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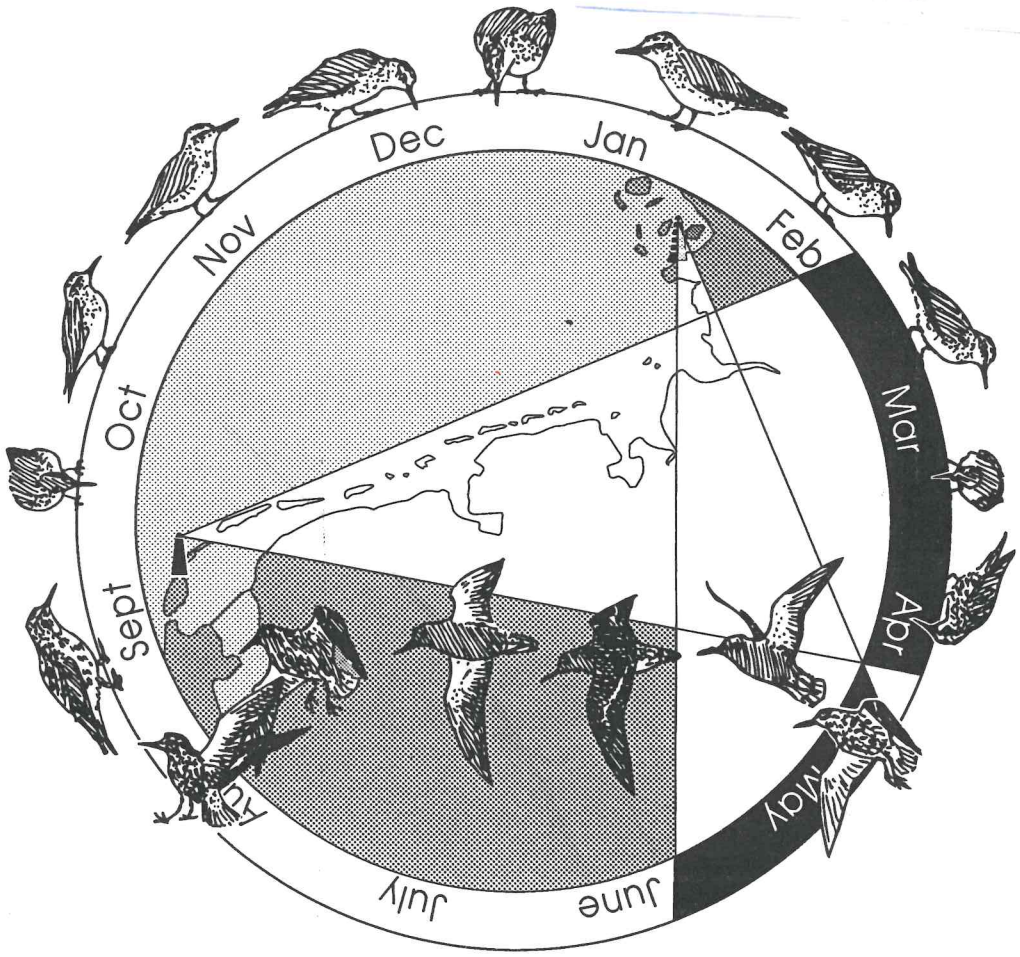
PREMIGRATORY FATTENING IN KNOTS: FOOD CONDITIONS, FEEDING TIME AND INTAKE RATES

INGRID TULP AND YVONNE VERKUIL



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PREMIGRATORY FATTENING IN KNOTS: FOOD CONDITIONS, FEEDING TIME AND INTAKE RATES

M.Sc. Study

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ABSTRACT

We studied the food supply and feeding behaviour of two subspecies of Knot (*Calidris canutus islandica* and *Calidris canutus canutus*) during the (pre)migratory (re)fuelling period in the Wadden Sea. *Islandica* was studied in March and April 1990 on Texel, The Netherlands, and *canutus* in May 1990 at Westerhever, Schleswig-Holstein, Germany. Faeces analyses showed that the diet of knots consisted of *Hydrobia ulvae* and *Macoma balthica*. Average biomasses of the two prey species *Hydrobia* and *Macoma* were 1.91 resp. 2.32 g AFDM m^{-2} on Texel and 17.14 resp. 3.87 g AFDM m^{-2} at Westerhever. The contribution of *Macoma* to the diet increased from 20 % to 50-100 % of the total AFDM per dropping when the biomass harvestable to knots increased from less than 1 to 2 g AFDM m^{-2} or more. Harvestable biomass increased due to the decrease in burying depth and the increase in body mass of *Macoma*. Knots selected size classes between 7-19 mm. Intake rates based on continuous observations of individual knots did not increase during the study period on Texel. Intakes rate in Westerhever were slightly higher. The values are relatively low and are probably underestimates. The biomass equivalent of the droppings increased significantly in the course of the period on Texel. But since measurements on defaecation intervals are lacking, no conclusions about actual intake rates are drawn. The foraging activities of knots during the middle part of the low water period did not change. We do not know whether they actively changed the length of the working day by using presumably, suboptimal, nocturnal feeding time, but as day length increased, the working time during day light hours also increased. The increasing prey harvestability and the longer days might have helped knots to increase energy uptake in the (pre)migratory period. In the discussion we point out that the considerable decrease in thermostatic costs in the course of spring permits the knots to spend an increasing amount of the energy intake on the accumulation of energy. Therefore we suggest that whether or not the knots manage to reach their optimal departure body mass, does not so much depend on increase in their energy intake, as well largely on the decreasing thermostatic expenses.

INTRODUCTION

The Wadden Sea is one of the major intertidal areas in northwest Europe that offers wintering and stopover possibilities to many wader species. Two subspecies of Knot (*Calidris canutus islandica* and *Calidris canutus canutus*) make use of the Wadden Sea and its food abundance during different periods. *C.c. islandica* arrive in autumn, from their breeding grounds in northeast Greenland and Canada, and stay throughout the winter in the Wadden Sea or move to the British estuaries or western France (Davidson & Wilson 1992). In late April/ early May they leave again for late spring staging areas: in western Iceland and northern Norway, from where they head north(west) to their breeding grounds approximately two weeks later (Davidson *et al.* 1986, Davidson & Wilson 1992, Morrison & Wilson 1992). Most *islandica* knots leave the Wadden Sea before the arrival of *Calidris canutus canutus*, which occurs in the first two weeks of May (Dick *et al.* 1987, Prokosch 1988, Piersma *et al.* 1992). *C.c. canutus* mainly visit the Wadden Sea coast of Schleswig-Holstein (Germany), but limited numbers occur for a short period on the west coast of France, in the Tejo Estuary in Portugal and in the Westerschelde in southwest Netherlands (Bredin & Doumeret 1987, Dick *et al.* 1987, Schekkerman *et al.* 1992). The *canutus* knots use the west European estuaries as refuelling sites on their way from the west and south African wintering areas to their breeding grounds in Siberia. Also on their way back south they interrupt their journey in western Europe and gain extra fuel stores to be able to make the last jump (Prokosch 1988).

Since knots depend entirely on only a few estuarine areas when migrating to and from their breeding grounds (Piersma 1987a), the food supply of the Wadden Sea clearly plays an important role in balancing the yearly energy budget of both knot species. In this report we will focus on the premigratory period of *islandica* knots in the Dutch Wadden Sea and of *canutus* knots in the German Wadden Sea. To be able to fly to the breeding grounds, knots have to store large fuel deposits. To find out how knots manage to gain enough energy stores, we made a distinction between several variables that might enable them to do so. The different possible pathways, eventually leading to mass gain (Fig.1), can at the first three branchings be divided in an active factor that can change due to the birds' effort and a passive factor that changes independently of the birds' effort and concerns the food conditions and the length of the daylight period. To gain mass a knot has not only to balance its budget, but has to end up with a positive balance at the end of the premigratory period. Therefore either its income must increase, or its expenses decrease. In other words, knots eat more per day, or pay less energy for thermoregulation and activity. Increasing air temperatures in the course of spring might reduce the costs of thermoregulation (Wiersma & Piersma 1993).

