

Low dietary importance of polychaetes in opportunistic feeding Sanderlings *Calidris alba* on Belgian beaches

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We studied abundance and feeding behaviour of wintering Sanderling *Calidris alba* at five beaches along the Belgian coast, and focused on the role of polychaete worms in their diet. On average 10.0 Sanderlings were present per km stretched beach, of which 87.8% were involved in foraging activities. Highest numbers of Sanderling occurred on the beach from 2 hours before to 4 hours after low tide. Detailed observations of individual birds revealed a mean pecking rate of 18.7 pecks per min. Birds exhibited several feeding modes, and we distinguished superficial pecking (mainly feeding on wreck) and probing for polychaetes. Feeding on wreck was observed frequently and throughout the tidal cycle. In contrast, probing for polychaetes was limited in time, and occurred primarily when the tide reached the upper intertidal zone, where peak densities of *Scolecopsis squamata* were found. Based on our observations, we conservatively estimated that during each tidal cycle this benthic species may provide only 2.0–9.0% of a Sanderling's daily energy demand. Numbers of Sanderlings appeared to be lowest when capture rates on polychaetes were highest. We therefore suggest that polychaetes are of minor importance for Sanderlings foraging along Belgian beaches.

Key words: Sanderling, feeding ecology, polychaetes, *Scolecopsis squamata*, sandy beaches

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INTRODUCTION

In winter, the Sanderling *Calidris alba* is typically found on sandy intertidal areas, and beach faces are favoured feeding grounds (e.g. Smit & Wolff 1981, Petracci 2002, Summers *et al.* 2002, van Turnhout & van Roomen 2005, van Turnhout & van Roomen 2008). Substantial research has been carried out on the Sanderling's feeding ecology in Nearctic regions (Silliman *et al.* 1977, Myers 1980, Myers *et al.* 1980, Castro 1987, Burger & Gochfeld 1991, Petracci 2002), but far less in western Europe. The limited information available on the Sanderling's diet along western

European coasts mainly comes from stomach and dropping analyses (Cramp 1983, Perez-Hurtado *et al.* 1997, Arcas *et al.* 2003). These types of analyses may give a skewed impression of the diet, since soft-bodied prey species are digested much easier than hard-shelled prey (Perez-Hurtado *et al.* 1997, Nuka *et al.* 2005).

The polychaete *Scolecopsis squamata* is mentioned as the main food item for Sanderling along the North Sea coast (Smit & Wolff 1981, Glutz von Blotzheim *et al.* 1984). However, studies confirming the actual dominance of this prey item are lacking, and Sanderling is known to take a large variety of other food items, including insects, peracarid crustaceans (amphipods and

isopods), shells and other, often stranded, organisms (Smit & Wolff 1981, Cramp 1983, Glutz von Blotzheim *et al.* 1984, van de Kam *et al.* 1999, Leopold *et al.* 2004, van Turnhout & van Roomen 2005).

We investigated the diet and feeding habits of Sanderling along the Belgian coast. The East Atlantic flyway population of Sanderling numbers 123 000 individuals (Wetlands International 2006), of which the Belgian coastline harbours a small wintering population. Total numbers wintering on the Belgian sandy beaches ranged from 180 to 709 individuals in the period 1988–1997 (Devos *et al.* 1998). The goal of the study was to assess the diet of Sanderling, in particular the role of polychaete worms, by direct field observations. To establish the importance of polychaetes, we investigated the foraging behaviour of Sanderling across the whole transverse gradient of beaches and estimated foraging success in relation to the tidal cycle and food availability. Based on our field observations, completed with literature data, we estimated the importance of polychaetes in the daily energy budget of Sanderling.

METHODS

Study site

Sanderlings were studied at five different transects along the Belgian coast (centred at 51°13'N, 2°54'E; Fig. 1), namely at Heist (Baai van Heist – BH, 700 m long), De Haan (Vosseslag – VOS, 350 m), Raversijde (RAV, 630 m), Lombardsijde (LBS, 345 m) and Oostduinkerke (Schipgat – SG, 400 m). An alternation of ridges and runnels was present at BH, VOS and SG. Beach profiles of VOS and SG are furthermore characterised by an interrupted slope at about 4 m above mean low water spring level (MLWS), separating the beach into a wide, gently sloping lower part, and a narrow, steep upper part (Degraer *et al.* 2003).

