the first wintering period in 1999, several droppings from each species were pooled in a bottle and fixed in 80% ethanol. Sampling dates (time) and bird species from which droppings were excreted are as follows; 18 January (0:00–2:00), *C. alpina*, *P. squatarola*, and *L. ridibundus*; 22 March (14:00–16:00), *C. alpina* and *L. ridibundus*; 3 May (12:00–14:00), *C. alpina* and *N. phaeopus* which had a stopover here.

Part of each sample of droppings (0.05–0.1 cc) was placed on a glass slide and examined under a microscope. This examination was repeated five times for each sample.

During the second wintering period from 1999 to 2000, droppings were fixed individually. Examination under a microscope was repeated five times for each sample as mentioned above. Sampling dates and bird species from which droppings were obtained are as follows: 25 November 1999 (0:00–2:00), *C. alpina* (29 individuals) and *L. ridibundus* (1); 23 January 2000 (0:00–2:00), *C. alpina* (13), *P. squatarola* (5), and *L. ridibundus* (2); 20 February (0:00–2:00), *C. alpina* (4) and *P. squatarola* (3); 22 March (12:00–15:00), *C. alpina* (7) and *L. ridibundus* (5); 22 April (12:00–15:00), *C. alpina* (14) and the Red-necked Stint, *C. ruficollis* (5); 6 May (12:00–15:00), *C. alpina* (26).

Survey of macrobenthic fauna

A sediment sample in a quadrat (25×25 cm, up to about 20 cm deep) was dug from the tidal flats (around station 4 or 5 in Fig. 1) at a height between mean low water level on neap tides (MLWN) and mean low water level on spring tides (MLWS) on 18 and 30 January, 6 and 22 March, 16 May, 13 July, 11 September, 25 November 1999 and 22 March 2000, and washed through a sieve of 1-mm mesh. All macrobenthic organisms sorted out were fixed in 80% ethanol and transferred to fresh 80% ethanol for preservation. They were identified to species, and the number of individuals and wet weight were recorded for each species.

On 25 April 1997, macrobenthic organisms were collected from all five sites (stations 1–5 in Fig. 1) by the same method.

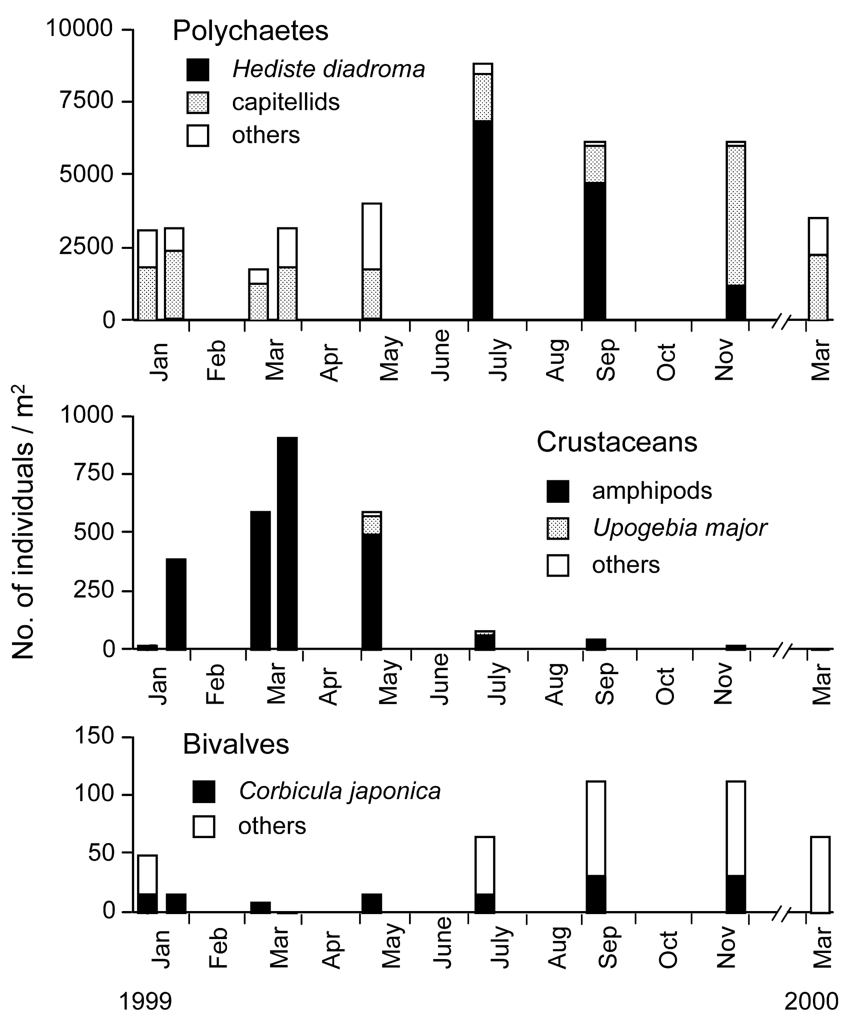


Fig. 3. Monthly changes in the density of polychaetes, crustaceans, and bivalves around station 4 or 5 on the tidal flats of Fujimae-higata from January to November 1999 and March 2000.