In our study we have concentrated on the income side of the energy budget. If daily energy intake does increase, this can be the result of either eating longer or eating more. The change in length of the working day can be a result of the knots' effort, in the sense that they can increase their feeding time during the low tide period or use suboptimal feeding time (e.g. night time feeding, shown by Zwarts *et al.* 1990a for knots wintering on the Banc d'Arguin, Mauritania), or just can be a result of longer daylength itself. Knots can increase their intake rate (=prey eaten per unit time) by changing their feeding behaviour, only when the behaviourial factors determining intake rate (such as encounter rate and handling time) are not already at maximum (Goss-Custard & Charman 1976, Piersma 1987b). Increase in intake rate can be facilitated if food resources increase and more prey become harvestable (*sensu* Zwarts *et al.* 1992). The harvestable proportion of the total food supply depends on the density, but also on the accessibility (burying depth) of the prey. The main prey species recorded for knots are *Macoma balthica* (Prater 1972, Goss-Custard *et al.* 1977a, Zwarts & Blomert 1992, Zwarts *et al.* 1992, Dekinga & Piersma 1993, Nehls 1993), *Cerastoderma edule* (Goss-

Custard 1977, Poot & Roelen 1992, Nehls 1993), *Mytilus edulis* (Prater 1972, Summers 1981, Alerstam *et al.* 1992, Nehls 1993) and other bivalve species (Piersma 1991, Tulp & de Goeij 1993), *Hydrobia ulvae* (Prater 1972, Dekinga & Piersma 1993, Nehls 1993) and *Littorina* spp. (Prater 1972, Summers 1981, Alerstam *et al.* 1992). In the (Dutch and German) Wadden Sea *Macoma*, *Hydrobia* and *Cerastoderma* make up the predominant part of the knots' diet. Since knot swallow prey whole, they can only handle a limited range of the bivalve size classes present (Zwarts & Blomert 1992). The upper threshold is limited by the size of their gape width, while the profitability of the prey determines the lower threshold. Unlike *Cerastoderma*, which lives at or just underneath the mudsurface, *Macoma* lives buried in the sediment. Since knots find their prey by probing in the mud, the length of their bill limits probing depth. The burying depth of *Macoma* changes over the seasons (Reading & McGrorty 1978, Zwarts & Wanink 1989) and can therefore strongly influence the fraction that is accessible to knots (Zwarts & Wanink 1991, Zwarts et al. 1992). The activity of prey is also liable to change, due to variations in the tidal cycle or temperature. To what extent an increased prey activity facilitates intake rate in the case of knots feeding on *Macoma* or *Hydrobia* is not known. Zwarts & Esselink (1989) measured highest feeding rates of Curlews *Numenius arquata* in spring, when the surface activity of their prey, *Nereis diversicolor* is high.

In this report we try to quantify each of the factors as described above (summarized in Fig.1) and evaluate which of these factors played a role in the premigratory fattening of the knots in the situation and the period studied.

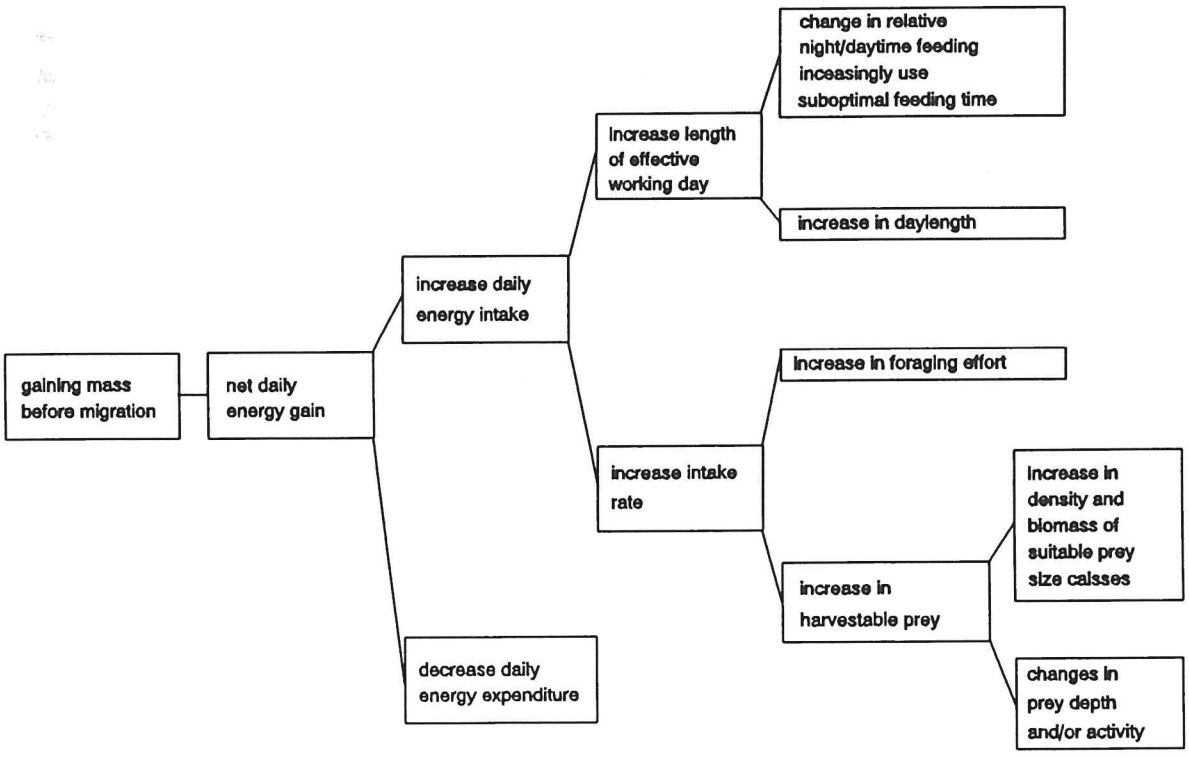

Fig.1. Scheme of possible pathways leading to mass gain in the period prior to migration.

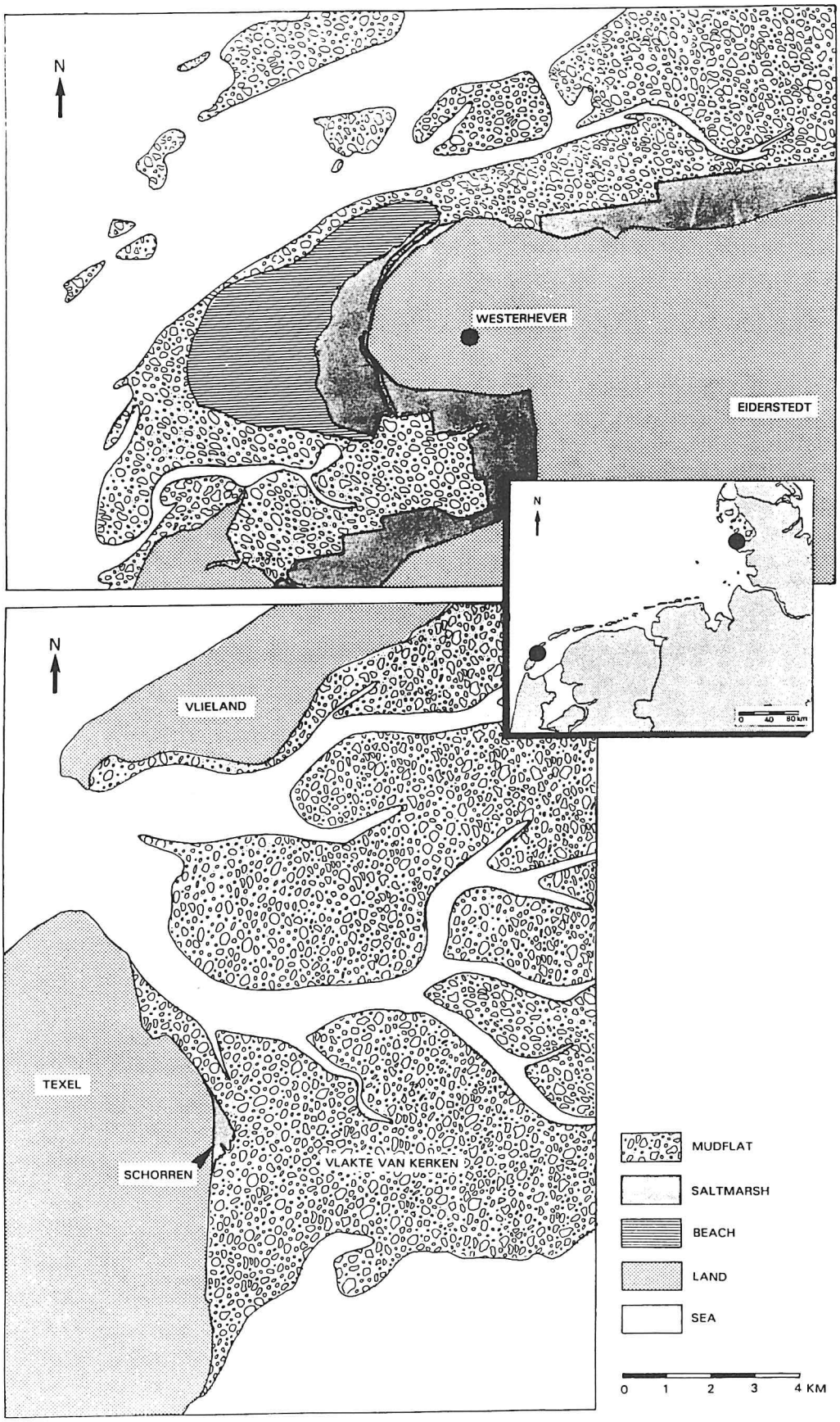

Fig.2. Map of the fieldwork areas situated in the German and Dutch Wadden Sea. Scales in both maps of the field work areas are identical.

STUDY AREAS

The fieldwork was carried out on the mudflats northeast of Texel named 'de Vlakte van Kerken'(53°21'N, 4°48'E) and in the intertidal area of the Eiderstedt peninsula of Schleswig-Holstein (Germany) north and northwest of Westerhever (54°26'N, 8°38'E)(Fig.2). Data were collected during spring 1990: from 14 February until 3 May on Texel and from 5 May until 2 June in Schleswig-Holstein.

'De Vlakte van Kerken' is the most western part of the Dutch Wadden Sea and makes up 40 km^2 of the total of 2500 km^2 Dutch tidal area. A dyke, which forms the eastern coastline of Texel forms the border of the tidal area. After the building of the dyke a natural saltmarsh ('De Schorren') has developed next to the dyke, which is used as a high tide roost. Another possible roosting place is Vlieland, the island next in row of the Wadden Sea isles, 7 km away. The tidal range in this area varies from 1-2 meter. At spring tide the mudflats sometimes do not become exposed, especially when combined with a (north)westerly wind. The opposite (the tidal flats stay exposed a complete tidal cycle) can occur at neap tide, and can be enforced by an easterly wind. The substrate is sandy and contains 3.5 % silt (< 50 μm).

