

Feeding ecology of dunlins *Calidris alpina* staging in the southern Baltic Sea, 1. Habitat use and food selection

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Abstract

The feeding habits of migrating dunlins *Calidris alpina* staging in different non-tidal coastal habitats in the southern Baltic Sea are described. The study also focuses on the structure of the benthic macrofauna of these habitats and the diet choice of dunlins. All investigations were carried out on Langenwerder Island (Wismar Bay), where different types of flats and beaches harbour a total of 30 to 40 species of marine macrofauna. The composition of the macrobenthos differed considerably between the eulittoral sandbank, the eulittoral mudflat, the pebble beach, and the sublittoral surroundings. Most dunlins were observed foraging in flocks of up to several hundred individuals on the eulittoral flats. Densities of up to 20 to 30 foraging dunlins ha⁻¹ occurred annually during peak migration in September and October. Macrobenthos biomass in these habitats fluctuated between 20 and 40 g AFDM m⁻². The mean total food consumption of dunlins during autumn migration was estimated at 0.01 g AFDM m⁻² d⁻¹. The predation pressure could be estimated at 3 to 6% of the suitable food supply. Dunlins staging on Langenwerder were able to attain a pre-migratory mass gain of 0.2 to 0.5% of their body weight per day within an 8 to 12-h daily feeding period. The birds fed predominantly on the polychaete *Hediste diversicolor* by probing. They selected small 7 to 31-mm-long individuals. When water levels were high, and the eulittoral flats inundated, many dunlins switched to foraging along the shorelines where a variety of small prey were taken from spilled macrophytes. Dunlins sometimes obviously ignored their most important food *H. diversicolor*, although available, by feeding on other prey such as juvenile fishes and shrimps, dipteran larvae or spilled amphipods. When feeding on amphipods, dunlins selected the smallest individuals. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Baltic Sea; *Calidris alpina*; food selection; macrobenthos

1. Introduction

Millions of shorebirds breeding in the boreal or Arctic zones spend the non-breeding season in temperate or tropical coastal habitats. Although they encounter a great variety of wetlands during their migration, most shorebirds are concentrated in only

a few huge intertidal areas such as the Wadden Sea or the Banc d'Arguin (Smit and Piersma, 1989). For shorebirds, the cyclic exposure of these intertidal mudflats in a predictable way offers access to the large amount of invertebrate macrobenthic prey (Zwarts and Wanink, 1993). The spatial distribution of foraging shorebirds in intertidal areas depends primarily on prey availability, which is triggered by lunar tidal changes in water level. However, har-

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vestable food stocks are also known to fluctuate seasonally and annually (Zwarts and Wanink, 1993). As a consequence, both the utilisation of a given intertidal area by shorebirds and their diet vary considerably in time and space (e.g. Nehls and Tiedemann, 1993; Piersma et al., 1993a,b; Tiedemann and Nehls, 1997). Furthermore, some shorebirds are specialised to such a degree that they depend on just a few intertidal areas along their migration route. In the extreme, the spatial concentration goes hand in hand with dietary specialisation. For example, the long-distance migratory knot *Calidris canutus* feeds almost exclusively on marine molluscs (Piersma et al., 1993a).

Other shorebird species, however, select their diet more opportunistically. Therefore, they are able to meet their daily energy requirements in a variety of coastal and freshwater habitats. Dunlins *Calidris alpina*, for instance, occur along most of the European coastline, while juveniles also migrate over land. In intertidal coastal habitats, dunlins mainly feed on marine polychaetes, molluscs and crustaceans (Ehlert, 1964; Höfmann and Hoerschelmann, 1969; Davidson, 1971; Viellard, 1973; Worrall, 1984; Durell and Kelly, 1990; Mouritsen, 1994). In wrack beds along rocky shores they rely on dipteran larvae and oligochaetes (Holgersen, 1953; Lifjeld, 1983; Dierschke, 1998), while in the food of dunlins migrating through inland Europe various molluscs, crustaceans, oligochaetes and insect larvae have been found (Viellard, 1973; Sterbetz, 1992). Although significant numbers of dunlins occur in windflat areas of the Baltic and Black Seas during migration (Chernichko et al., 1991; Kube et al., 1994), little is known about their diet and feeding ecology in this habitat. The only investigations on the diet of dunlins in windflats showed that ragworms *Hediste diversicolor* were the preferred prey on a sandbank in southern Sweden (Baltic Sea) and brine shrimps *Artemia salina* in the Sivash (Black Sea) (Bengtson and Svensson, 1968; Verkuil et al., 1993).

Windflats are coastal habitats with unpredictable fluctuations in water level. Changes in water level are forced by wind direction and wind force as well as atmospheric pressure (Brosin, 1965). Occasionally, prolonged periods of high water levels as well as mortality of macrobenthic invertebrates during peri-

ods of severe winter weather or prolonged draught make windflats unsuitable as feeding substrate for dunlins and other waders (Kube, 1994; Dierschke, 1997). Staging in the Baltic Sea then requires alternative feeding habitats (Kube, 1994). This is of importance especially for juvenile dunlins, the majority of which migrate through the Baltic (Leslie and Lessells, 1978). In contrast to adults, which cross the Baltic in long-distance flights and apparently only stop over during adverse weather, juveniles appear to migrate in several shorter flights leading to stopovers at various sites along the coast (Kube et al., 1994; Dierschke, 1997). As almost 90% of dunlins staging in the Baltic use windflats (Kube et al., 1994), this kind of habitat including alternative feeding locations plays an important role in the survival of juveniles, and thus in recruitment.

This study highlights several features of dunlin feeding habits on the southern Baltic Sea coast to test whether these sites meet the demands of staging dunlins with respect to the role in population dynamics (survival). We chose the Island of Langenwerder in Wismar Bay (southwestern Baltic Sea) as the study site because there an array of habitats allowed us to investigate how dunlins meet their energetic requirements in windflats and how they respond to unavailability of windflats as foraging habitat during inundation. The study focuses on the structure of the benthic macrofauna communities and the diet choice of dunlins.

2. Study area

Langenwerder is a small island of 0.22 km². It is situated in the outer Wismar Bay only 200 m off the Island of Poel (54°02'N, 11°30'E, Fig. 1). Waters around Langenwerder are mesohaline, with salinity values varying between 8 and 16 PSU (Sammour, 1989). The island is a network of small sandy dunes, reed beds, creeks, and some ponds. Langenwerder has been protected as a nature reserve since 1924 because of its large sea- and shorebird colonies (Brenning, 1990). Wardens are the only humans living there.