RESULTS

Macrobenthic fauna in the tidal flats

A total of 27 species of macrobenthic organisms were collected (Appendix 1), including 16 polychaetes, four crustaceans and four bivalves.

Polychaetes were dominant throughout the year in terms of both density (maximum 8,850 individuals/m^2 in July 1999; Fig. 3) and biomass (maximum 392 g/m^2 in September 1999; Fig. 4). In summer (July and September), small, young individuals of a nereidid polychaete (*Hediste diadroma*) were densest. As the density of *H. diadroma* decreased during the following autumn and winter, its body size increased considerably (Fig. 5). Therefore, the biomass of *H. diadroma* was the greatest (40–370 g/m^2) of all benthic organisms throughout the year, except for less than 1 g/m^2 in May 1999 and March 2000 (during or just after reproduction). During the reproductive period of *H. diadroma* (March 1999), we collected a large, nearly mature female that had eggs 110–140 µm in diameter in its coelom. The density (1,300–4,800 individuals/m^2) and biomass (16–57 g/m^2) of capitellid polychaetes (mainly *Notomastus* sp. and *Heteromastus* sp.) were also relatively high throughout the year. A relatively high density of a spionid polychaete (*Prionospio (Minuspio) japonica*) was recorded from winter to spring (300–2,100 individuals/m^2).

Among crustaceans, amphipods (mainly *Grandidierella* sp.) were dense from March to May (2.8–3.9 g/m^2), and juveniles of *Upogebia major* were found in May and July (1.2–1.8 g/m^2). Among bivalves, *Corbicula japonica* was dominant (maximum biomass 159 g/m^2).

In April 1997, a nereidid polychaete (*Neanthes succinea*) was dominant in terms of biomass (55–87 g/m^2) at four sites (stations 2–5), whereas a goniadid polychaete (*Goniada* sp.) (15 g/m^2) and an amphipod (*Grandidierella* sp.) (14 g/m^2) were dominant at station 1 (Fig. 6). *Hediste diadroma* was absent except for the occurrence of a juvenile at station 5. The biomass of capitellid polychaetes (mainly *Notomastus* sp. and *Heteromastus* sp.) was also large at station 4 (46 g/m^2), and a large bivalve (*C. japonica*) was collected at station 5 (74 g/m^2).

Contents of droppings of *Calidris alpina*

During the first wintering period in 1999, body parts (chaetae, aciculae, or jaws) of nereidid polychaetes were commonly found in pooled samples of droppings from *Calidris alpina* (Fig. 2a) in January and March, but were not found in May (Table 1). Similar results were obtained during the