The mudflats in Schleswig Holstein are part of an extensive intertidal area along the German coast. The study area covers about 20 km^2. Compared to the situation on Texel the strip of tidal flats and saltmarshes along the coast is much narrower. The silt fraction of the sediment amounts to 5 %. The saltmarshes are not shaped naturally, but are in fact land reclamations with a meadowlike appearance, drained by narrow channels and grazed by sheep. These saltmarshes are used by the waders as roosting sites at high tide. Also the sand beach in the intertidal area funtions as a roosting site.

METHODS

Densities and biomass of the benthic fauna were measured at sites were flocks of knots were seen foraging. Beside at these sites, samples were also taken on a few spots, which were rarely or never visited by knots (in total 16 locations on Texel, 7 at Westerhever, Fig.3). The sampling programme served to determine the density of benthic food stocks for knots and was restricted to the prey species: *Macoma balthica*, *Cerastoderma edule*, and *Hydrobia ulvae*. The density of bivalves was measured by randomly taking a series of 20 cores (dimensions: 181 cm^2x30 cm deep) from each spot. *Hydrobia* densities were determined by taking 5 cores, measuring 180cm^2x10 cm on each spot. The samples were sieved over a 1 mm mesh sieve for bivalves and 0.5 mm mesh sieve for *Hydrobia* in the field and gathered in labelled plastic bags. The bags were taken to the laboratory and the animals were sorted to species and size. The size distribution of the bivalves was measured. The animals were placed in crucibles and dried at 60°C for two days in a ventilated drying-oven. The crucibles were put in a dessicator with silica gel to cool. The weights of the crucibles+contents were determined. After incineration at 550°C the crucibles again were placed in a dessicator to cool, and weighed. The ash-free dry mass (AFDM) was calculated for each invertebrate group.

Another part of the sampling program concerned the depth distribution of *Macoma balthica*. At most of the sampling sites cores were taken from the sediment. The mud column was put vertically upon the sediment and with a knife or a ruler very thin slices were cut from it in vertical direction. Once a *Macoma* was exposed, the distance between the upper side of the *Macoma* and the surface of the sediment core was measured. The bivalves found and measured were put in plastic cubs labelled with the corresponding depth classes (0.0-0.5 cm, 0.5-1.0 cm, ... 4.5-5.0 cm, 5.0-6.0 cm, 6.0-7.0 cm,...11.0-12.0 cm). This was continued until about 50 *Macoma* were found. The

depth-specific bivalves were then put in plastic bags and sorted and measured per depth class in the lab. From each *Macoma* the inhalant siphon was removed, put in a platinum crucible, dried and ashed following the same procedure as described above (except for the drying period: in this case 1 day instead of 3). Animals were further treated the same way as animals from density samples (see Zwarts & Wanink 1989 for comprehensive method description).

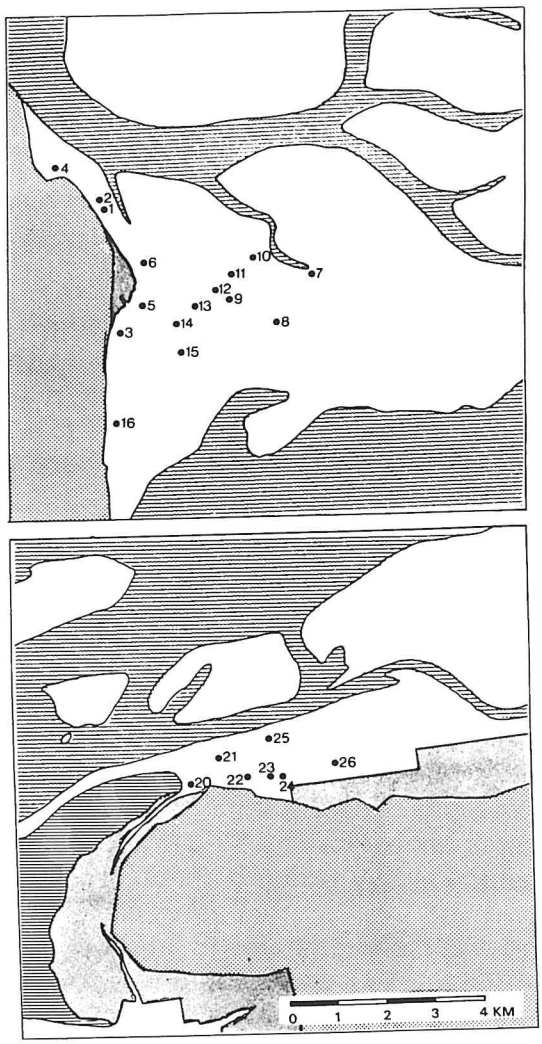

Fig.3. Location of sampling sites near Texel (upper panel) and Westerhever (lower panel).

Bird counts were carried out regularly. In this report results of low water maxima per day are presented.

During 28 (Texel) and 19 (Westerhever) low water periods, data on activity of knots were collected. Flocks of knots were followed as they left the roost and started foraging. The birds were observed with 10x40 binoculars and a 80x Questar mirror telescope. A group of knots was observed as long as possible. When one flock disappeared out of sight the same or a new group was tracked down and approached while walking on the mudflats. Every 15 minutes activity scans were made (in total 182 on Texel and 153 in Westerhever), during which the behaviour of about 100 knots of the group was scanned. Distinction was made between foraging, sleeping, preening,

running, walking, standing, and bathing.

Data on prey choice and intake rates were obtained during continuous observations on individual birds. A bird was observed constantly as long as possible (range 5-20 minutes), while recording the number of prey items eaten per unit time and, when possible, prey species and estimates of prey size. In total 651 (Texel) and 81 (Westerhever) minutes of continuous observation on 136 and 8 birds respectively were recorded. In Westerhever knots were almost exclusively foraging on *Hydrobia* (result from faecal analysis), which is too small a prey to see being swallowed. Only on 31 May we observed knots eating *Macoma*, so all observations on intake rates in Westerhever refer to that day. On Texel continuous observations were carried out during 18 low water periods. Knots were mainly foraging on *Macoma*, while *Hydrobia* formed an additional part of the diet. At a few instants a *Macoma* was rejected by a knot that was being observed. At such occassions we gathered the rejected bivalves, that were still laying on the mud surface after the group of knots had left the area. AFDM of these 'rejected' *Macoma* was measured according to the method described earlier.

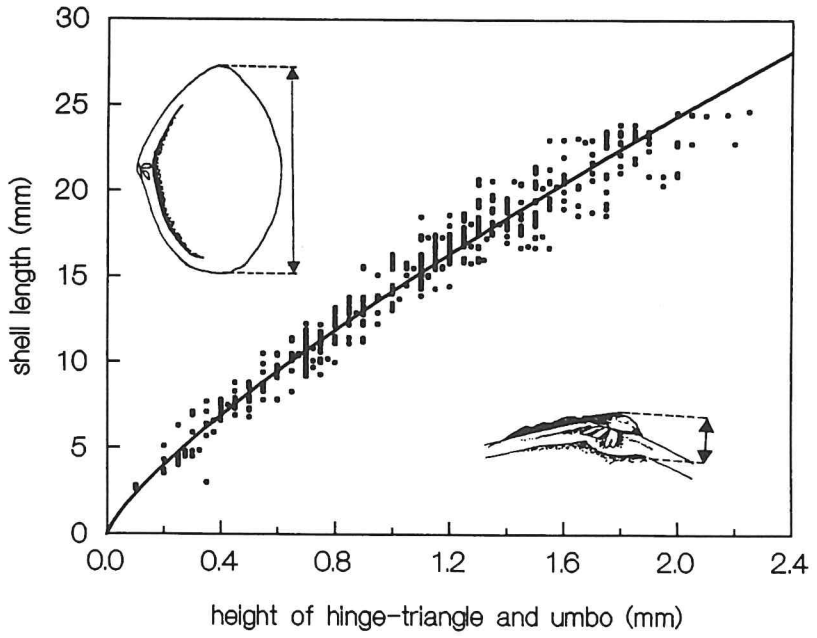

Fig.4. Regression of shell length (SL) on hinge + umbo (HU). The regression equation is given by: $SL = 14.143 \cdot HU^{0.786}$ (based on in total 510 measurements, by five observers, including the authors, from Dekinga & Piersma 1993).

As soon as a group of knots left an area where we had observed them foraging for at least half an hour, we collected a faeces sample of 50-100 droppings. In total 24 faeces samples were collected. The analysis of droppings was carried out according to the methods described by Dekinga & Piersma (1993). The samples were frozen and later dried in the laboratory at 60°C. After sieving over a 0.3 mm mesh, recognizable parts (intact or fragmented *Hydrobia ulvae* and hinges of *Macoma balthica*) were collected, using a binocular microscope. Shell size of eaten *Macoma balthica* was estimated from the hinges according to the regression equation given in Fig.4. The length of intact Hydrobia and the width of the last whorl of broken shells was measured. Of the latter the shell height (H) was reconstructed from shell width (W) according to the equation: $H = 1.729 \cdot W^{1.326}$. Since small *Hydrobia* are more likely to

pass the digestive tract undamaged we corrected the length of intact *Hydrobia* according to Dekinga & Piersma (1993). The shell fractions were selected to species and weighted. From shell mass, biomass equivalents (mg AFDM ingested per dropping produced) could be estimated using the formulas presented by Dekinga & Piersma (1993).