The shore of Langenwerder has never been fixed by construction works and the shape of the island has changed remarkably over time. Especially the

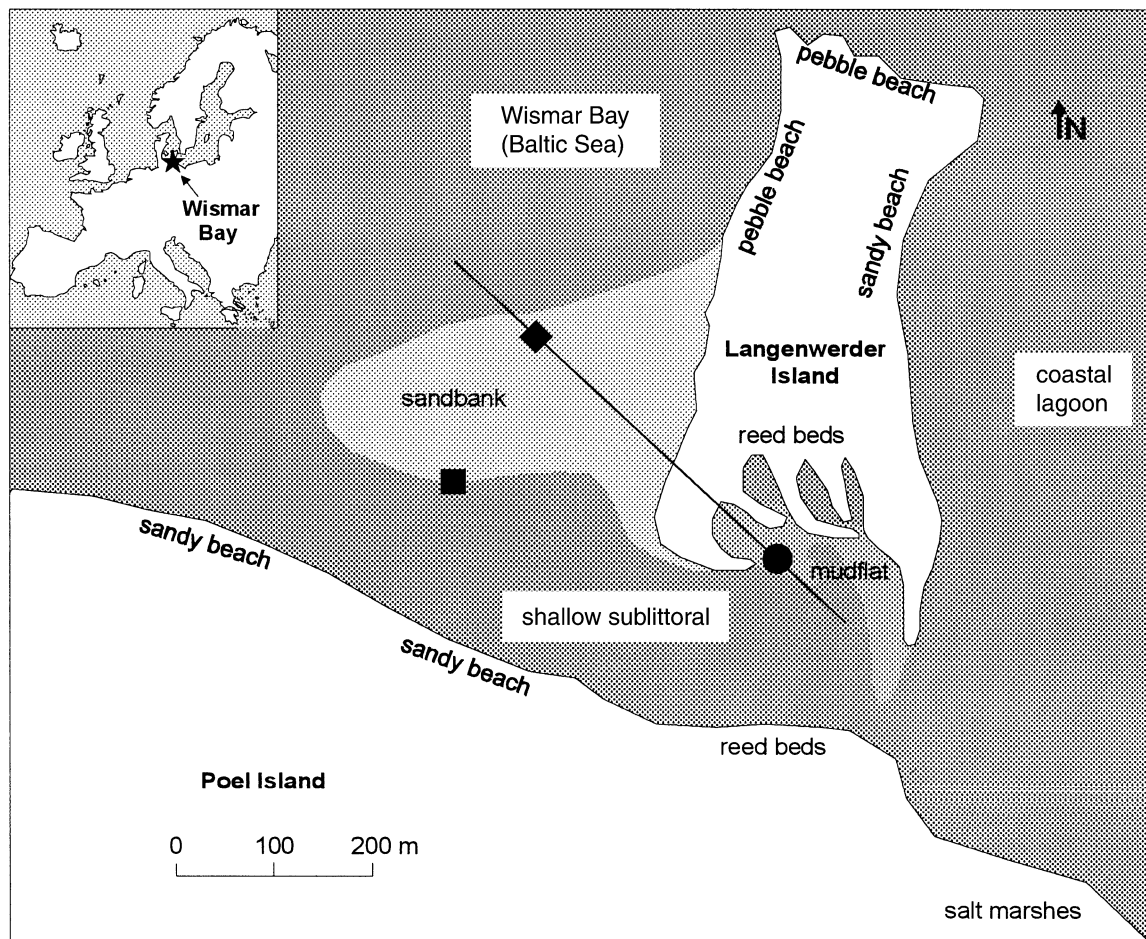


Fig. 1. Study area. Symbols indicate macrobenthos sampling sites: northern part of the sandbank, southern part of the sandbank, and lagoon (see Figs. 5 and 8). The line denotes the course of the transect shown in Fig. 4.

western and northern shores are very dynamic as westerly winds prevail in the southwestern Baltic Sea. The northwestern beaches are flat and consist mainly of coarse gravel, pebbles and stones. Large amounts of eel grass *Zostera marina* and red and green algae are spilled ashore occasionally during storms and aggregate into rotting beds along the shore. The eastern shoreline is sandy and steep, thus not providing feeding habitats for waders.

A large sandbank, including approximately 15 ha of windflats, is situated off the southwest coast of Langenwerder (Fig. 1). The mean grain size of the fine sand fluctuates between 0.1 and 0.15 mm. The organic content of the sediment does not exceed

0.5% (Sammour, 1989). Another smaller windflat area (approximately 3 ha) is located in a sheltered lagoon at the southern edge of the island (Fig. 1). The sediment in the lagoon is muddy with a mean grain size value of 0.08 mm. The organic content varies between 0.5 and 2% (Sammour, 1989). The sandflat in the west is exposed more often than the mudflat in the southern lagoon. On the nearby Island of Poel, the shoreline opposite to Langenwerder is bordered by 20 ha of salt marshes and brackish ponds which are flooded occasionally during high water.

3. Methods

3.1. Bird numbers and feeding distribution

Since 1964, wardens of Langenwerder have carried out daily counts of all migratory shorebirds around the island from April to November. These data have been summarised by Brenning (1985, 1987, 1993). Daily wader catches, using Ottenby traps and mist nets, have since 1974 been carried out during autumn migration between July and October or November (Krägenow, 1980; Brenning, 1987).

3.2. Macrobenthos

The composition of the endobenthic macrofauna of windflats was determined quantitatively by taking three replicate core samples at three stations (sandbank north and south, mudflat) in monthly intervals in 1987/1988 (Sammour, 1989) and 1990, and at two stations (sandbank south, mudflat) in September/October 1994 and 1995 (Fig. 1). Sediment cores of 250 cm² were taken at each station in 1987 and 1990 down to a depth of 10 cm. A corer of 100 cm² was used in 1994 and 1995 to extract 20-cm-deep sediment cores per station. All samples were washed over a 0.5 mm sieve. Samples were preserved in a 4% neutral formalin/seawater solution. Organisms were extracted after three months of storage. Ash-free dry mass (AFDM) was calculated from fresh mass (FM) data by conversion factors determined by incineration at 500°C for 8 h. These factors were in the range of figures given by Rumohr et al. (1987). Large adult specimens of soft-shell clams *Mya arenaria*, lugworms *Arenicola marina* and *H. diversicolor*, longer than 75 segments, could not be sampled quantitatively with the corers, because their burying depth was more than 10 to 20 cm. Densities of *A. marina* were estimated by counting the visible faecal mounts during periods of high water.

The length of all *H. diversicolor* sampled in October 1994 and 1995 was measured in two ways: (1) stretched length of worms stored in 4% formalin and (2) the number of segments. The number of segments (SGM) was converted to worm length (WL, in mm) by:

$$WL = 0.032 \text{ SGM}^{1.588} \quad (R^2 = 0.786, n = 43)$$

The length of broken worms was estimated from a comparison with intact worms of similar width. In 1995 we also measured the shell height of mudsnails *Hydrobia ventrosa* and the length of the amphipod *Corophium volutator* (rostrum to telson). The composition of epibenthic macrofauna of windflats was determined qualitatively by taking occasional dredge samples.

In October 1994 thousands of *Hyperia galba*, an amphipod living as a parasite in *Aurelia aurita* (Buchholz, 1953), were washed ashore and accumulated on the sandbank. These amphipods were eaten by dunlins. We collected all *H. galba* from a 1-m-wide transect and measured their maximum length.

The composition of the fauna of the northwestern pebble beaches was analysed qualitatively in 1990, 1994 and 1995. Finally, we identified the fauna of the spilled seagrass along the northwestern shores. Fresh, wet, and green eel grass was checked qualitatively for marine macrobenthic animals in 1990, 1994 and 1995. A core sample of 90 cm² and 5 cm depth was collected in July 1994 from a bed of rotting eel grass and algae to analyse the size spectra of dipteran larvae.

3.3. Foraging behaviour and diet of dunlins

Qualitative observations on the feeding behaviour of dunlins were made in different coastal habitats both during spring migration (April) and autumn migration (August–October) between 1988 and 1995. These observations covered all characteristic and relevant foraging habitats for waders along the shoreline of the southern Baltic Sea. Notes were made on flock size, main activity, feeding behaviour and food items in relation to water level and season.