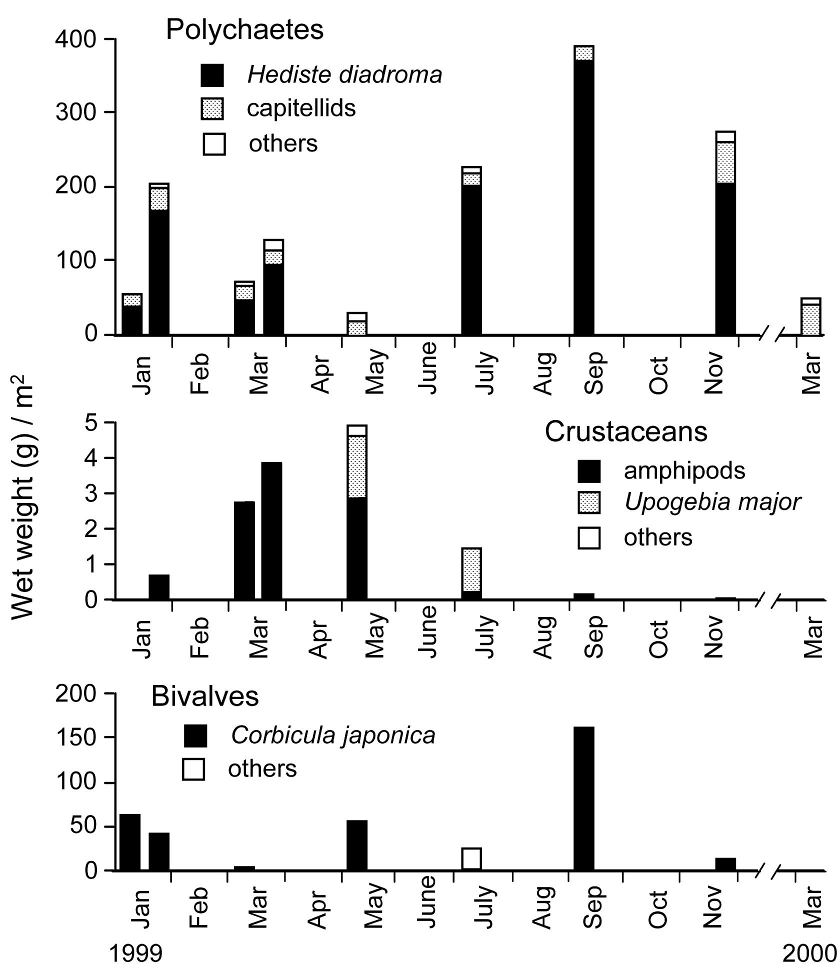


Fig. 4. Monthly changes in the biomass of polychaetes, crustaceans, and bivalves around station 4 or 5 on the tidal flats of Fujimae-higata from January to November 1999 and March 2000.

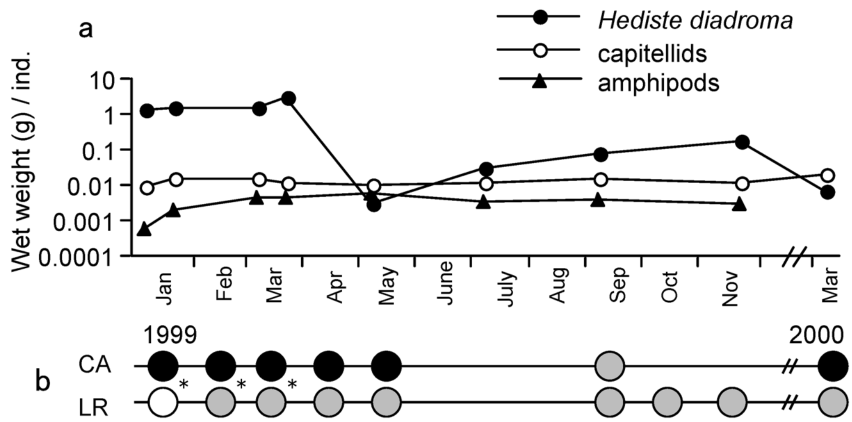


Fig. 5. **(a)** Monthly changes in the individual biomass (wet weight/individual) of representative macrobenthic organisms [*Hediste diadroma* (Polychaeta), capitellids (Polychaeta), and amphipods (Crustacea)] around station 4 or 5 on the tidal flats of Fujimae-higata from January to November 1999 and March 2000. **(b)** Monthly records of individual numbers of the Dunlin *Calidris alpina* (CA) and the Black-headed Gull *Larus ridibundus* (LR) observed in the same place from April 1999 to March 2000 (data from Nagoya City, 2001). Data from January to March (*) represent those in 2000. Black circles, more than 500 individuals; gray circles, 51–500 individuals; white circle, 11–50 individuals.

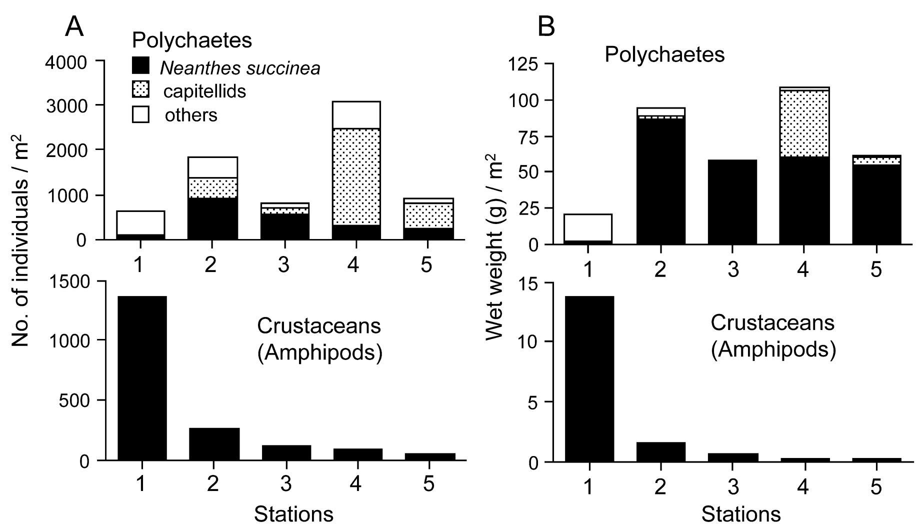


Fig. 6. Variation in the **(A)** density and **(B)** biomass of polychaetes and crustaceans (all amphipods) at five stations on the tidal flats of Fujimae-higata on 25 April 1997.