In this report we divided the complete two field work periods in 4 (Texel) and 2 (Westerhever) two week periods. Unless stated otherwise, the classification of the periods is as follows: period 1: 1-15 March, period 2: 16-31 March, period 3: 1-15 April, period 4: 16 April-3 May, period 5: 5-17 May, period 6: 18-31 May. Concerning period 4, the observations were continued until 30 April, while benthos sampling lasted until 3 May. Measurements of the waterlevel during the period on Texel were obtained from Rijkswaterstaat in Den Burg (Texel) (measured at Oudeschild, Texel, 53°9'N, 4°41'E, 10 km south of the study area). Statistical analyses were carried out using Systat 5.0 (Wilkinson 1990). Meteorological data were obtained from the KNMI at De Bilt. The measurements taken at De Kooij were used in the calculations on thermostatic costs on Texel and at Westerhever.

RESULTS

Presence of knots and movements in response to the tide

The numbers present on Texel in spring are given in Fig.5. In early April numbers of knots increased rapidly. This influx of birds can be due to early spring movements of birds that have spent the winter in the English estuaries (Wash, Teesmouth, Firth of Forth, Moray Firth, west coast), the Dutch delta and western France (Davidson & Wilson 1992). By the end of April all of the (*islandica*) knots had left, which is rather early compared to other studies (Prokosch 1988, Davidson & Wilson 1992, Swennen 1992).

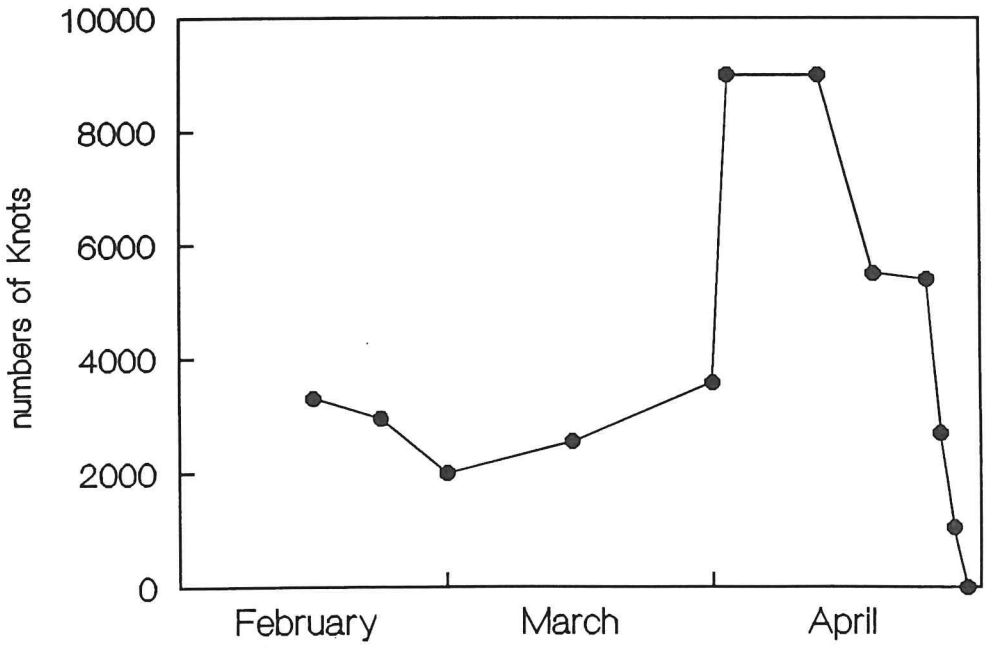

Fig.5. Number of knots on the Vlakte van Kerken on Texel in the course of spring 1990.

On 8 and 9 May, the first days of the fieldwork period at Westerhever, we saw flocks of knots depart in a northwesterly direction (Piersma *et al.* 1991). According to Prokosch (1988) most of the *islandica* knots leave in the first two weeks of May. By mid May groups of *canutus* knots, judged from timing of arrival and slimmer appearance, arrived, probably coming from their African wintering areas (Piersma *et al.* 1992). Throughout the rest of the study period the number of knots remained constant at 2000-3000 inidividuals. On 28, 29 and 30 May we recorded the first departures of *canutus* knots, taking off for the northeast, the direction of Siberia.

On Texel knots roosted at the saltmarsh area next to the dyke and after high tide flocks could often be seen flying in from Vlieland, where they probably also had been roosting (Fig.1, Fig.6). On a few occasions, when even the saltmarsh became flooded at high tide, knots roosted at the inner side of the dyke. From their roosting sites they first visited the highest part of the mudflats just offshore and when the water receded further, they followed the water's edge as indicated in Fig.6. Their main feeding areas were located about 5 km offshore near a gully. At spring tides, large areas east of this gully became exposed and most of the knots could be seen foraging there.

In Westerhever the situation was better surveyable. Knots roosted on the saltmarshes indicated in Fig.6, and/or came flying in from saltmarsh areas further east. During the complete low tide period they stayed on the narrow strip of mudflat up to a few hundred meters offshore. Only on rare occasions they moved to areas further north.

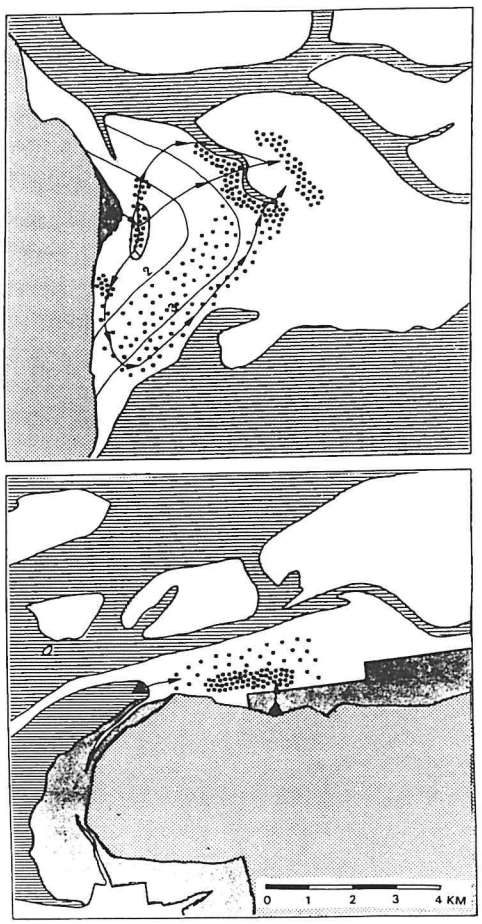

Fig.6. Dispersal of knots over the mudflats during low tide at the two study sites, Texel (left panel) and Westerhever (right panel). Triangles represent the locations of high tide roosts. Arrows indicate movements of knots following the receding water. Numbers indicate the different heights of the tidal flat. The higher the value, the shorter the area stays exposed. The tidal flat, visited by the birds in Westerhever was narrow and with little relief. The density of dots corresponds with the frequency and intensity of visits by knots.