The food of dunlins was examined in stomach contents of 22 casualties from ringing operations in September/October 1994 and 1995. In addition, stomach-flushing was applied to freshly trapped birds in late July/early August 1994 ($n = 15$) and in October 1994 ($n = 19$). A plastic tube (outer diameter 4 mm) was passed down the oesophagus to the stomach. With a syringe, c. 10 cm³ seawater were flushed into the stomach resulting in the regurgitation of at least part of the stomach contents (cf. Martin and Hockey, 1993). Samples were stored in

5% formalin and later examined for prey remnants under a stereo microscope. The size of *H. diversicolor* eaten was estimated by measuring the jaw size (JS, tip to innermost tooth, cf. Zwarts and Esselink, 1989), which is correlated with worm length (in no. of segments, SGM) by:

$$JS = 0.06 e^{0.0326 SGM} \quad (R^2 = 0.923, n = 100)$$

In case the size distribution of a prey species was known in both the sediment (p) and the diet of dunlin (r) the selectivity (D) for given size classes was tested as:

$$D = (r - p) / (r + p - 2rp)$$

with negative and positive values indicating avoidance and preference, respectively (Jacobs, 1974).

4. Results

4.1. Seasonal variations in dunlin numbers

The autumn passage of dunlins through Langenwerder took place in several waves of adult and juvenile birds, starting in mid-July and ending in late October (Fig. 2). Whereas adult dunlins stayed for only 1 to 3 days, juvenile birds stayed for about 10 days on average (Brenning, 1987; Dierschke, 1997). Adult migration peaked in late July/early August with maximum numbers counted on 1 day fluctuating between 50 and 300 individuals. Juveniles usually arrived from mid-August onwards. Annual maxima of juveniles counted on 1 day ranged from 150 to 1200 individuals between 1976 and 1995 (Fig. 3). Although the timing of juvenile migration varied between years (Brenning, 1987), no significant changes in mean migration patterns and mean bird numbers were observed throughout the period from 1976 to 1995. Relative differences between the average maxima of 5-day periods of the decades 1976–1985 and 1986–1995 indicated a somewhat later start of adult migration and a 50% increase in mean juvenile numbers during the second period of observation (Fig. 2). The latter is coincident with breeding success, which was low in some years in the late 1970s/early 1980s and markedly higher in the early 1990s (Rösner, 1997).

From late autumn onwards numbers of staging dunlins were strongly related to the local weather

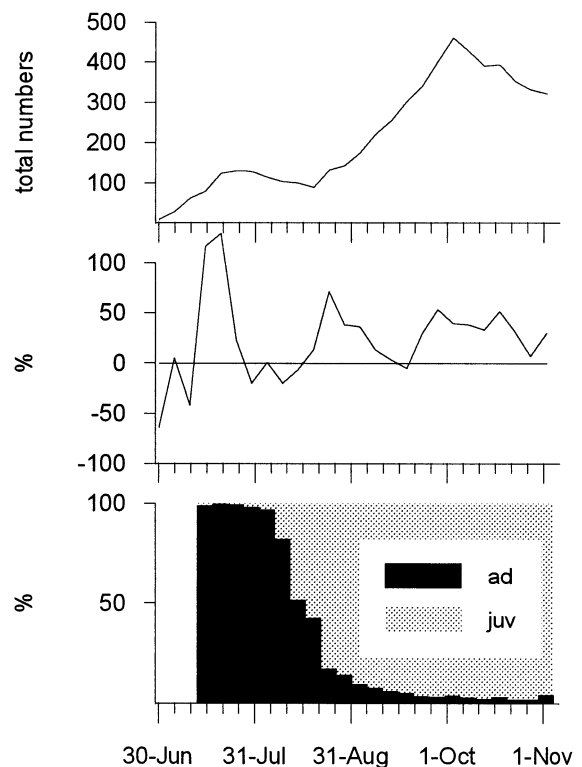


Fig. 2. Phenology of autumn migration of dunlins on Langenwerder. Upper panel: average maxima of 5-day periods from 1976 to 1995; central panel: relative differences between average maxima of 5-day periods of the decades 1976–1985 and 1986–1995, positive values indicate higher numbers during the second observation period and vice versa; lower panel: seasonal changes in the proportion of adult and juvenile birds during autumn migration; data derived from results of trapping.

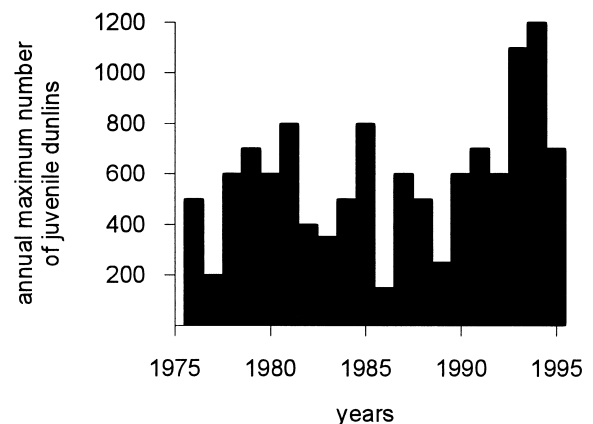


Fig. 3. Annual maximum numbers of juvenile dunlins staging on Langenwerder from 1976 to 1995.

conditions. In September and October, increasing numbers of dunlins tended to stay longer and probably tried to overwinter on Langenwerder. However, most birds left the island when temperatures dropped below 0°C and the surface of windflats froze. Apart from the exceptionally mild winters of the years 1988–1993, when up to 300 birds remained on Langenwerder in January, dunlins usually returned in February or March. About 100 to 300 birds stayed on the island between March and May without showing a clear spring migration peak. No dunlins occurred on Langenwerder in June (Brenning, 1993; Kube et al., 1994).

4.2. Macrobenthos

Langenwerder had a regular occurrence of 30 to 40 species of marine macrofauna between 1987 and 1995. The composition of the macrobenthos differed considerably between the sandbank, the mudflat, the pebble beaches, and the sublittoral habitats (Fig. 4). Species number, total abundance, and total biomass were very low on the northern edge of the sandbank. These parameters revealed much higher values on the southern edge of the sandbank and in the sheltered southern lagoon. Biomass values there fluctuated between 20 and 40 g AFDM m⁻² from 1987 to 1990 (Fig. 5). More than 50% of the total biomass was made up of the bivalves *M. arenaria* and *Mytilus edulis*. Due to the patchy distribution of these two species, no seasonal patterns of total biomass values could be detected.

Biomass values of *H. diversicolor* were highest in spring, when large adult individuals prevailed (Fig. 6). High densities of juvenile worms were

observed between August and October (see also examples in Fig. 8). While the biomass of *Hydrobia* spp. was more or less stable throughout the study period, the biomass of *C. volutator* fluctuated strongly both seasonally and annually (Table 1, Fig. 7; see also Meißner and Bick, 1997). From September to October, 20 to 30% of specimens of *H. ventrosa* (by far the dominant mudsnail species on the windflats) measured >2 mm, but only 5% exceeded 3 mm; the maximum shell height was 3.5 mm (see also Bick and Zettler, 1994). Adult specimens of *C. volutator* attained up to 8 mm length (see also Meißner and Bick, 1997).

The structure of the benthic communities of the windflats has changed significantly as a result of natural changes in the shape of the sandbank in the early 1990s. The velocity of water currents between Langenwerder and Poel islands decreased, sediments became more muddy and sometimes oxygen depletion events occurred in summer. As a result, *M. edulis*, *A. marina*, *Cerastoderma lamarcki* and some other benthic species almost disappeared from the shallow waters south of Langenwerder. *M. arenaria*, *Macoma balthica* and *H. diversicolor* were the only dominant macrofauna species whose biomass had not changed (Table 1).