Table 1. Occurrence of nereidid body parts in fecal droppings from 5 shorebird species (*Calidris alpina, C. ruficollis, Pluvialis squatarola, Numenius phaeopus, Larus ridibundus*). Values and symbols in perentheses indicate the occurrence of *Hediste*-specific simple chaetae.

Date	*C. alpina*	*C. ruficollis*	*P. squatarola*	*N. phaeopus*	*L. ridibundus*
18 January 1999	+ (+)[1)]	nd	+ (–)	nd	+ (–)
22 March 1999	+ (–)	nd	nd	nd	+ (+)
3 May 1999	–	nd	nd	+ (–)	nd
25 November 1999	26 (8)/29[2)]	nd	nd	nd	1 (1)/1
23 January 2000	13 (9)/13	nd	5 (4)/5	nd	2 (0)/2
20 February 2000	4 (2)/4	nd	3 (2)/3	nd	nd
22 March 2000	6 (1)/7	nd	nd	nd	5 (2)/5
22 April 2000	12 (3)/14	2 (0)/5	nd	nd	nd
6 May 2000	9 (2)/26	nd	nd	nd	nd

1) Results from pooled samples of several droppings (+: present, –: absent, nd: no data).
2) No. of droppings with nereidid parts/ No. of droppings examined.

second wintering period. Most (85–100%) of the droppings from *C. alpina* contained nereidid body parts from November 1999 to April 2000, whereas only 23% of droppings contained them in May 2000 (Table 1, Figs. 7A, 8a, c, d). The nereidid body parts included simple chaetae (Fig. 8c),

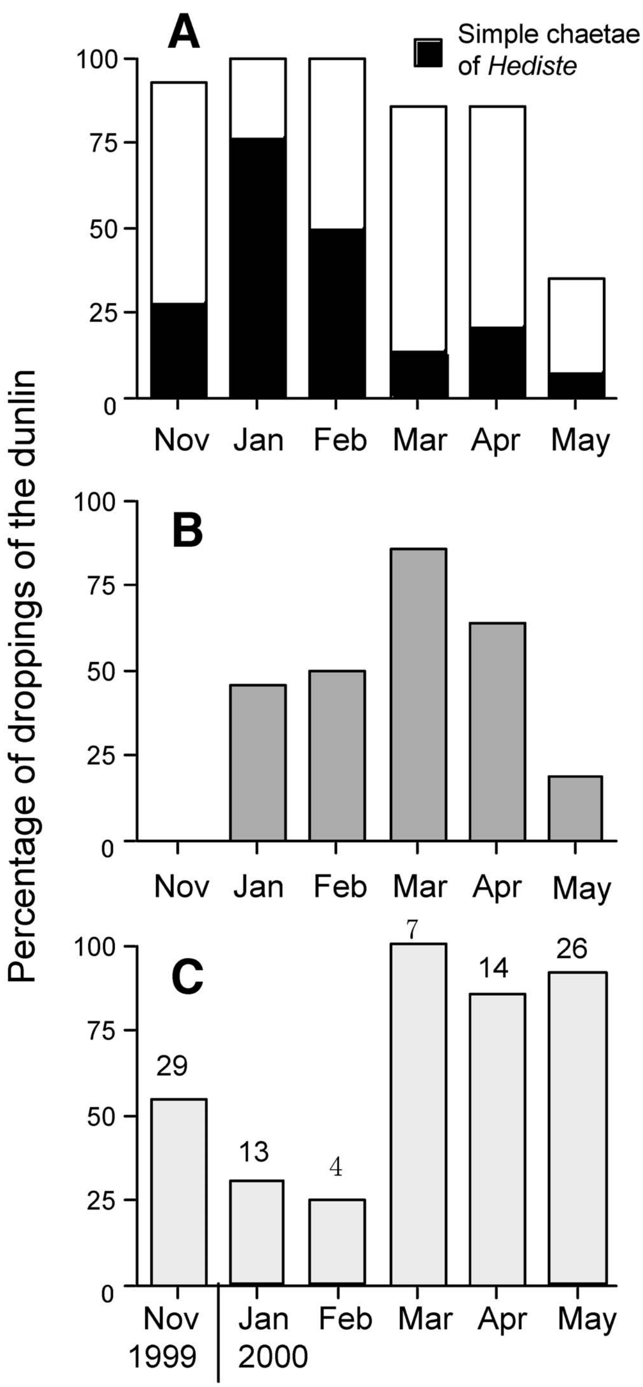


Fig. 7. Monthly changes in the percentage of fecal droppings from the Dunlin *Calidris alpina* containing **(A)** body parts of nereidid polychaetes, **(B)** chaetae of capitellid or spionid polychaetes, and **(C)** body parts of crustaceans. Black bars in A indicate the percentage of droppings containing simple chaetae of worms of the genus *Hediste*. The number at each bar in (C) indicates the number of droppings examined.

which are specific to the posterior parapodia of the genus *Hediste* (Sato and Nakashima, 2003). The simple chaetae were found more frequently from November 1999 to February 2000 (28–70% of *C. alpina* droppings) than from March to May 2000 (8–21% of droppings) (Fig. 7A).