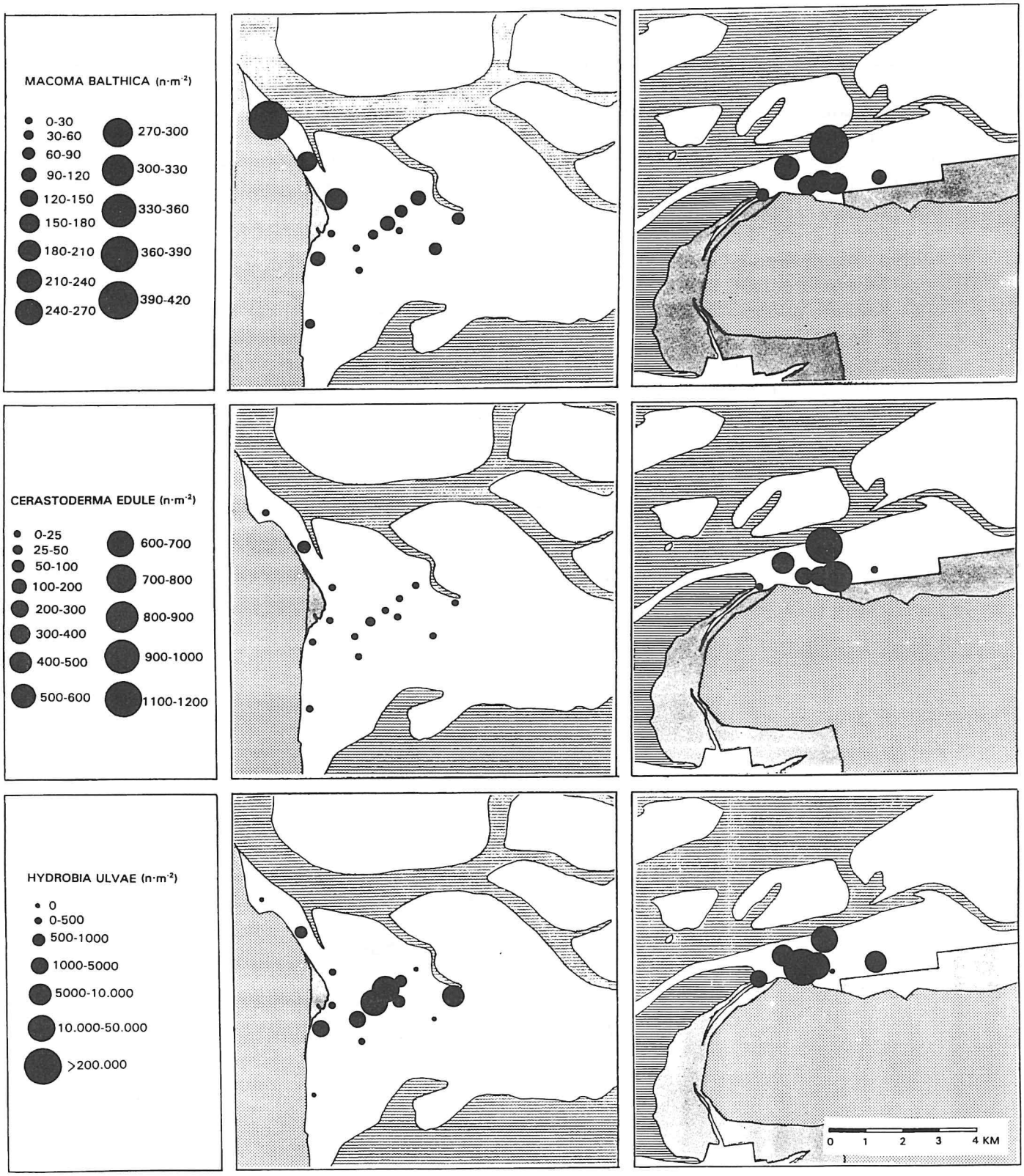

Fig.7. Densities of *Macoma balthica*, *Cerastoderma edule* and *Hydrobia ulvae*. Densities presented are mean values for the whole study periods, in March and April on Texel (left panels) and in May in Westerhever (right panels).

Densities of benthic prey species

The most abundant molluscs on Texel and in Westerhever were *Macoma balthica*, *Cerastoderma edule* and *Hydrobia ulvae* (Fig.7). The numbers of bivalves and mudsnails per square meter on Texel are average values for March and April, the period *islandica* was studied. The average numbers per square meter given for Westerhever are measured in May, the stopover period of *canutus*. The cockles present on Texel and in Westerhever were too large to be ingested by knots (captive knots seldom took cockles over 10 mm long (Goss-Gustard 1977a) and 12 mm is the upper size threshold according to Zwarts & Blomert (1992). So the main prey species for knots on Texel and in Westerhever were *Macoma* and *Hydrobia*. Average biomass of *Macoma* on Texel was 2.32 g AFDM m^{-2} (range 0.08-10.78 g AFDM m^{-2}). The annual average along the Frisian coast, in the eastern part of the Wadden Sea is 17.22 g AFDM m^{-2} (Zwarts *et al.* 1992). Biomass of *Macoma* in March 1990 on the Balgzand, a mudflat area south of De Vlakte van Kerken, was 2.94 g AFDM m^{-2} (average of 50 samples along a transect, range 1.0-5.0 g AFDM m^{-2}, Beukema, pers. comm.). Average biomass of *Macoma* in Westerhever was less variable and higher, 3.87 g AFDM m^{-2} (range 0.62-7.04). Average biomass of *Hydrobia* on Texel was 1.91 g ADFM m^{-2} (range 0-17.39), at Westerhever it was no less than 17.14 g AFDM m^{-2} (range 0-93.73).

Table 1. Densities and biomass of *Macoma balthica* on Texel. Densities in n m^{-2}, biomass (in brackets) in g m^{-2}. Plots where knots were seen foraging are indicated with a *. In Fig.3 the locations of the plots are given.

plot		period 1		period 2		period 3		period 4	
1	*	239	(2.5)			117	(1.6)		
3	*	147	(2.8)			54	(1.6)		
4		677	(4.7)					128	(3.2)
5		46	(0.5)			11	(0.3)		
6	*			90	(1.3)			272	(10.8)
7	*			71	(1.5)			82	(6.3)
8	*							71	(4.2)
9				14	(0.4)			22	(1.0)
10	*					87	(1.6)	150	(5.1)
11	*					125	(7.4)	49	(1.9)
12	*					106	(2.8)	125	(7.1)
13						52	(1.5)	33	(1.3)
14						14	(0.4)	16	(0.6)
15						22	(0.8)	16	(0.8)
16	*					3	(0.1)	63	(4.7)

Table 2. Densities and biomass of *Hydrobia ulvae* on Texel. Densities in n m^{-2}, biomass (in brackets) in g m^{-2}. Plots where knots were seen foraging are indicated with a *. In Fig.3 the locations of the plots are given.

plot		period 1		period 2		period 3		period 4	
1	*	0	(0.0)			1785	(1.5)		
3	*	0	(0.0)			2644	(1.0)		
4		0	(0.0)					0	(0.0)
5		0	(0.0)			1012	(1.7)		
6	*			337	(0.5)			0	(0.0)
7	*			5898	(1.4)			10849	(4.3)
8	*							0	(0.0)
9				0	(0.0)			1371	(0.5)
10	*					0	(0.0)	0	(0.0)
11	*					0	(0.0)	1251	(0.3)
12	*					33384	(9.5)	18585	(7.4)
13						19402	(6.2)	47835	(17.4)
14						501	(0.8)	5136	(2.4)
15						87	(0.1)	816	(0.4)
16						0	(0.0)	0	(0.0)

Table 3. Densities and biomass of *Macoma balthica* in Westerhever. Densities in n m^{-2}, biomass (in brackets) in g m^{-2}. Plots where knots were seen foraging are indicated with a *. In Fig.3 the locations of the plots are given.

plot		period 5		period 6	
20				71	(0.8)
21	*	220	(3.8)	218	(4.5)
22	*	177	(2.6)		
23	*	212	(5.5)	171	(4.3)
24	*	193	(5.5)		
25	*			302	(7.0)
26				73	(0.6)

Table 4. Densities and biomass of *Hydrobia ulvae* in Westerhever. Densities in n m^{-2}, biomass (in brackets) in g m^{-2}. Plots where Knots were seen foraging are indicated with a *. In Fig.3 the locations of the plots are given.

plot		period 5		period 6	
20				1926	(1.1)
21	*	14995	(7.7)	522	(0.4)
22	*	220783	(93.7)		
23	*	33645	(10.1)	68868	(22.7)
24	*	0	(0.0)		
25	*			27280	(15.0)
26				8041	(3.5)

Not all sampling plots were equally frequently visited by knots (see Fig.3 and 6). In Table 1-4, frequently visited plots are indicated with an asterisk. While we have rarely seen knots foraging on plots 1, 2 and 4, although these plots have high prey densities, knots probably preferred the most quiet plots (as far as possible from the dike) to the plots with the highest food supply. No samples were taken in the area just across the gully, due to the inaccessibility by foot. But being a favourite spot to the knots (Fig.6) it might hold good food resources, unknown to us but maybe very useful to the knots. Although Zwarts *et al.* (1992) found that knots responded to differences in prey densities, on Texel no evident relation between distribution of the birds and food supply seems to exist. In Westerhever plot 26 was avoided, which is probably due to low densities of both *Macoma* and *Hydrobia*.

Not the total amount of this benthic prey stock is harvestable for knots, the proportion accessible (not too deep), ingestable (not too big) and profitable (not too small) can vary highly between locations and among seasons (Zwarts & Wanink 1989, Zwarts & Wanink 1991). The prey selection and prey depth distribution will be discussed to obtain insight in possible changes in amounts of harvestable prey during spring.

Prey size selection

The faeces analyses (Zwarts & Blomert 1992, Dekinga & Piersma 1993, this report) and the collected *Macoma balthica*, rejected by knots (Fig.22) showed that not all prey sizes were eaten. Knots select ingestable (not too big) and profitable (not too small) size classes. In our study areas, knots selected size classes between 7 and 19 mm (Fig.8). Taking the handling time into account, Zwarts & Blomert (1992) predicted that *Macoma* smaller than 6 mm should be rejected in order to maximize the intake rate. However, the actual lower acceptance threshold of knots along the Frisian coast was 9 mm. They argued that since knot are touch feeders the recognition time should be added to the handling time. Because small prey are more difficult to encounter, this would especially reduce the profitability of small prey. The lower size threshold ranged from 7 to 10 mm (Fig.8).

On Texel we found a relative increase in the density of *Macoma* size classes larger than 15 mm in the course of spring. In April only *Macoma* of 10-15 mm moved deeper, individuals larger than 15 mm predominantly remaining in the upper 3 cm of the mud (as will be discussed later, Fig.10 and 11). Simultaneously with this decrease in accessibility of the smaller half of suitable size classes in April and relative increase in the accessibility of individuals larger than 15 mm, also the upper size limit of the individuals selected by knots increased from 18 to 19 to 20 mm (Fig.8). In Westerhever the same size classes were selected in both periods (10-18 mm). The selection index of one size class depends on the relative densities of the various size classes accessible (Cayford and Goss-Gustard 1992). To show this dependency we calculated an expected selection, based on the frequency of size classes selected in the first two weeks of March divided by the frequency of accessible size classes in the period concerned. Comparing this expected selection with the selection index based on actually selected size classes in the period concerned (dashed line), it is evident that knots on Texel, forced by relative increase in abundance of larger *Macoma*, during the season changed their selection. In comparison with the tops of the expected selection-curves, the tops of the actually selected curves are wider and move in the direction of the larger size classes. In the last two periods more *Macoma* above 15 mm were selected than in the first period.