The fauna of the pebble beaches mainly consisted of three species: spat of *M. edulis* and amphipods *Orchestia gamarellus* and *O. platensis*. All three species occurred in high densities of well over 100 ind. m⁻². Other macrobenthic invertebrates commonly found along the northwestern beaches originated from the sublittoral eel-grass beds, from which they were washed ashore (Fig. 4).

Beds of rotting eel grass and algae deposited

Table 1

Biomass values (mean ± sd) of dominant macrofauna species on the southern edge of the sandbank of Langenwerder in October in different years (1985, 1986 and 1987; from Sammour, 1989)

Species	biomass (g AFDM m ⁻²) in October					
	1985	1986	1987	1990	1994	1995
<i>Hydrobia</i> spp.	9.1 ± 4.3	5.5 ± 4.1	4.2 ± 1.7	8.3 ± 3.7	?	0.3 ± 0.2
<i>Mytilus edulis</i>	11.7 ± 21.6	20.2 ± 23.6	1.6 ± 3.5	3.6 ± 3.2	?	–
<i>Mya arenaria</i>	3.7 ± 6.8	0.3 ± 0.4	5.1 ± 5.2	0.6 ± 1.0	?	3.0 ± 2.4
<i>Macoma balthica</i>	1.0 ± 1.2	0.3 ± 0.4	0.6 ± 0.7	1.5 ± 2.0	?	1.3 ± 1.2
<i>Hediste diversicolor</i>	2.8 ± 2.8	0.9 ± 0.8	4.7 ± 0.9	1.7 ± 1.2	3.6 ± 2.4	3.6 ± 0.8
<i>Corophium volutator</i>	0.04 ± 0.04	0.4 ± 0.6	0.8 ± 1.2	–	0.1 ± 0.1	0.02 ± 0.01

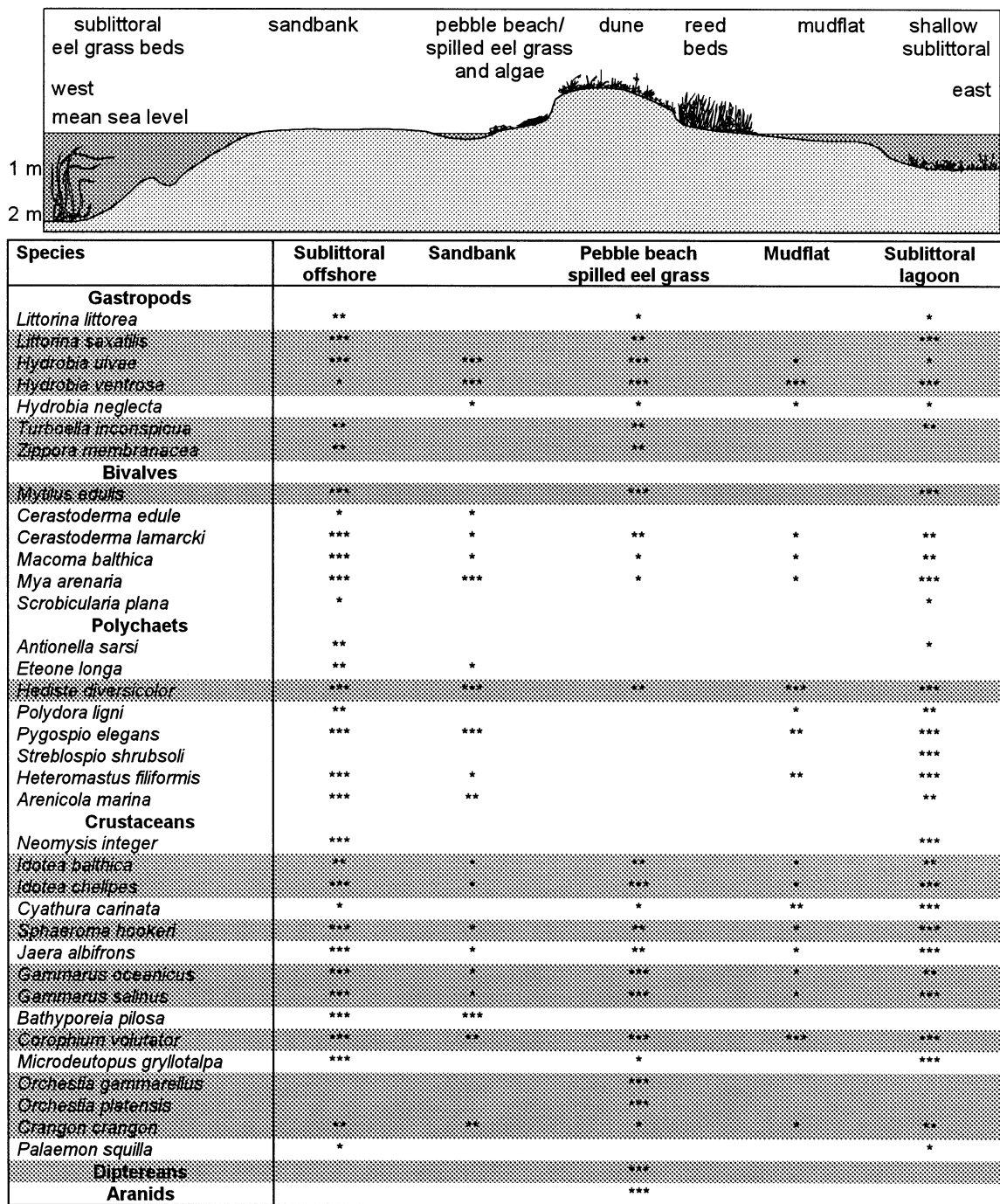


Fig. 4. Composition of macrobenthos in different habitats on Langenwerder. Shaded species were found to be prey items of dunlins.

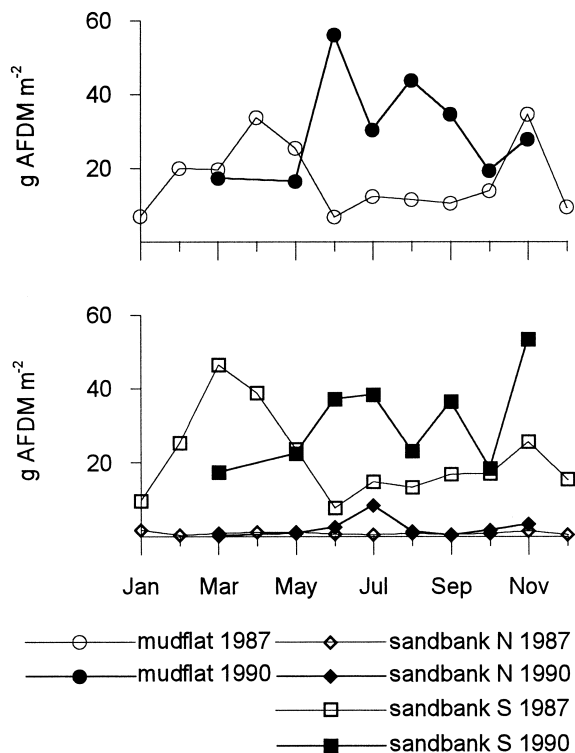


Fig. 5. Seasonal variations in total macrofauna biomass (g AFDM m⁻²) at three stations in windflats at Langenwerder in 1987 and 1990 (data of 1987 were obtained from Sammour, 1989). See Fig. 1 for the location of sampling sites.

on the beaches were inhabited by terrestrial invertebrates during summer and autumn with dipterans and araneids prevailing. A density of 58 000 ind. m⁻² of sepsid larvae was found on 31 July 1994. Furthermore, we observed larvae of Syrphidae and imagines of Anthomyiidae, Sepsidae, and Ephydriidae.