Data collection

We collected information on habitat selection, foraging behaviour and diet of Sanderlings during 47 observation days between 23 February 2005 and 25 March 2006, during the months with highest numbers of Sanderling (October–March). On each observation day, numbers of Sanderlings present at the transect were counted each hour and the percentage of birds involved in foraging activities was estimated. It was noted whether the birds were associated with the water line or located on the emerged parts of the intertidal zone. In between these hourly 'transect scans', detailed behavioural observations of randomly chosen individual

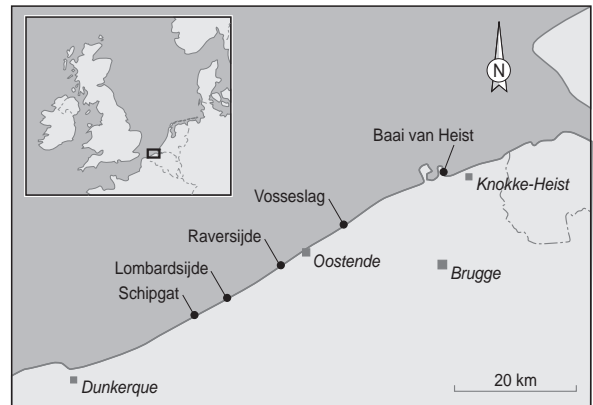


Figure 1. Location of the study transects along the Belgian coast.

birds were made for up to five minutes, making use of a telescope and a tape recorder. While observing individual birds, their location on the beach (water line, intertidal, supralittoral) and activity (searching for food, feeding, running, resting, sleeping, preening, flying) was assessed continuously. Each foraging event was recorded. Foraging events were subdivided in 'pecking' (superficial pecks, bill not clearly penetrating the sediment), 'probing' (bill clearly penetrating the sediment) and 'spooning' (bill clearly penetrating the substrate, bill swishing from side to side). The success of these foraging attempts was deduced from 'snatching' movements of the bill. Obviously, our measure for foraging success is a minimum estimate as we may have missed ingestion of the smallest items.

Whenever possible, the caught prey was identified. During the observations of individual birds, the bird's location on the beach relative to the water line was assessed continuously. Thus, for birds foraging close to the water line, the time at which they were observed in combination with actual water levels gave the exact location on the beach expressed in height above MLWS. To link foraging characteristics of Sanderling to food densities we used macrobenthos data by Degraer *et al.* (2003), collected in the same transects. These results need to be interpreted with care since benthos sampling took place in 1997.

We defined *foraging rate* as the total number of foraging events per min of foraging time (searching and feeding). *Foraging efficiency* was defined as the percentage of successful foraging events. Similarly, we distinguished *probe percentage* as the percentage of probes to the total number of foraging events, and *probing efficiency* as the percentage of successful probes to the total amount of probes.

Statistics

To compare numbers of Sanderling and foraging characteristics among environmental factors (transects, tidal cycle and height above MLWS), the non-parametric Mann–Whitney U test (for pair-wise comparisons) and Kruskal–Wallis test were used (SPSS 9.0).

RESULTS

Foraging activity

The total number of Sanderlings present per km of shoreline averaged 10.0 ($n = 303$, SE 1.5) and varied between 2.6 individuals per km at LBS and 14.6 at RAV (Fig. 2). On average, 87.8% of the birds present at the transects were foraging. Of all foraging birds, 85% were located within 2 m of the water line, 13% on emerged parts of the intertidal area, and only 2% were seen on the tide line (supralittoral). Total numbers and foraging numbers of Sanderling significantly differed among the transects (total number: $\chi^2_4 = 54.7$, $P < 0.0005$; foraging number: $\chi^2_4 = 53.1$, $P < 0.0005$).

Foraging birds were present at the transects throughout the entire tidal cycle. Nevertheless, abundance on the beach and foraging numbers tended towards a tidal pattern, with highest numbers from 4 to 10 hours after high tide (or coinciding with low tide; total number: $\chi^2_{11} = 17.8$, $P = 0.085$; foraging number: $\chi^2_{11} = 18.9$, $P = 0.061$; Fig. 3).