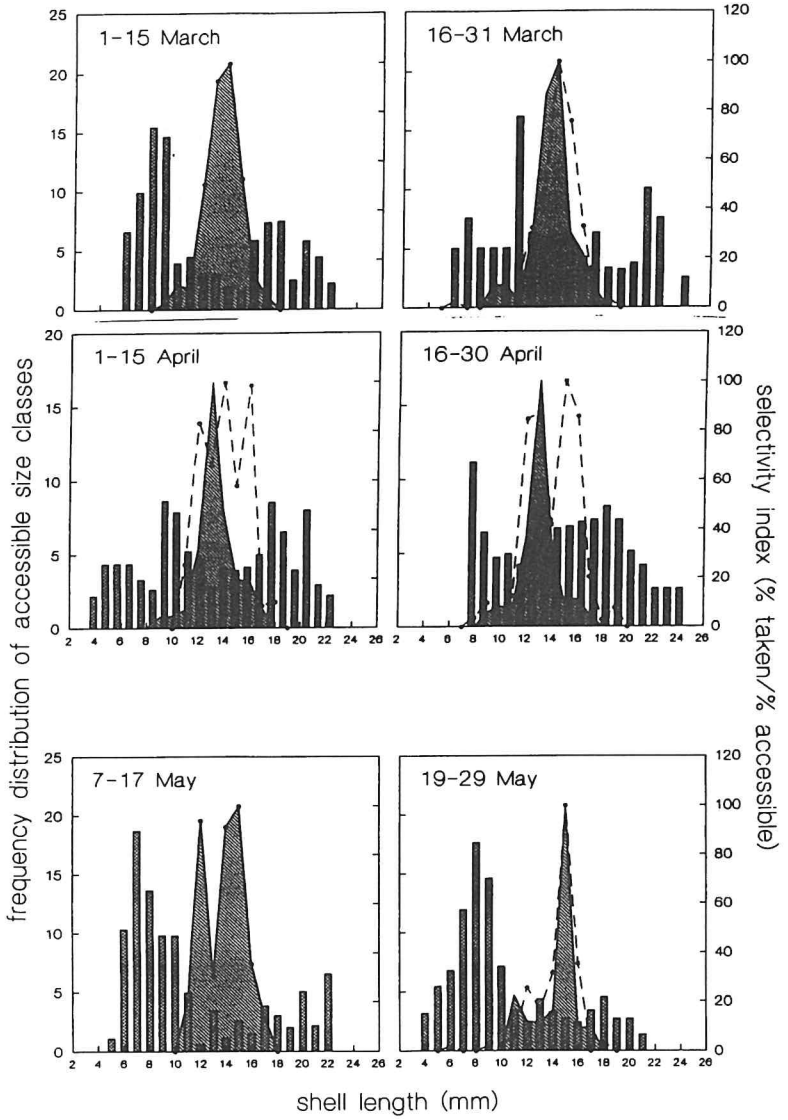

Fig.8. Selection of size classes of *Macoma balthica* reconstructed from hinge heights in the faeces samples. The bars indicate the size class distribution of accessible prey items. The expected selection (percentage of selected size classes in the first period divided by the precentage accessible size classes in the period concerned), is represented by the hatched area. The dashed line indicates the actual selection (frequency of the actually eaten size classes divided by the frequency of accessible size classes in the same period). The numbers in each panel indicate the different periods.

The size distribution of *Hydrobia ulvae* eaten, has been estimated by measuring the unbroken and broken shells. It is expected that the selected size classes will correspond to the size distribution of available size classes. Knots are not forced to select particular size classes of *Hydrobia*, since all available size classes are equally ingestable. Selection on larger size classes would increase the yield of foraging, but this is not observed in knots (Zwarts and Blomert 1992). However, knots on Texel seemed to select the larger size classes (Fig.9). On the other hand, in Westerhever knots seemed to select the smaller size classes. Since small *Hydrobia* pass the digestive tract undamaged, a larger proportion of small size classes is found among unbroken *Hydrobia* in the faeces than is actually ingested. To prevent an underestimation of prey sizes, measurable fragments of broken *Hydrobia* were also measured (Dekinga & Piersma 1993). Nevertheless, this has led to an underestimation of prey sizes for the faeces samples from Westerhever (if

we assume it is not very likely that knots selected *Hydrobia* smaller than 2 mm). *Hydrobia* in the faeces collected in Westerhever were more fragmented. Knots at Westerhever somehow crushed their prey more efficiently, because the large *Hydrobia* were broken more often than the smaller ones. And even the small snails were more often completely fragmented, so in the large amount of very small pieces hardly no measurable fragments could be found. In samples of 50 faeces from Texel on average 133.4 (SD 62.4) measurable fragments were found, in samples from Westerhever only 16.8 (SD 5.7). The amount of intact Hydrobia did not differ largely (Texel: n = 96.8, SD = 54; Westerhever: n = 122.8, SD = 29.2), but the intact *Hydrobia* were much smaller than in faeces from Texel. This may be the reason for the underestimation of prey sizes eaten at Westerhever. Presumably, *canutus* knots are accustomed to small prey and therefore have a tighter pylorus that leaves only the smallest items through undamaged (as hypothesized by Piersma, Koolhaas & Dekinga 1993).

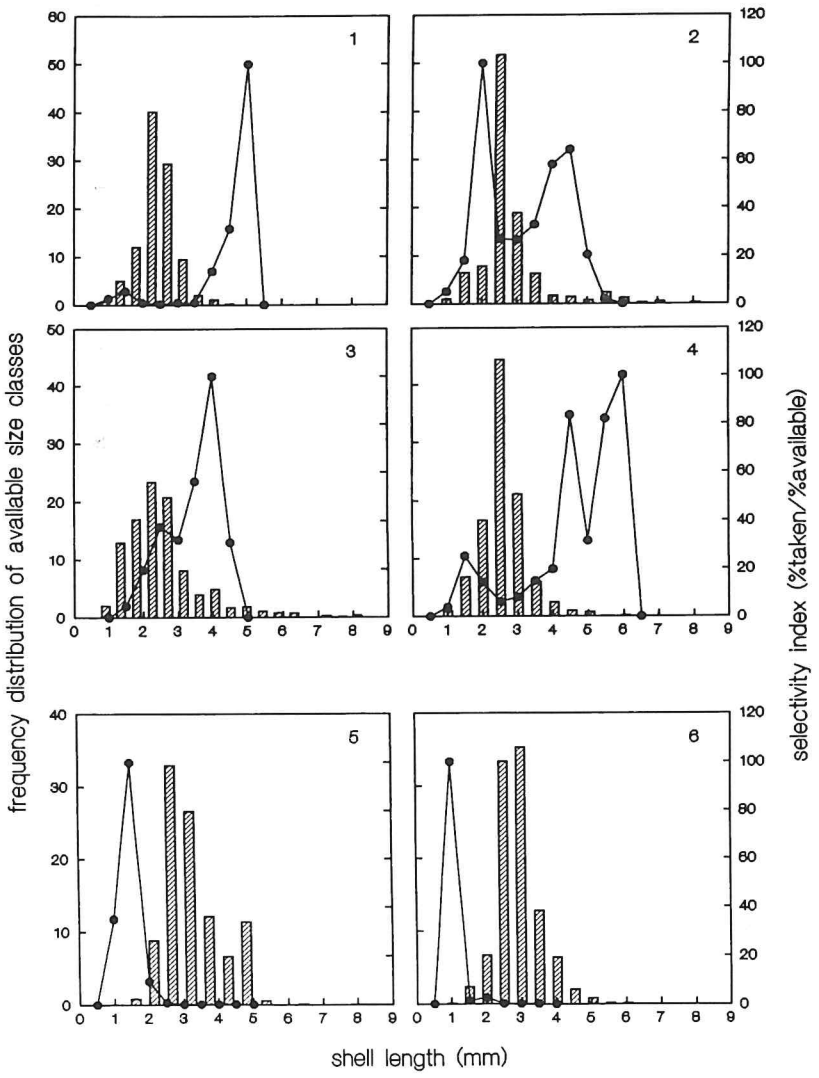

Fig 9. Selection of size classes of *Hydrobia ulvae* based on measured intact and broken *Hydrobia* in the faeces samples. The bars indicate the size class distribution of accessible prey items. The line indicates the selection (frequency of the eaten size classes divided by the frequency of accessible size classes). The numbers in each panel indicate the different periods.

Accessibility of prey to knots

Because *Hydrobia ulvae* lives at the surface or just buried in the upper 3 cm (Barnes 1981), all prey items sampled and given in Table 2 and 4 were considered to be accessible.

Macoma balthica lives buried beneath the surface at varying depths (until ± 10 cm, Reading & McGrorty 1978, Zwarts & Wanink 1991). The 3.5 cm long bill of a knot limits probing depth, so bivalves buried deeper than 3 cm will be out of reach of the knots' bill (Goss-Gustard *et al.* 1977a). Therefore the depth distribution of preferred prey of knots strongly affects the amount of harvestable prey. The proportion inaccessible *Macoma* varied between the periods, due to differences in burying depth of the bivalves (Fig.10). *Macoma* decreased its burying depth in spring. The same seasonal variation in burying depth was observed by Reading & McGrorty (1978) and Zwarts and Wanink (1989). The vertical migration of *Macoma* in spring on Texel coincided with the premigratory period of knots. *Macoma* moved closer to the surface in the second half of March so that the largest proportion of animals occurred in the upper 2 cm. In the second half of April burying depth became larger again (on average 3 cm). In June mean burying depth was 3.5 cm again (own obs.). At Westerhever, in the second half of May, *Macoma* also moved closer to the surface (Fig.11 and 12).