4.3. Foraging behaviour and diet of dunlins

Most dunlins were observed foraging in flocks of up to several hundred individuals on the windflats. Mean densities of up to 20 to 30 foraging juveniles ha⁻¹ occurred annually in this habitat in September and October. As many as 50 juveniles ha⁻¹ were observed in autumn of 1993 and 1994. Densities of foraging birds were much lower during winter, spring, and summer (5–15 ind. ha⁻¹). The spatial distribution of flocks was related to the water level and to the onset of exposure. The birds searched for

prey preferably along the waterline. During periods of falling water levels they fed on both sides of the waterline, on wet sand and in shallow water less than 5 cm deep. During periods of rising water levels they gathered mainly in the shallow water. No dunlins occurred on the windflats during inundation periods. They also avoided foraging on the windflats after longer periods of exposure. The longer a certain flat was exposed, the fewer flocks used it as a feeding ground. Exposed sandflats were left earlier by the birds than exposed mudflats.

On windflats, dunlins usually fed on small worms by probing. During periods of very low water levels in autumn, some individuals were also observed to hunt juvenile shrimps *Crangon crangon* and small gobiid fish trapped in small puddles. During an unusual event of mass spilling of the amphipod *Hyperia galba*, lasting for 3 days in October 1994, dunlins intensively used this sudden food supply.

Especially during periods of high water levels, when the windflats were inundated, many dunlins switched to foraging along the northwestern shorelines and a variety of small prey were taken from leaves of floating eel grass. Small flocks of 10 to 50 individuals could be observed foraging on the pebble beaches also during periods of falling and low water levels throughout the year. On such occasions they searched visually for amphipods and spat of *M. edulis* growing between the stones. However, the relative importance of the northwestern shorelines as a foraging habitat was low during autumn migration, as the total number of dunlins foraging along the beach usually did not exceed 200 individuals. The relative importance of the northwestern shorelines increased in winter and spring when total numbers of dunlins were much lower.

During the summer, dunlins often fed on dipteran larvae and other terrestrial arthropods living in and on the rotting eel grass and algae washed ashore.

As mentioned above, most of the dunlins disappeared from Langenwerder during longer periods of exposure and during periods of complete inundation. The birds often spent these periods on the nearby salt marshes of Poel. Although we sometimes observed them feeding on terrestrial invertebrates there, most birds used this habitat only as a roost. Dunlins returned to the windflats of Langenwerder within a few hours as soon as foraging conditions there improved.

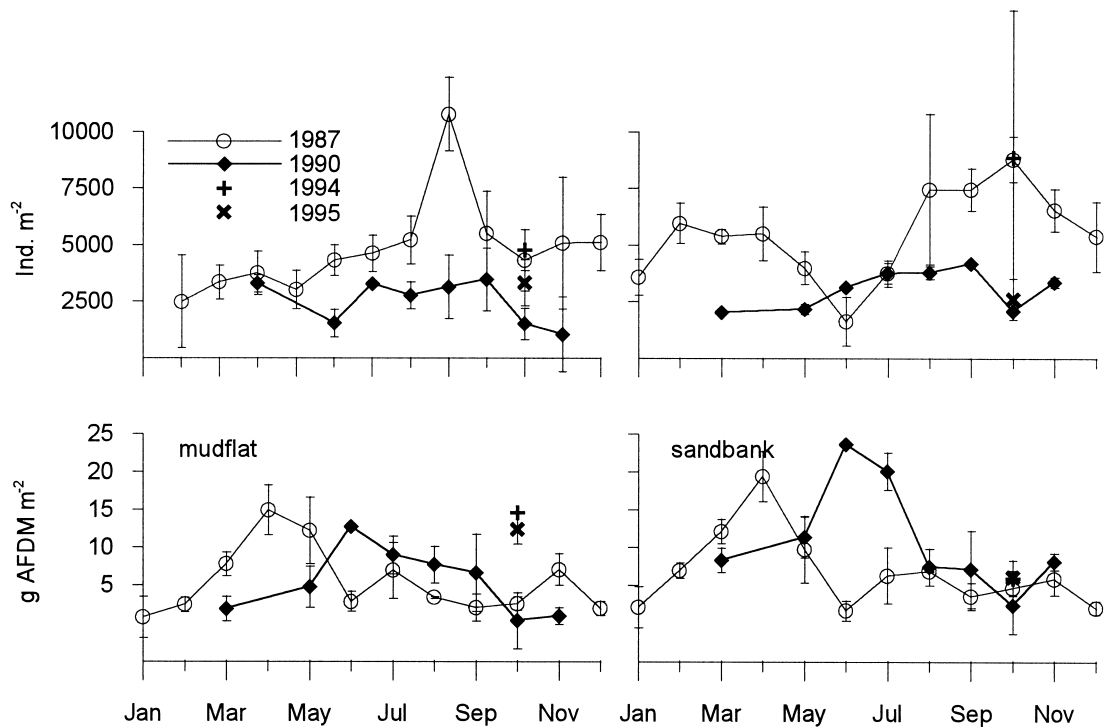


Fig. 6. Seasonal variation in density and biomass of *Hediste diversicolor* (mean \pm sd) in the southern part of the sandbank and in the southern lagoon of Langenwerder in 1987 and 1990. October values of the years 1994 and 1995 are given in addition (data of 1987 were obtained from Sammour, 1989). See Fig. 1 for the location of sampling sites.

4.4. Diet selection

The stomachs of adult and juvenile dunlins caught on the windflats in 1994 and 1995 mainly contained jaws of *H. diversicolor* (up to 961 jaws in one stomach). They also contained crustaceans, shell fragments of several gastropods and *M. edulis*, but these represented only a small number of individuals compared to *H. diversicolor*. Remains of dipteran larvae were mainly found in the stomachs of birds trapped on spilled algae and eel grass or on the pebble beach (Table 2).

Due to the frequent switching between the mudflat and the sandflat, it was impossible to assign the stomach content of dunlins to any of the two windflats. Therefore, the sizes of the ragworms derived from the stomach contents were compared with those in both habitats. According to both frequency and selectivity, worms of 30 to 60 segments (7–22 mm) were favoured in October 1994 (Fig. 8). Longer worms were eaten, too, but because these deep-liv-

ing worms could not be sampled quantitatively, no clear result was obtained with regard to selectivity. In October 1995, juvenile dunlins selected for larger ragworms than in the year before (45–75 segments, i.e. 14–31 mm). The median number of segments of the worms (indicating their size) was 40 in October 1994 ($n = 1596$ jaws), but 59 in October 1995 ($n = 407$ jaws; median test: $\chi^2 = 332$, $df = 1$, $P < 0.001$; see Fig. 8). Stomach-flushing of adult dunlins in late July and early August 1994 resulted in a median number of 43 segments ($n = 452$ jaws). Due to the large sample size, the difference between adults in summer and juveniles in autumn in the size of ragworms eaten was significant in 1994 (median test: $\chi^2 = 38.9$, $df = 1$, $P < 0.001$). Despite the variation in bill length, which allows for different probing depths in the sediment, no individual differences were recognised concerning prey size (Fig. 9).