Capillary chaetae (Fig. 9a) and hooded hooks (Fig. 9b), which seemed to be derived from capitellid and spionid polychaetes, were found more frequently from January to April 2000 (38–86% of *C. alpina* droppings) than in November 1999 and May 2000 (0–19% of droppings) (Table 2, Fig. 7B)

Crustacean body parts were also commonly found in droppings of *C. alpina* (Fig. 10). Some were identified as parts of the appendages of an amphipod, *Grandidierella* sp. (Fig. 10b). The crustacean body parts were found more frequently from March to May 2000 (86–100% of droppings) than from November 1999 to February 2000 (25–55% of droppings) (Table 3, Fig. 7C)

Contents of droppings from the other shorebirds

Body parts of nereidid, capitellid, and spionid polychaetes and crustaceans were also found in droppings from *Calidris ruficollis*, *Pluvialis squatarola* (Fig. 2b), *Numenius phaeopus*, and *Larus ridibundus* (Fig. 2c, Tables 1–3).

Nereidid body parts were found in all fecal samples from *P. squatarola* (a pooled sample in January 1999, and eight individual samples from January to February 2000) and *L. ridibundus* (pooled samples in January and March 1999, and eight individual samples from November 1999 to March 2000). Many of these samples contained *Hediste* simple chaetae.

DISCUSSION

Our results show that five species of shorebirds (*Calidris alpina*, *C. ruficollis*, *Pluvialis squatarola*, *Numenius phaeopus*, and *Larus ridibundus*) foraging in Fujimae-higata during migration or wintering exploit as food sources dominant macrobenthic invertebrates such as nereidids, capitellids, spionids (polychaetes), and an amphipod (crustacean). Of all the food sources, two nereidid species (*Hediste diadroma* and *Neanthes succinea*) with relatively large body size and large biomass in the tidal flats seemed to be the most important diet. A similar result was obtained on the tidal flats of the Ichinomiya-gawa estuary, central Japan, where nereidid (the genus *Hediste*) and capitellid polychaetes were dominant (Akiyama, 2000); nereidid body parts (chaetae or jaws) including *Hediste* simple chaetae were present in 78% of 100 droppings of *C. alpina*, and 44% of them also contained capitellid body parts (hooded hooks).

Calidris alpina subsists mainly on insects on Arctic breeding grounds (Holmes, 1966), whereas it feeds mainly on macrobenthic invertebrates on tidal flats during migration or wintering (Akiyama, 1988). Although the food items taken by *C. alpina* are somewhat variable depending on its wintering sites (Akiyama, 1988) or light conditions (diurnal or nocturnal) (Mouritsen, 1994), nereidid polychaetes represented by *Hediste* species seem to be the most important diet for *C. alpina* not only in Asia but also in Europe. In the inner part of the Ariake Sea, western Japan, Kawaji and Shiraishi (1979) found that jaws of a *Hediste* species, probably *H. japonica* (Sato and Nakashima, 2003), were most abundant in four stomachs of *C. alpina*, followed by shells of