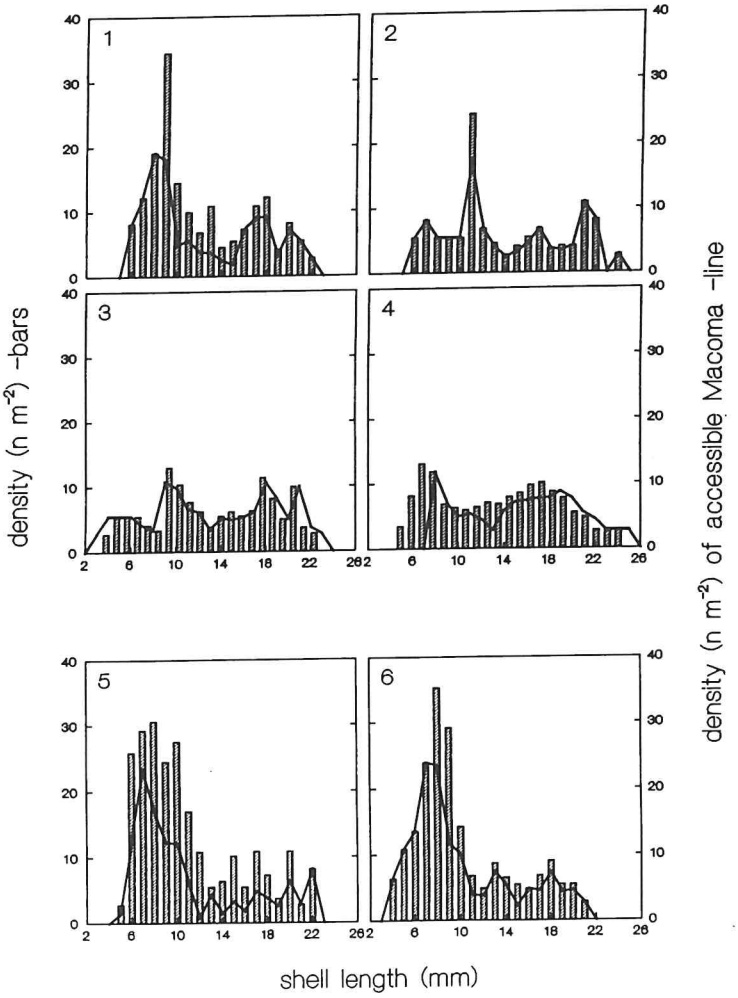

Fig.10. Frequency distributions of size classes of *Macoma balthica* present (bars). The solid line indicates the frequency distribution of size classes accessible to knots (present in the upper 3 cm of the mud). Numbers indicate the successive two week periods.

In all four periods, the mean depth of the suitable sizes classes (10-18 mm) is somewhat larger than the overall mean depth (Fig.13). Since larger *Macoma* generally bury deeper than smaller ones (Reading & McGrorty 1978), and since depth remains the same for all animals >10 mm, this seems to be a normal pattern (Zwarts & Wanink 1989). Nevertheless, we did not find all suitable size classes on equally accessible depths (Fig.11); the larger *Macoma* tended to be buried more superficially. On 7 of 12 sampling dates on Texel, this negative correlation between shell size and burying depth was significant (Table 5a). For the suitable size classes (10-18 mm), the negative relation between burying depth and shell size was significant in period 1 and period 3 (Fig.11, Table 5b). Hulscher (1983) also found this inverse relationship between shell length and burying depth. He supposed that these larger individuals were infected with trematodes. So the harvestable proportion of *Macoma* varies per shell length class. In our case, a larger proportion of the large (≥ 15 mm) size classes was accessible than of the small (<15 mm) size classes (Fig.11). Possibly this is also the case in Westerhever (Fig.11) although no significant (negative) relationship between burying depth and shell size could be found (Table 5a,b).

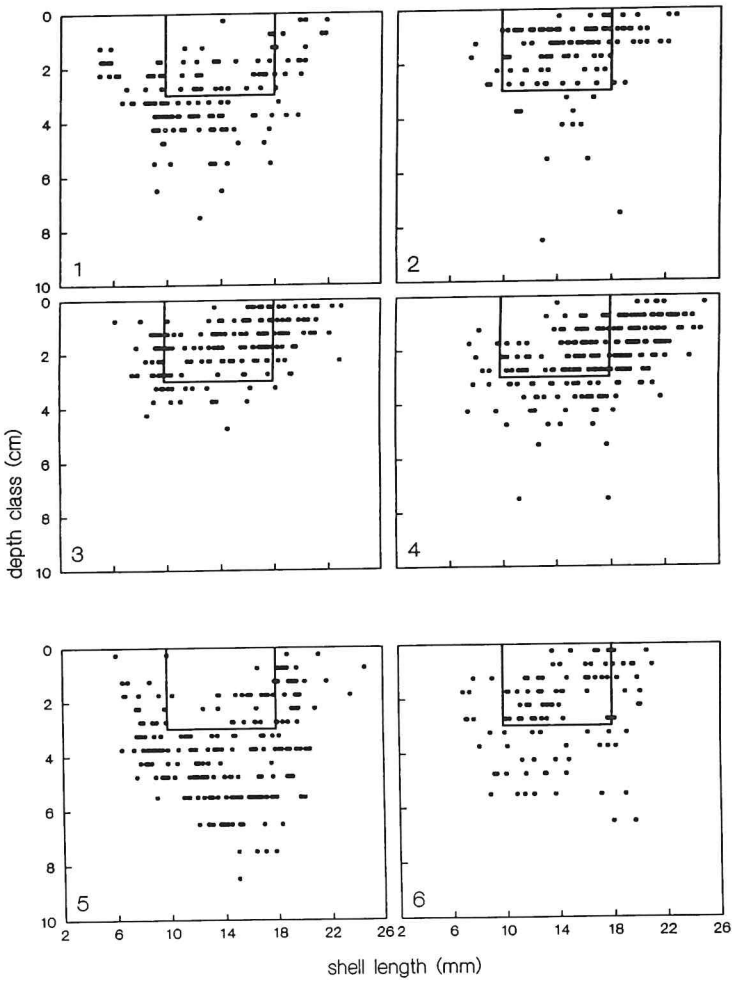

Fig.11. Depth and size distribution of *Macoma balthica*. The boxes indicate the part of the total *Macoma balthica* present, which is accessible (not too deep), ingestible (not too big) and profitable (not too small) for knots (n for the successive periods: 135, 125, 160, 228, 207 and 87). On 30 % of the sampling days (3 days per period) at Texel, a significant negative correlation between burying depht and shell length (adjusted for siphon mass) was found (see Table 5a). For the suitable size classes (10-18 mm) this negative correlation was significant in period 1 and 3 (see Table 5b). In May in Westerhever no significant correlation was found.

Table 5a. Results of multiple regression analyses to test the correlation between shell length, siphon mass and burying depth of *Macoma balthica*. The model used is $\ln(\text{depth}) = a + b \cdot \text{shell lenght}^2 + c \cdot \text{sipnon mass}^2 + \text{date}_i + \text{shell length}^2 \cdot \text{date} + \text{shell length}^2 \cdot \text{siphon mass}^2 \cdot \text{date}$. To avoid intercorrelation between the variables shell length and siphon mass, a principal components analysis was carried out. The factors derived from this analysis, shell length^2 and siphon mass^2, were used in this model. The tests on the homogeneity of slopes for period 1-4 (Texel) and period 5-6 (Westerhever) showed that the shell length^2·date interaction and the siphon mass^2·date interaction were both significant on Texel ($p = 0.001$ and $p = 0.049$, $n = 648$). Concerning the periods 5-6, only the siphon mass^2·burying depth relation differed significantly among dates ($p = 0.269$ and $p = 0.018$, $n = 266$). To test the relation between shell length^2, siphon mass^2 and burying depth, multiple regressions were carried out separately per sampling date. In these tests all shell length classes of *Macoma* were selected (A). A dash indicates that a variable was not involved in the regression, or that none of the variables correlated significant with burying depth. Levels of significance: *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$

sampling date		period	R^2	siphon mass^2 p	shell length^2 p	ANOVA sign. level	n
March	6	1	6.8	0.049	-	*	44
	7	1	18.2	0.005	0.134	**	44
	12	1	47.0	-	0.001	***	47
	14	1	67.3	0.001	0.001	***	37
	16	2	16.3	0.042	0.031	*	33
	26	2	40.6	0.001	-	***	55
April	2	3	25.2	0.008	0.008	***	43
	11	3	21.6	0.001	-	***	65
	13	3	5.8	0.047	-	*	52
	30	4	5.7	0.048	-	*	52
May	1	4	26.6	0.001	0.145	***	107
	3	4	31.0	0.001	0.125	***	69
	10	5	8.4	0.025	-	*	49
	13	5	0.0	-	-		46
	14	5	57.2	0.001	-	***	48
	17	5	0.0	-	-		64
	20	6	25.0	0.022	0.117	**	40
	25	6	42.2	0.001	-	***	47

Table 5b. Results of multiple regressions of shell length^2, siphon mass^2 on burying depth of *Macoma balthica*, tested for the suitable size classes for Knots (10-18 mm). Sampling data were lumped per period. Multiple regressions were carried out per period. A dash indicates that a variable was not involved in the correlation, or that none of the variables correlated significantly with burying depth. Levels of significance: *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$

period	R^2	siphon mass^2 p	shell length^2 p	ANOVA sign. level	n
1	9.7	0.022	0.012	**	86
2	13.4	0.001	-	***	100
3	20.3	0.001	0.003	***	115
4	4.7	0.007	-	**	133
5	22.5	0.001	0.114	***	128
6	33.4	0.001	_	***	71

The change in burying depth of suitable size classes for knots on Texel is significant ($p=0.001$, $n=378$, only suitable size classes, 10-18 mm, considered). To test this we carried out an analysis of covariance. See Table 5a for explanation of the model we used. The assumption of homogeneity of slopes is plausible ($p=0.068$, $n=378$). This allowed us to test the effect of date (adjusted for shell length^2 and siphon mass^2) on burying depth of suitable size classes. For data from Westerhever, however, the shell length^2·siphon mass^2·date interaction is significant ($p=0.007$, $n=165$, size classes 10-18 mm), so no analysis of covariance could be carried out to test the difference in burying depth of suitable size classes for knots among dates.