Mean foraging rates ranged from 13.4 in BH to 24.4 in RAV, and mean foraging efficiency from 1% in LBS to 11% in BH (Table 1). A Kruskal–Wallis analysis revealed a significant difference between foraging rates and foraging efficiencies at the transects (foraging rate: $\chi^2_4 = 17.7$, $P = 0.001$; foraging efficiency: $\chi^2_4 = 82.4$, $P < 0.0005$). Pair-wise comparisons indicated that foraging

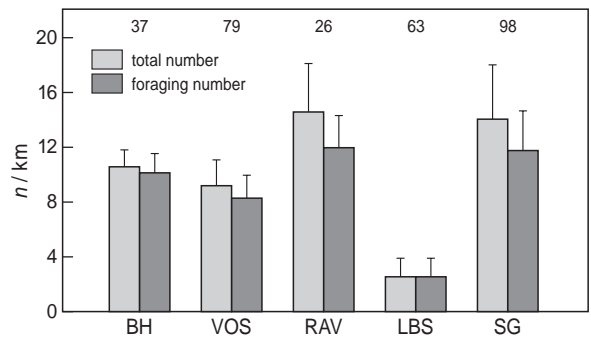


Figure 2. Mean numbers of Sanderling (\pm SE) at five transects (the numbers above the graph denote the numbers of scans).

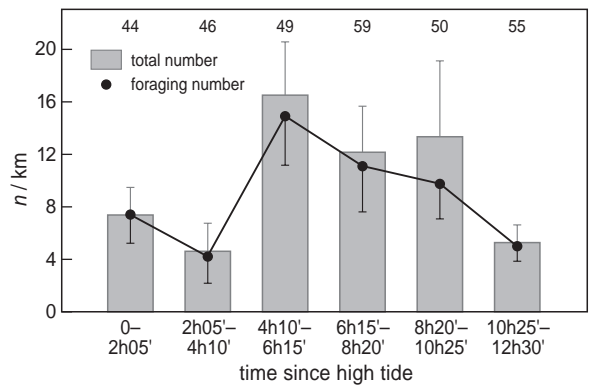


Figure 3. Mean numbers of Sanderling (\pm SE) per tidal stage (the numbers above the graph denote the numbers of scans).

performance of birds at BH differed from those at the other transects (Table 1). Averaged over all transects, foraging efficiency was 7%. Foraging efficiency was highest during probing (15%), and less so during pecking (6%) and spooning (1%).

Table 1. Foraging rates (number of foraging events per minute) and foraging efficiency (% successful foraging events) of Sanderling at five transects along the Belgian coast.

Transect	Foraging rate			Foraging efficiency		
	Mean \pm SD	Test ¹	<i>n</i>	Mean \pm SD	Test ¹	<i>n</i>
BH	13.39 \pm 5.68	a	127	10.9 \pm 9.8	a	125
VOS	19.91 \pm 13.06	b	105	5.6 \pm 11.6	b	104
RAV	24.41 \pm 22.18	ab	70	3.4 \pm 5.6	b	69
LBS	17.54 \pm 8.47	b	17	1.2 \pm 1.8	b	17
SG	20.11 \pm 13.96	b	104	5.0 \pm 6.6	b	102
Total	18.65 \pm 14.04		423	6.5 \pm 9.3		417

¹Same letter indicates no difference ($P > 0.05$, Mann–Whitney test).

Diet

In total, we observed 1182 successful foraging events, and in 41% of these cases we were able to identify the prey taken (Table 2). Identification of prey varied by the foraging mode, with 78% of the prey identified when the bird was probing, 62% when spooning, and only 25% of the prey were identified when pecking. Among the identified prey, polychaete worms (most likely *Scolecopsis squamata*, see Discussion) were consumed most (22%), followed by bivalves (17%) that were predominantly eaten as wreck washed ashore by incoming tides. Occasionally, Sanderlings were observed taking small crabs, anemones and insects (washed ashore), or they were taking advantage of foraging Oystercatchers, eating leftovers in broken mussel shells.

Table 2. Numbers and types of prey taken by Sanderling along the Belgian coast.

	Number of prey caught
Polychaetes	263
Bivalves	
<i>Mytilus edulis</i>	19
<i>Donax vittatus</i>	27
<i>Ensis</i> sp.	66
Unidentified	85
Crustaceans	17
Anemones	7
Unidentified	698
Total	1182

Energetic importance of polychaetes

Combining data from all transects, there was a clear tidal effect on probe percentage and probing efficiency (probe percentage: $\chi^2_5 = 28.3$, $P < 0.0005$; probing efficiency: $\chi^2_5 = 27.6$, $P < 0.0005$; Fig. 4A). Generally, probing for worms occurred most often just before high tide. Accordingly, most successful probes were observed during incoming tide, with maximum success occurring right before high tide. While probing was observed during receding tide as well, success was lower (Fig. 4A).