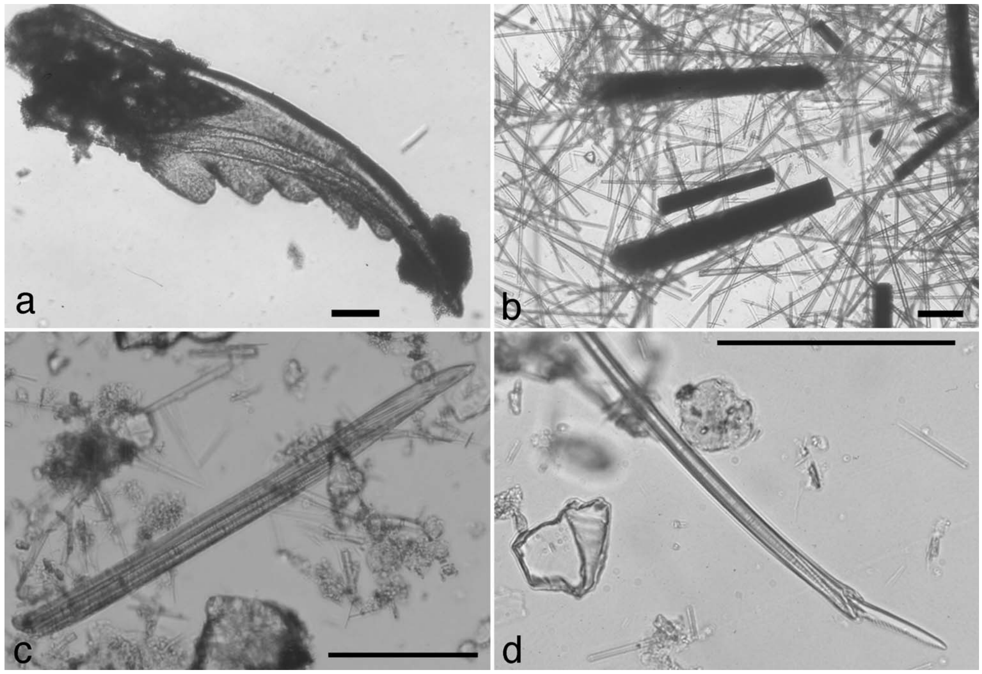


Fig. 8. Micrographs of body parts of nereidid polychaetes found in fecal droppings from the Dunlin (*Calidris alpina*) (a, c, d) and Black-headed Gull (*Larus ridibundus*) **(b)**. **(a)** A jaw, 23 January 2000. **(b)** Many compound chaetae and thick black aciculae, 22 March 2000. **(c)** A simple chaeta typical of worms of the genus *Hediste*, 18 January 1999. **(d)** A heterogomph falciger, 18 January 1999. Scale bars, 100 μm.

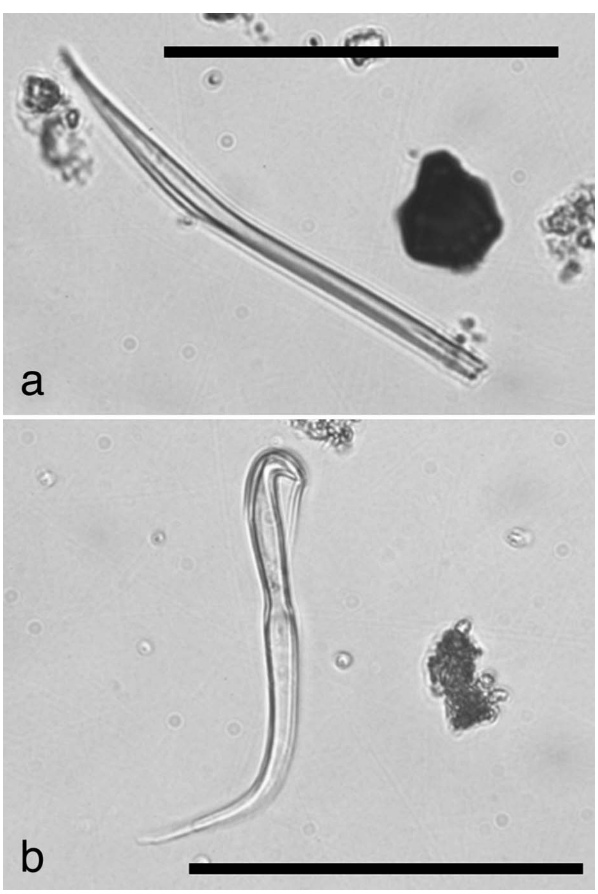


Fig. 9. Micrographs of chaetae of capitellid or spionid polychaetes found in fecal droppings of the Dunlin (*Calidris alpina*), 23 January 2000. **(a)** A capillary chaeta. **(b)** A hooded hook. Scale bars, 100 μm.