As mollusc shells were crushed in the stomach, information on size classes taken by dunlins was scant. Three intact *M. edulis* were 0.6, 1.7 and 2.3

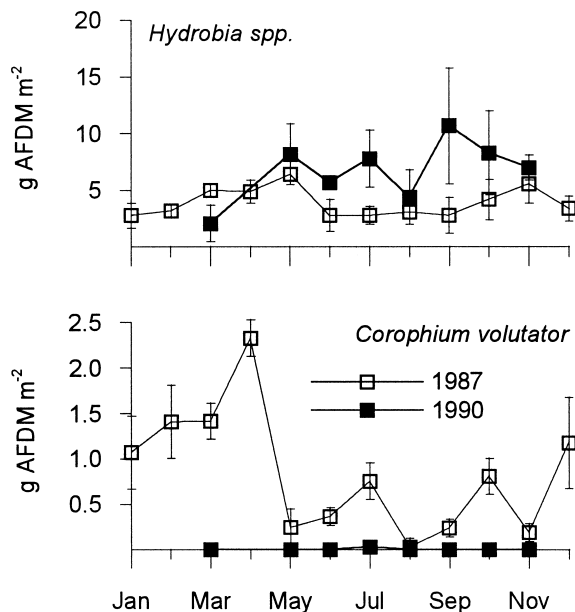


Fig. 7. Seasonal variation in biomass of *Hydrobia* spp. and *Corophium volutator* (mean \pm sd) in the southern part of the sandbank of Langenwerder in 1987 and 1990 (data of 1987 were obtained from Sammour, 1989). See Fig. 1 for the location of the sampling site.

mm long, but according to fragments the largest mussels eaten seemed to be 4 mm long. Shell heights of gastropods were 1.3 mm in one *Littorina saxatilis* and between 1.0 and 3.4 mm in six *Hydrobia* spp. Stomach-flushing of dunlins feeding on the sandbank strewn with spilled *Hyperia galba* provided 21 intact individuals of this amphipod. Compared to the sample collected along the waterline, dunlins only took the smallest third of the size classes available (Fig. 10). Also when feeding on dipteran larvae in eel grass and algae washed ashore, dunlins selected the smaller larvae (Fig. 11).

5. Discussion

5.1. Diet composition

The main contribution of *H. diversicolor* to the diet of dunlins found in this study is paralleled by the only comparable study from the Baltic Sea. On a sandbank at Saltviken (southern Sweden) dunlins mainly fed on *H. diversicolor*, but avoided

oligochaetes and *C. volutator* although these occurred in roughly the same density (Bengtson and Svensson, 1968). The very small portion of *C. volutator* in the diet on Langenwerder might be explained by low abundance during the study in 1994/1995 (cf. Table 1), although in general crustaceans (and oligochaetes) can be underrepresented in stomach analyses due to the lack of hard and indigestible body parts (Puttick, 1978; Lifjeld, 1983).

Despite their high abundance in the sediment, *Hydrobia* spp. seem to be eaten by dunlins on Langenwerder only occasionally. As dunlins preferred mudsnails of 2 to 4 mm shell height in the Severn Estuary, England (Worrall, 1984), about one third of *Hydrobia ventrosa* present in the windflats of Langenwerder should be regarded as profitable prey. In sharp contrast, mudsnails belong to the most important prey species in the Wadden Sea (Ehlert, 1964; Mouritsen, 1994) and in British estuaries (Davidson, 1971; Goss-Custard et al., 1977; Evans et al., 1979; Worrall, 1984; Durell and Kelly, 1990), even though *H. diversicolor* is the main prey there, too.

The positive selection of *H. diversicolor* longer than 7 mm (or 30 segments) on Langenwerder is in accordance with the 'lower prey size acceptance rule' postulated by Zwartz and Wanink (1993), who describe the lower prey size acceptance threshold as a function of the predator's body mass:

minimum prey mass (mg DM)

$$= 0.0012 \text{ body mass (g)}^{1.20}$$

Dunlins arriving on Langenwerder in autumn with a mean body mass of 45 g (Brenning, 1987; Dierschke, 1997) are predicted to take prey heavier than 0.115 mg DM, which on Langenwerder is equal to *H. diversicolor* longer than 8 mm (or 32.5 segments). The preference for small size classes of 7 to 31-mm-long *H. diversicolor* on Langenwerder is paralleled by observations in other studies. Applying formulae relating jaw size to worm length from Langenwerder to a photo of ragworm jaws from a stomach of a dunlin shot in the German part of the Wadden Sea (Ehlert, 1964) shows that most worms eaten measure between 19 and 31 mm. In the Dutch part of the Wadden Sea, 90% of *H. diversicolor* eaten are longer than 20 mm (Zwarts et al., 1990a), while in the West African Banc d'Arguin an average length of 10 mm has been calculated from energy

Table 2

Occurrence (in %) of prey in stomachs of juvenile dunlins at Langenwerder

Age, Month:	Adults, August		Juveniles, October			
Habitat:	Wind flat	Spilled algae and eel grass	Wind flat	Spilled algae	Pebble beach	Spilled <i>Hyperia</i>
<i>n</i> :	11	4	25 ^a	3	8	5 ^a
Mollusca			56		75	60
<i>Hydrobia</i> spp.			24 (1.5)		25 (0.5)	20 (0.2)
<i>Turboella inconspicua</i>			8 (0.2)			
<i>Zippora membranacea</i>			8 (0.2)			
<i>Littorina saxatilis</i>			8 (0.5)		38 (2.0)	40 (0.4)
<i>Mytilus edulis</i>			28 (1.3)		63 (4.4)	20 (0.4)
Polychaeta						
<i>Hediste diversicolor</i>	82 (29.5)	25 (0.5)	88 (59.2)	33 (2.3)	50 (6.9)	40 (0.4)
Crustacea	27		36	33	25	100
<i>Orchestia</i> spp.					13	
<i>Hyperia galba</i>						100
<i>Corophium volutator</i>	9					
Chelicerata						
Acari	9					
<i>Erigone</i> spp.					13	
Insecta	73	100	24	67	63	
Dipteran larvae	18	75		33		
Dipteran pupae	45	100	12	67	38	
Dipteran imagines				33	25	
Green plant fragments			4		25	20
Seeds			4		13	20
Grit			68		38	20

In addition to the frequency in *n* samples, between brackets the average number of individuals per sample is given for molluscs and *H. diversicolor*.

^a Including one adult bird.

requirements and intake rates (Zwarts et al., 1990a). In British estuaries, ragworms of 20 to 40 mm are preferred (Goss-Custard et al., 1977; Worrall, 1984), the lower size limit being 5 mm (Worrall, 1984). At least in the southern Baltic, where *H. diversicolor* reproduces relatively late in July/August (Dierschke et al., 1999), the selection might be explained by the fact that especially the smaller ragworms are very abundant in autumn. Furthermore, longer ragworms live in deeper burrows (Esselink and Zwarts, 1989; Dierschke et al., 1999) and are therefore more difficult to catch and/or less likely to be encountered with a bill of about 30 mm length. A reason to avoid large ragworms could be the long handling time, as they have to be washed before dunlins can swallow them (pers. observation; see also Ehlert, 1964).