Probing and capture of polychaetes was concentrated at upper intertidal areas (probe percentage: $\chi^2_4 = 40.2$, $P < 0.0005$; probing efficiency: $\chi^2_4 = 25.1$, $P < 0.0005$; Fig. 4B). At all transects, birds were observed probing at lower parts of the intertidal as well. However, this occurred to a lesser extent and probing efficiency was much lower. In general, successful probing was concentrated in the limited area where *S. squamata* occurred in peak densities (Fig. 5).

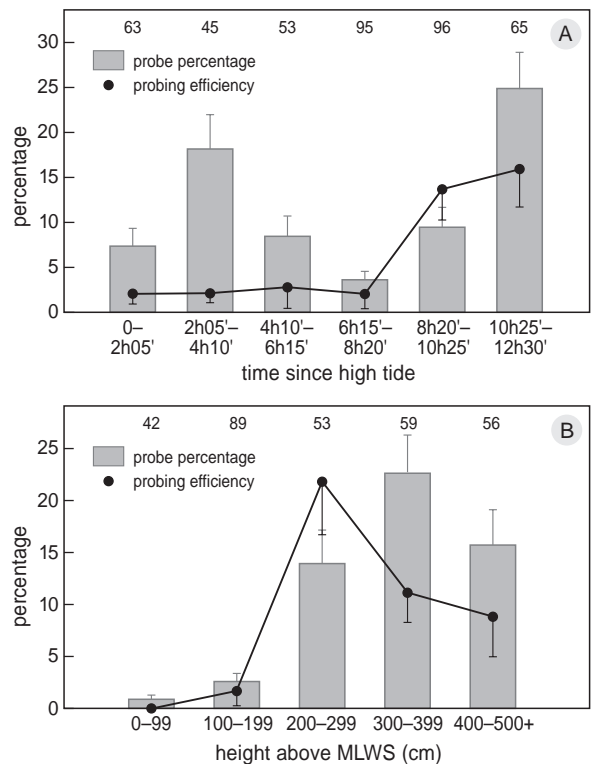


Figure 4. Mean probe percentage (+SE) and mean probing efficiency (-SE) in relation to the tidal stage (A) and height above mean low water spring level (B) (the numbers above the graph denote the number of observation bouts).

Assuming that all caught polychaetes were *S. squamata*, we can calculate the daily energy intake that this polychaete would support. According to Castro (1987), the basal metabolic rate (BMR) of Sanderling is 48.1 kJ/day. Taking the relationship of Net Energy Intake (NEI) to BMR for waders as reported by Kersten & Piersma (1987) (NEI is 2.4–4.9 multiples of BMR) and assuming an assimilation efficiency of 85% (Kersten & Piersma 1987), a Sanderling's daily energy intake varies between 136 and 277 kJ/day. Furthermore, the mean weight per individual *S. squamata* has been reported as 1.6 and 3.0 mg AFDW (Degraer *et al.* 1999 and Dankers *et al.* 1983, respectively). The caloric content of benthic animals ranges between 22 and 26 kJ/g AFDW, with a mean of 23.7 kJ/g AFDW for the taxon *Annelida* (Beukema 1997). Taking this variation into account, a daily energy intake of 136–277 kJ corresponds to 5.2–12.6 g AFDW of benthic prey per day, or 1735–7650 individuals of *S. squamata* each day. Based on the variation in probing efficiency with the tide (Fig. 4), and assuming that an individual Sanderling is present at the beach during a full tidal cycle, it follows that