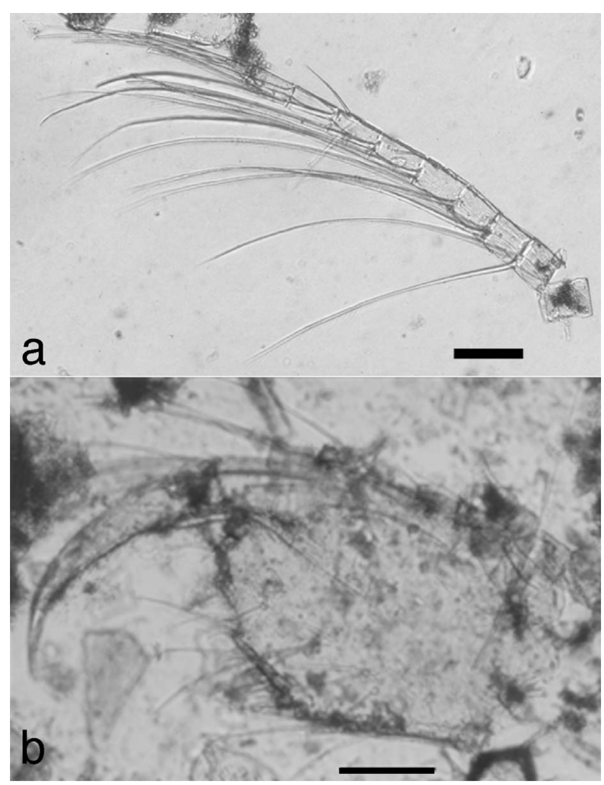


Fig. 10. Micrographs of body parts of crustaceans found in fecal droppings from the Dunlin (*Calidris alpina*). **(a)** An appendage. **(b)** Probably a gnathopod from an amphipod. Scale bars, 100 μm.

Table 2. Occurrence of capitellid or spionid body parts in fecal droppings from 5 shorebird species. Values and symbols as shown in Table 1.

Date	*C. alpina*	*C. ruficollis*	*P. squatarola*	*N. phaeopus*	*L. ridibundus*
25 November 1999	0/29	nd	nd	nd	0/1
23 January 2000	5/13	nd	1/5	nd	2/2
20 February 2000	2/4	nd	3/3	nd	nd
22 March 2000	6/7	nd	nd	nd	3/5
22 April 2000	9/14	2/5	nd	nd	nd
6 May 2000	5/26	nd	nd	nd	nd

Table 3. Occurrence of crustacean body parts in fecal droppings from 5 shorebird species. Values and symbols as shown in Table 1.

Date	*C. alpina*	*C. ruficollis*	*P. squatarola*	*N. phaeopus*	*L. ridibundus*
18 January 1999	–	nd	+	nd	+
22 March 1999	+	nd	nd	nd	–
3 May 1999	+	nd	nd	+	nd
25 November 1999	16/29	nd	nd	nd	1/1
23 January 2000	4/13	nd	0/5	nd	2/2
20 February 2000	1/4	nd	1/3	nd	nd
22 March 2000	7/7	nd	nd	nd	5/5
22 April 2000	12/14	5/5	nd	nd	nd
6 May 2000	24/26	nd	nd	nd	nd

Fluviocingula nipponica (gastropod). In Ore-sound in southern Sweden (Bengtson and Svensson, 1968), the Danish Wadden Sea (Mouritsen, 1994), Mellum near Helgoland in Germany (Ehlert, 1964), and the Severn Estuary in South Wales (Worrall, 1984), *Hediste diversicolor* was judged from analyses of stomach contents and/or regurgitated pellets or fecal droppings to be by far the most important dietary item of *C. alpina*, although *Hydrobia* spp. (gastropods), *Macoma balthica* (a bivalve), and/or *Corophium volutator* (a crustacean) were also commonly found. Wolff (1969) showed that the distribution of *C. alpina* agreed very well with that of *H. diversicolor* in the Delta area of the Netherlands. In California, USA, another nereidid species, *Neanthes succinea*, which was dominant there, comprised the major component of gizzard contents of *C. alpina* (Recher, 1966).

Goss-Custard *et al*. (1977) found that *H. diversicolor* was also the most important prey species for the Redshank (*Tringa tetanus*) and Curlew (*Numenius arquata*), by direct observation of feeding behavior and surveys of macrobenthic fauna.

On the other hand, an analysis of fecal droppings demonstrated that *H. diversicolor* was not more important in the diet of *C. alpina* than other small polychaetes such as *Nephtys* spp., phyllodocid and spionid species, and mollusks such as *Hydrobia ulvae*, although *H. diversicolor* was the main prey item taken by the Grey Plover (*Pluvialis squatarola*) in the Wash, southeastern England (Dit Durell and Kelly, 1990). Small oligochaete worms seemed to be of considerable importance in the diet of *C. alpina* in the Wash (Dit Durell and Kelly, 1990) and Teesmouth (Evans *et al*., 1979).

Foraging habits of many shorebirds such as *C. alpina* seem to be closely related to the life histories of their major prey species, *Hediste* spp. In contrast to Europe, where *Hediste* worms consist of a single species (*H. diversicolor*), in Asia *Hediste* worms comprise three similar but morphologically distinct species (*H. japonica*, *H. diadroma*, and *H. atoka*); *H. diadroma* and *H. atoka* are commonly distributed across a wide range of Japanese estuaries and often occur sympatrically, whereas *H. japonica* is distributed in the inner part of the Ariake Sea in Japan and the coast of the Yellow Sea (Sato and Nakashima, 2003; Sato, 2004). All *Hediste* worms collected from Fujimae-higata during the present survey were identified as *H. diadroma*. The life span of this species is one year (Qiu and Wu, 1993, see Sato and Nakashima, 2003). At the end of its life, reproductive swarming occurs in winter or early spring: sexually mature males and females simultaneously swim up to the surface just after high tide at night during spring tides, and die after spawning (Sato and Tsuchiya, 1987; Sato, 1999; Hanafiah *et al*., 2006). In Fujimae-higata, reproductive swarming of *H. diadroma* was recorded on 28 February 2002 (Sato and Nakashima, 2003).