The same holds true for the amphipod *Hyperia galba*: large individuals were carried to the water for washing and were perhaps negatively selected

because of the resulting handling time. This compares to semipalmated sandpipers *Calidris pusilla* avoiding large individuals of *C. volutator*, for which unprofitable handling times were found (Gratto et al., 1984). Thus, the preference for small prey can be interpreted either as opportunism or as the minimisation of time spent feeding. In addition, long handling times in large prey might provoke kleptoparasitism by gulls or other waders (Warnock, 1989).

5.2. Consumption and food supply

Windflats are the most important feeding areas for dunlins staging in the southern Baltic Sea (Kube et al., 1994). The mean feeding density on Langenwerder of 5 to 15 ind. ha⁻¹ is in accordance with estimates from other Central European staging areas (e.g. Graumann et al., 1980; Erfurt and Dierschke, 1992; Nehls and Tiedemann, 1993; Dierschke,

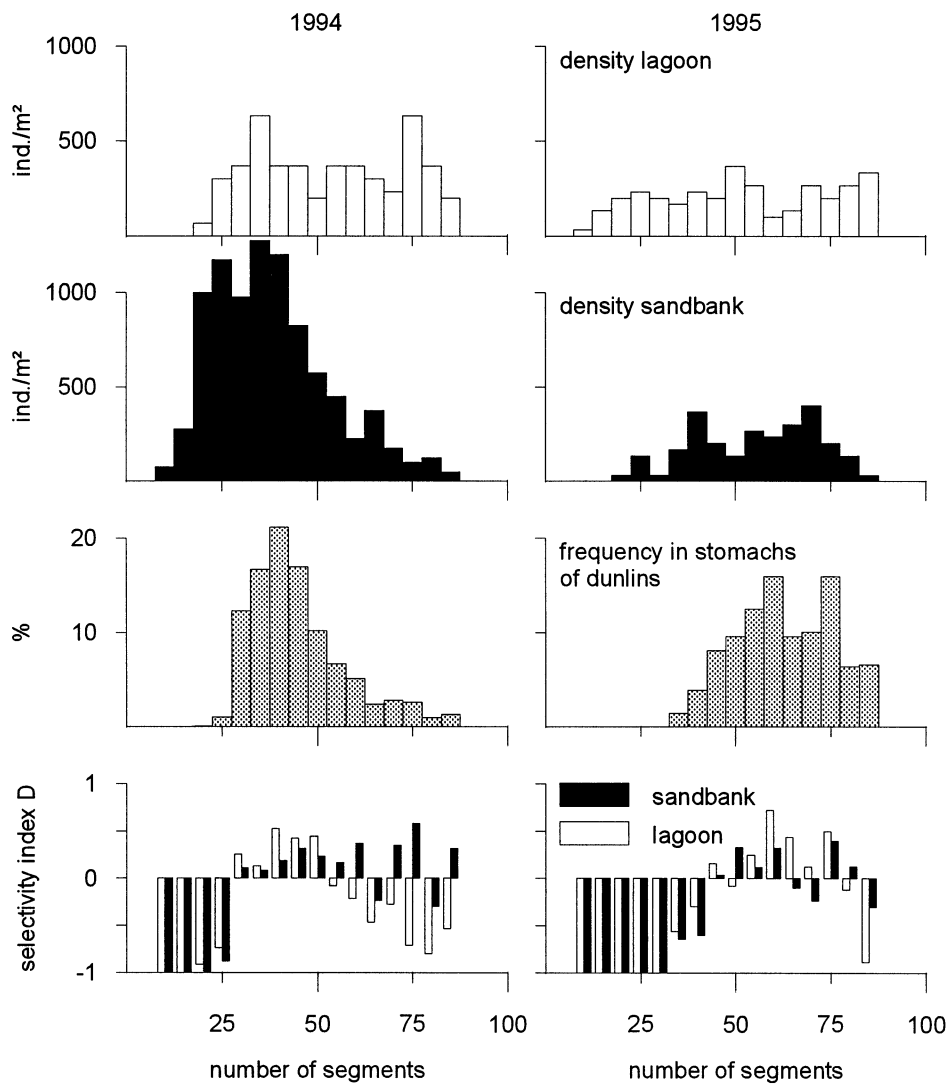


Fig. 8. Upper panels: length-frequency distributions (expressed in numbers of segments) of *Hediste diversicolor* on Langenwerder in the southern part of the sandbank, in the southern lagoon and in stomachs of dunlins trapped in October 1994 and 1995. Selectivity indices are shown in the lower panel by the index *D* of Jacobs (1974).

1997). During September and October, however, juvenile dunlins regularly occur on Langenwerder in densities of 20 to 50 ind. ha⁻¹. The main question arising from these high density values is how dunlins can find enough food to attain a pre-migratory mass gain of 0.2 to 0.5% of body weight per day as measured by Brenning (1987) and Dierschke (1997).

Dunlins wintering in tidal habitats at the Banc d'Arguin, Mauritania, feed 6 to 10 h daily to obtain

their energy requirements and 8 to 12 h to obtain a body mass increase of about 1% per day (Zwarts et al., 1990a,b). The metabolic requirements are a function of body mass. The total daily food consumption of a dunlin staging on Langenwerder in autumn with a mean body mass of 48 g (Brenning, 1987; Dierschke, 1997) can be estimated at 3.9 to 4.5 g AFDM d⁻¹. This figure is calculated by using the formulas of Zwarts et al. (1990a)⁽¹⁾ and Lasiewski

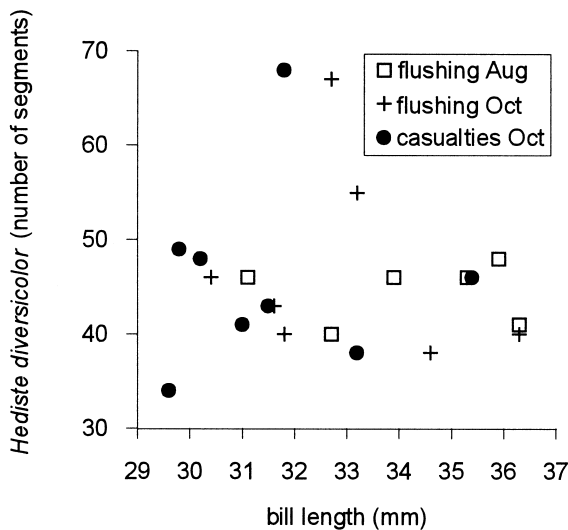


Fig. 9. Bill length of dunlins in relation to the median length (number of segments) of *Hediste diversicolor* found in their stomachs on Langenwerder (worm length was calculated from jaw length, see Section 3 for details).

and Dawson (1967)⁽²⁾:

$$\text{gross food intake per bird (g AFDM d}^{-1}\text{)} \\ = 47.6^{(1)} \text{ (or } 55.3^{(2)}\text{) body mass (kg)}^{0.723}$$

The estimated biomass value of the mean daily food consumption of 4.2 g AFDM d⁻¹ can be converted to a number of prey items per day in accordance to the selected size spectra observed in autumn 1994 and 1995. Dunlins staging on Langenwerder had to take a minimum of 6203 *H. diversicolor* per day in autumn 1994 and a minimum of 1468 *H. diversicolor* per day in autumn 1995. In order to meet this estimate within 6 to 10 h, dunlins would have to obtain an intake rate of 10 to 17 *H. diversicolor* per min in 1994 and 2 to 4 *H. diversicolor* per min in 1995. These hypothetical intake rates agree well with the intake rates of 5 to 18 *H. diversicolor* per min that we observed in the southern Baltic (Dierschke, 1997; Kube, 1994). Hence, dunlins staging on Langenwerder should generally be able to find enough food to attain a pre-migratory mass gain of 0.2 to 0.5% of body weight per day within a period of 8 to 12 h daily feeding time. In fact, two different situations were observed in October 1993 and 1994. In October 1993, time budgets revealed by scan sampling during daylight hours resulted in