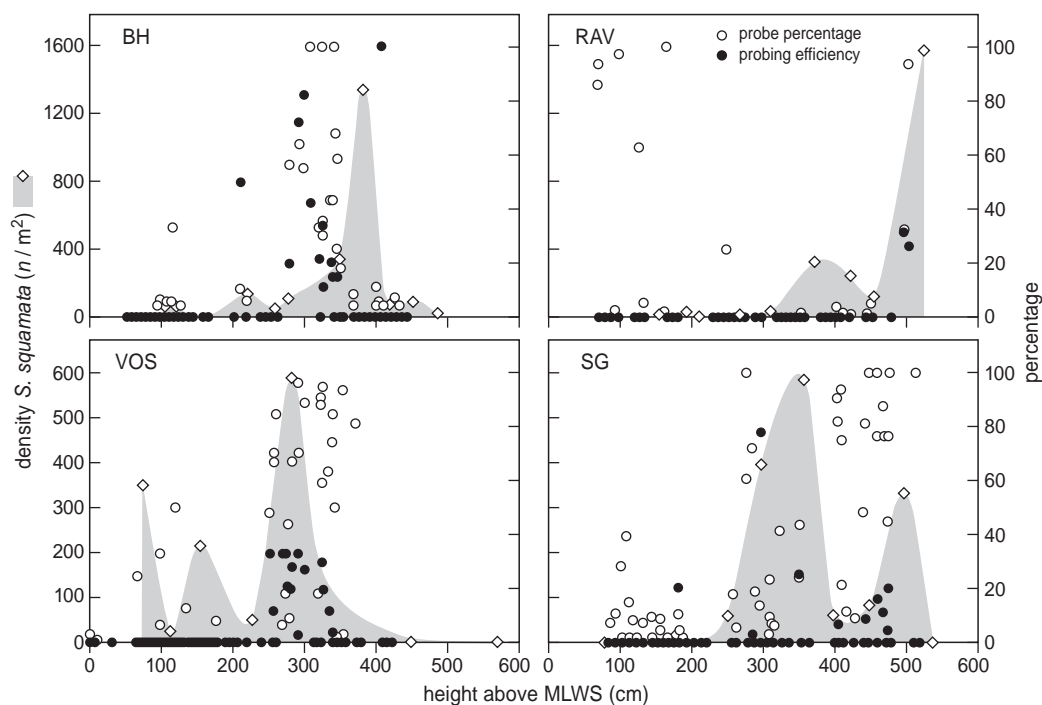


Figure 5. Probe percentage and probing efficiency of foraging Sanderling in relation to height above mean low water spring level (MLWS) for four transects. Indicated are densities of *S. squamata* as measured in the same transects.

Table 3. Comparing the total number of polychaetes caught per tidal cycle and the number needed to cover daily energy needs.

Tidal stage (time after high tide)	Polychaetes caught per min	Polychaetes caught per tidal stage	
		A ^a	B ^b
0–2h05'	0.03	4.1	1.8
2h05'–4h10'	0.14	17.2	4.9
4h10'–6h15'	0.02	2.1	2.1
6h15'–8h20'	0.02	2.8	2.1
8h20'–10h25'	0.29	36.8	29.7
10h25'–12h30'	0.74	93.1	29.7
Total number of polychaetes per tidal cycle		156.1	70.3
Number of polychaetes required to cover daily energy needs		1735–7650	
Energy need covered by polychaete intake		2.0–9.0%	0.9–4.0%

^aAssuming all individuals forage throughout the tidal cycle.

^bAssuming bird presence in transects (Fig. 3) reflects foraging activities (for example, 100% of birds are foraging at 4h10'–6h15' and only 32% at 10h25'–12h30').

polychaetes may fulfil 2.0–9.0% of the bird's daily energy demand per tidal cycle. When the tidal-dependent variation in foraging activity is considered (Fig. 3) an even smaller percentage of the energy needs is covered (Table 3).

DISCUSSION

Of the identified prey items, polychaetes were the most numerous, followed by wrecked bivalves. Apart from these resources, Sanderlings took advantage of each possible food source that came available. Several times, they were observed pecking on insects washed ashore or cleaning out broken mussel shells left by Oystercatchers. The diet composition as found in our study is comparable to diet descriptions in literature (Smit & Wolff 1981, Cramp 1983, Glutz von Blotzheim *et al.* 1984, Perez-Hurtado *et al.* 1997, van de Kam *et al.* 1999, Petracci 2002, Leopold *et al.* 2004, Nuka *et al.* 2005, van Turnhout & van Roomen 2005). Only amphipods and isopods, which stand out as prey in stomach and dropping analyses, are lacking. As amphipods and isopods are abundant on Belgian beaches (Degraer *et al.* 1999, 2003, Van Hoey *et al.* 2004) they may have been missed in our direct field observations.

Polychaetes were captured almost exclusively through probing at intertidal zones above 2.5 m above MLWS. Most probably these worms belong to the species *S. squamata*, since this is the only polychaete occurring in significant densities at the upper intertidal area of Belgian beaches. Moreover, faecal samples collected around high water in March 2006 exclusively

held chaetae of *S. squamata*. Throughout the year, the higher intertidal areas hold densities of several hundreds or thousands of individuals/m² (Degraer *et al.* 1999, 2003, van Hoey *et al.* 2004, Speybroeck *et al.* 2007, Van Ginderdeuren *et al.* 2007). There seems to be limited seasonal variation in *S. squamata* densities, and numbers drop to a minimum during autumn to build up throughout winter and spring. Other studies show a lower density and biomass in March compared to September (Degraer *et al.* 1999). There is a slight inter-annual variation in *S. squamata* densities (Speybroeck *et al.* 2007, Souza & Borzone 2000).