During the stay of many migratory shorebirds at Fujimae-higata, *i.e*., from autumn to the next spring, individuals of *H. diadroma* grew to almost maximum body size in the late phase of their life cycle, with their weight much larger than that of any other macrobenthic species (Fig. 5). The high percentage occurrence of *Hediste* chaetae in feces of *C. alpina* from November to February (Fig. 7) suggests that shorebirds selectively catch large individuals of *H. diadroma*, though the density of the latter was then relatively low (Fig. 3). After February, however, the percentage occurrence of *Hediste* chaetae decreased, and the percentage occurrence of smaller food items such as capitellids, spionids, or amphipods increased. This suggests that *C. alpina* changed its main prey species when the majority of large *H. diadroma* individuals disappeared after reproduction.

A high percentage occurrence of nereidid body parts in droppings of *C. alpina* was maintained even in March and April (Fig. 7), when most adults of *H. diadroma* disappeared from the tidal flats, suggesting that another nereidid, *Neanthes succinea*, may also be a main prey species during this period. During this time, *N. succinea* was dominant at many sites (Fig. 6), and it increased in individual body size just before its reproductive swarming from May to July (Imajima, 1996). The low percentage occurrence of nereidid chaetae in feces of *C. alpina* in May indicates that many *N. succinea* adults also disappeared after reproduction, and therefore, that nereidid prey for shorebirds may be limited in May, when many shorebirds migrate farther north. The involvement of different nereidid species with different life cycles on the same tidal flats appears to enhance their stability as a major food resource for migratory shorebirds, as implied by Sato and Nakashima (2003).

Larus ridibundus is an omnivorous species. The variety of items in its diet is always large, including invertebrates, plant material, fish, carrion and refuse (Fossi *et al*., 1995). Our results show that nereidid polychaetes and amphipods comprise the major food component for *L. ridibundus* at Fujimae-higata. The unusual abundance of nereidid chaetae in some feces of *L. ridibundus* (Fig. 8b) suggests that this species may catch swarming nereidid adults at the surface of the water. Swarming adults of not only *H. diadroma* (probable swarming period February to April) and *N. succinea* (May to July) but also *Tylorrhynchus osawai* (October to December; Hanafiah *et al*., 2006), which commonly inhabit the upper reaches of Japanese estuaries and move downstream on the ebb tide during swarming, seem to be available around Fujimae-higata.

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Appendix 1. List of macrobenthic species collected from tidal flats at Fujimae-higata, Nagoya during the present study

Nemertinea
- gen. sp.

Mollusca
- Bivalvia
  - *Corbicula japonica* Prime, 1864
  - *Meretrix lusoria* (Röding, 1798)
  - *Laternula (Exolaternula) marilina* (Reeve, 1863)
  - *Musculista senhousia* (Benson, 1842)

Annelida
- Polychaeta
  - Phyllodocidae
    - *Eteone* sp.
  - Goniadidae
    - *Goniada* sp.
  - Glyceridae
    - *Glycera alba* (O.F. Müller, 1776)
  - Pilargiidae
    - *Sigambra hanaokai* (Kitamori, 1960)
  - Nereididae
    - *Hediste diadroma* Sato and Nakashima, 2003
    - *Neanthes succinea* (Frey et Leuckart, 1847)
  - Nephtyidae
    - *Nephtys polybranchia* Southern, 1921
  - Polynoidae
    - gen. sp.
  - Spionidae
    - *Prionospio (Minuspio) japonica* Okuda, 1935
    - *Pseudopolydora* cf. *kempi* (Southern, 1921)
    - *Polydora cornuta* Bosc, 1802
  - Capitellidae
    - *Capitella* sp.
    - *Heteromastus* sp.
    - *Notomastus* sp.
  - Oweniidae
    - gen. sp.
  - Ampharetidae
    - gen. sp.
- Oligochaeta
  - gen. sp.

Echiura
- *Urechis unicinctus* (von Drasche, 1881)

Arthropoda
- Crustacea
  - Cumacea
    - gen. sp.
  - Amphipoda
    - *Grandidierella* sp.
  - Decapoda
    - *Upogebia major* (de Haan, 1841)
    - Juveniles of a shrimp