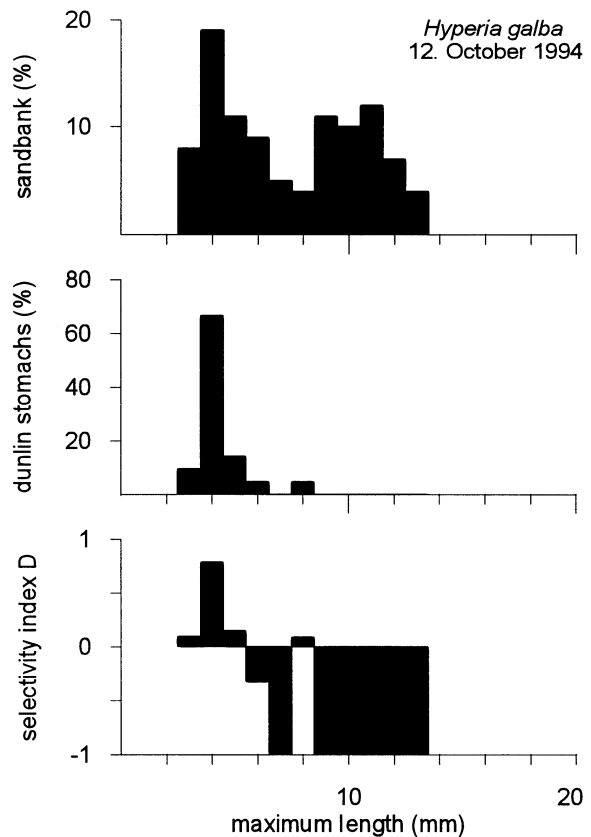


Fig. 10. Upper panels: length-frequency distribution of *Hyperia galba* on the sandbank of Langenwerder and in stomachs of dunlins trapped there on 12 October 1994. Selectivity indices are shown in the lower panel by the index *D* of Jacobs (1974).

a total foraging time of 5.9 h d⁻¹, while recaptured juvenile dunlins lost mass at a rate of -0.4 g d⁻¹ (Dierschke, 1997). However, when they foraged for 10.6 h d⁻¹ in October 1994, recaptured individuals gained mass at a rate of 0.5 g d⁻¹ (i.e. 1% d⁻¹; Dierschke, 1997). Again, observed values agree well with the hypothetical ones, demonstrating the suitability of the Langenwerder windflats as a stopover site for dunlins.

The total food consumption by on average 500 juvenile dunlins staging on Langenwerder in October can be estimated at 0.01 g AFDM m⁻² d⁻¹. Thus consumption is at a level comparable to the high estimates for dunlins wintering at the Banc d'Arguin, Mauritania (Zwarts et al., 1990a). Dunlins on Langenwerder extract some 1.35 g AFDM

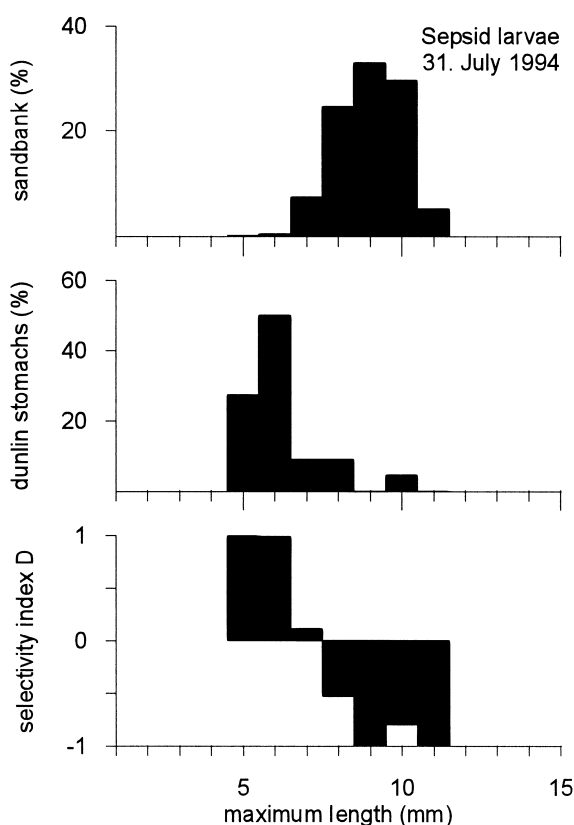


Fig. 11. Upper panels: length-frequency distribution of sepsid larvae (Diptera) collected from a bed of rotting eel grass and algae on Langenwerder and in stomachs of dunlins trapped there on 31 July 1994. Selectivity indices are shown in the lower panel by the index D of Jacobs (1974).

$\text{m}^{-2} \text{y}^{-1}$, which is less than 10% of the total annual production of *H. diversicolor* (the P/B ratio of *H. diversicolor* ranges from 2.5 to 3; Kristensen, 1984). The supply of suitable *H. diversicolor*, the main prey on the windflats of Langenwerder in October 1994 and 1995, fluctuated between 5 and 11 g AFDM m^{-2} . The relative predation pressure in October (food consumption in g AFDM $\text{m}^{-2} \text{month}^{-1}$ divided by suitable food supply in g AFDM m^{-2}) can be estimated at 3 to 6%. During other months the relative predation pressure is only 1 to 2%.

By focussing simply on these average values, one would presume that dunlins should be able to fulfil their daily metabolic energy requirements on Langenwerder without any problem. But this is certainly not the case, as only very small parts of the entire

windflat area are suitable for feeding at any one time. The size of the suitable feeding area changes frequently and in an unpredictable way due to the stochastic fluctuations in water level. In addition, dunlins sometimes overexploit certain parts of the windflat during longer periods of stagnation in water level (see Dierschke et al., 1999) and prey density might locally become unprofitable. As a consequence, dunlins staging in non-tidal coastal habitats frequently have to change their foraging habitat. The switching between different foraging sites is supposed to be caused predominantly by the irregular fluctuations in water level which determine site accessibility and prey availability (Verkuil et al., 1993; Kube, 1994). The results of our investigations suggest that prey profitability plays an important role, too, as dunlins feeding on Langenwerder sometimes obviously ignored their most important food *H. diversicolor*, although available, by feeding on other prey such as small fish, *C. crangon*, dipteran larvae and spilled *H. galba*.

The versatility in the diet of dunlins both on a global and on a local scale enables them to make frequent use of wetlands with unpredictable feeding conditions such as the southern Baltic Sea or the Sivash (Black Sea). The flexible usage of a broad spectrum of prey species seems to be advantageous because severe winters and prolonged periods of windflat exposure occasionally cause high mortality among macrobenthic invertebrates (Kube, 1994; Dierschke, 1997). Therefore, an array of alternative foraging habitats at a certain site is required for non-tidal wetlands to become important stopover sites. Though the energy requirements of a given number of individuals may then be met for a longer period, the carrying capacity of the alternative foraging habitats often differs considerably. Hence, some of the dunlins will have to leave their preferred site temporarily and use alternative sites nearby (Verkuil et al., 1993; Kube, 1994). Other individuals move further onwards along their migration route when foraging conditions become unfavourable (Kube et al., 1994).

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