Although abundant, *S. squamata* provided no more than 10% of the daily energy need of Sanderlings, and when considering the apparent time that Sanderlings were roosting, this value was as low as 4% (Table 3). However, we regard this as minimal estimates of the importance of polychaetes. First, because it is likely that Sanderlings select for the most profitable prey and ignore the smaller, as other waders do (Sutherland 1982, Zwarts & Wanink 1984, Thompson *et al.* 1986, Meire 1993, Hulscher 1996). Individual *S. squamata* weigh up to 10 mg AFDW (Dankers *et al.* 1983; Mooij, unpubl. data), which is more than three times the maximum mean weight that we used in this study. Secondly, Sanderling can double the intake of polychaetes by nocturnal foraging (waders, including Sanderlings, are known to forage at night – Burger & Gochfeld 1991, Rohweder & Baverstock 1996) and exploiting polychaetes during both tidal cycles.

When simulating food intake based on *maximum* observed capture rates of polychaetes (6 polychaetes per min) and assuming selective feeding on the largest polychaetes, we estimate that less than three hours of foraging would be enough to satisfy daily energy requirements. However, such high intake rates were observed rarely (0.5% of all individuals) and on average, successful foraging on polychaetes was limited to 40 minutes per rising tide, which can be explained from the worms' biology. Since *S. squamata* occurs at the upper intertidal area, it is buried in the sediment and unavailable to Sanderlings during most of the tidal cycle. When the rising tide reaches their burrows, the worms start feeding at the surface and do become available to foraging Sanderlings. Accordingly, successful probing was restricted to the short period when the rising tide crossed the narrow zone where *S. squamata* occurs in peak densities (Fig. 5). Probing for polychaetes mainly occurred close to the water line where penetrability of the sediment is highest and foraging cost lowest (Perkins 1958, Myers *et al.* 1980, Pienkowski 1981, Grant 1984, Mouritsen & Jensen 1992).

Strikingly, feeding activity of Sanderlings was lowest during high tide, when worms were well available. Hence the numbers of foraging Sanderling present on the beach (Fig. 3) showed no relationship with the intake rates that Sanderling achieved when feeding on polychaetes (Fig 4A) ($r = -0.26$, $n = 6$, ns). We therefore hypothesise that due to the restricted, tidal-dependent availability of polychaetes, these worms are of minor importance to Sanderlings foraging on Belgian beaches. Rather than being staple food, polychaetes seem a secondary choice only exploited by Sanderlings that continue foraging during high tide.

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SAMENVATTING

De aantallen Drieteenstrandlopers *Calidris alba* en hun foeragegedrag werden onderzocht op vijf verschillende stranden langs de Belgische kust. De aandacht ging hierbij onder meer uit naar het belang van de Gemshoornworm *Scolecopsis squamata* (een borstelworm) in het menu. Gemiddeld bevonden zich op de stranden 10,0 Drieteenstrandlopers per strekkende kilometer. Hiervan was 87,8% actief met voedsel zoeken. De grootste aantallen strandlopers waren aanwezig van 2 uur voor tot 4 uur na laagwater. Er werd onderscheid gemaakt tussen twee foerageermethoden: het boren naar borstelwormen en het pikken naar aangespoeld organisch materiaal. Aanspoelsel (vooral kleine insecten en aangespoelde schelpdieren) werd gedurende de hele getijdencyclus opgepikt. Daarentegen werden borstelwormen in een korte periode rond hoogwater gepikt. Op dat moment bereikt het water de zone waar de Gemshoornwormen in hoge dichtheden voorkomen. Een schatting gebaseerd op onze waarnemingen geeft aan dat borstelwormen elke getijdencyclus voorzien in 2–9 % van de dagelijkse energiebehoefte van een Drieteenstrandloper. Het belang van wormen in de energievoorziening van de Drieteenstrandlopers in België lijkt dus beperkt te zijn. Deze veronderstelling wordt versterkt door de waarneming dat de strandlopers het minst actief zijn in de periode dat ze de wormen het gemakkelijkst kunnen pakken.

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