Periodical variation in siphon mass and burying depth of *Macoma balthica*

Why does *Macoma* move to higher depth layers, and thus increase the predation risk, in the same period when knots and many other migratory waders are present in large numbers? Apart from the relation between burying depth and shell size, burying depth is also correlated with siphon size (Reading & McGrorty 1978, Zwarts and Wanink 1989). *Macoma* has two separate siphons, an exhalent and an inhalent one with which they defaecate and take up food and oxygen from the surface and the overlying water , respectively (Reading & McGrorty 1978, de Vlas 1985). *Macoma* is a deposit feeder, which grazes deposited algae and diatoms from the surface around its burrow, but it is also able to filter food from the water (suspension feeding). In winter, when food on the surface is absent, *Macoma* shifts to filter feeding. In spring, the growing season, *Macoma* starts to graze from the increasing food, deposited on the surface (Hummel 1985).

Thus the first reason for moving higher in the substrate in early spring is that *Macoma* extends part of the siphon above the mud surface to start deposit feeding; in this case siphon size may remain the same. Secondly, *Macoma* may be forced to move higher because juvenile plaice *Pleuronectus platessa* feed on the siphon tips. These flatfish have a significant impact on siphon mass by grazing siphos in April, May and June, and maybe also in March (de Vlas 1985). Other potential consumers are shrimps and shore crabs; the first cause a maximum effect in June, July and August, the main consumption of the latter is in July and August (de Vlas 1985). Besides moving higher, *Macoma* may switch from deposit feeding to suspension feeding to be able to keep feeding after siphon cropping (Zwarts and Wanink 1989, Kamermans 1992). But because siphon predation inhibits growth of *Macoma*, finally the animals may even stop

feeding completely. Then *Macoma* may bury deeper after siphon cropping to avoid further cropping, and thus more loss of body mass (Kamermans 1992). Moving deeper also prevents predation by birds. When siphon cropping occurs, the choice between burying shallow or deep, is a compromise between feeding (which involves running the risk of being eaten) and being deprived of food (but staying alive).

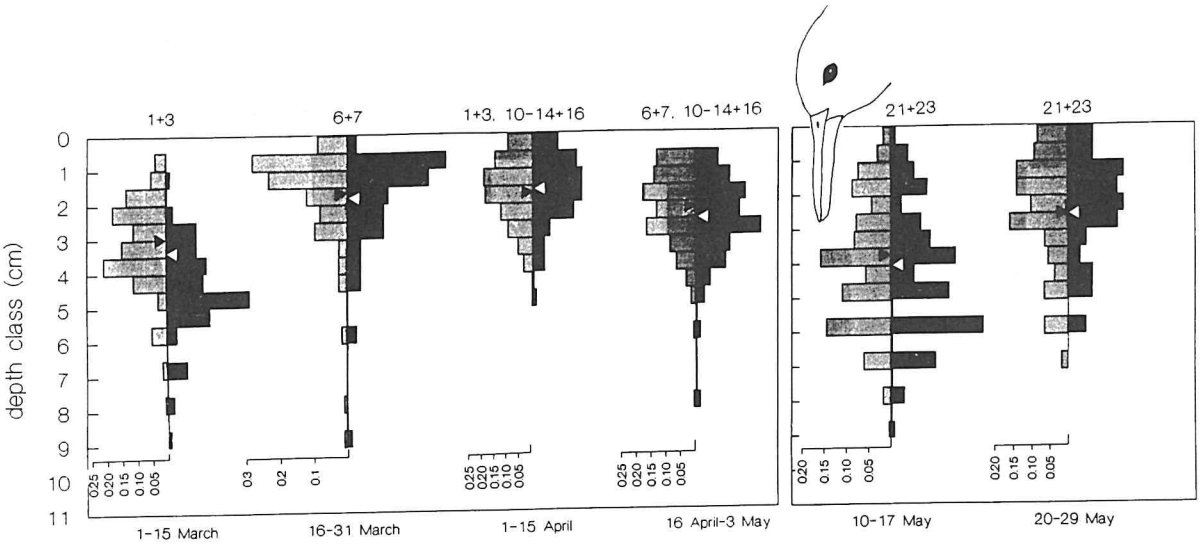

Fig.12. Depth distribution of *Macoma balthica* in the different periods (1-4: Texel, 5-6: Westerhever). The shaded frequency distribution represents all size classes. In the dark frequency distribution only the suitable size classes are included. White and black triangles are mean values for the size classes concerned. The small scales within the figure show the proportion per depth class. On the upper line sampled plots in each period are indicated.

Our measurements show that on most sampling dates on Texel, siphon size correlated significantly with burying depth (Table 5a). Within a certain size class (in Fig.15, 17-19 mm) individuals with larger siphons lived deeper. In the second half of March, when burying depth of *Macoma* decreased (Fig.12), the siphon mass of all size classes decreased (Fig.13). Presumably in this period siphons were cropped by juvenile flatfish. In the first weeks of April, when *Macoma* remained buried very superficially, the siphon mass had increased. In the last week of April and the first days of May, *Macoma* moved deeper with similar siphon mass as in the previous period. Possibly *Macoma* took the risk of predation to increase the opportunities for feeding by extruding the siphon (which requires more shallow burying depth) in the first half of April (Zwarts and Wanink 1989). Two weeks later the body mass of *Macoma* of a certain size class had increased (Fig.14). This better condition provided the possibility to bury deeper.

In Westerhever, simultaneously with a decrease in burying depth, the siphon mass decreased (Fig.12 and 13). On all dates but two, siphon mass correlated with burying depth (Table 5a). Presumably here siphon cropping occurred more in the last weeks of May than in the first two weeks.

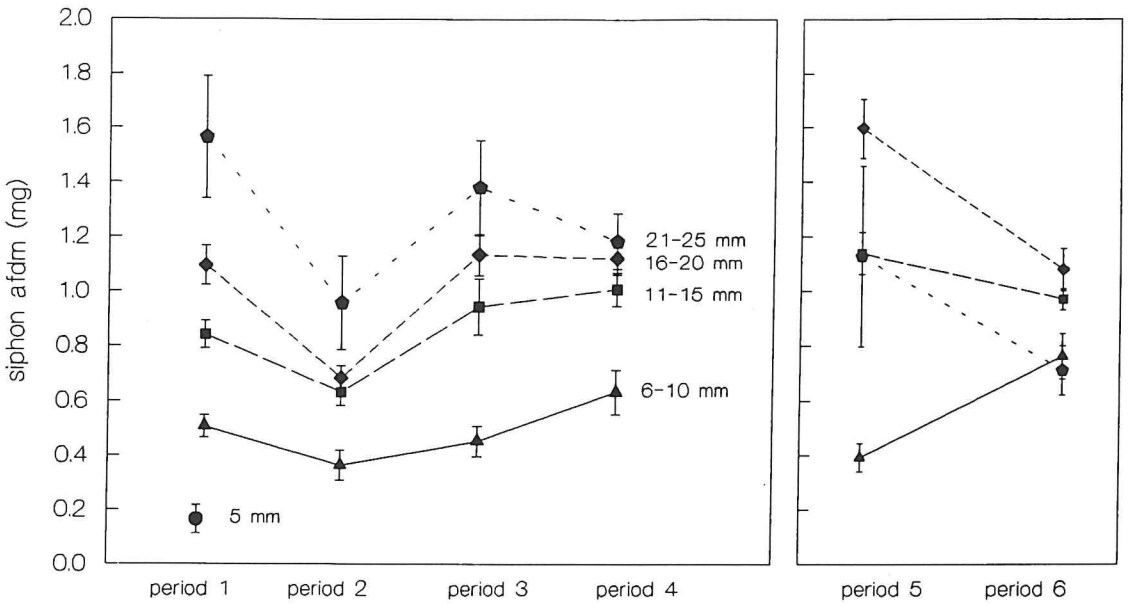

Fig.13. Siphon AFDM of five shell size classes of *Macoma balthica*, in the different periods on Texel (left panel) and in Westerhever (rigth panel). Vertical lines indicate standard errors.

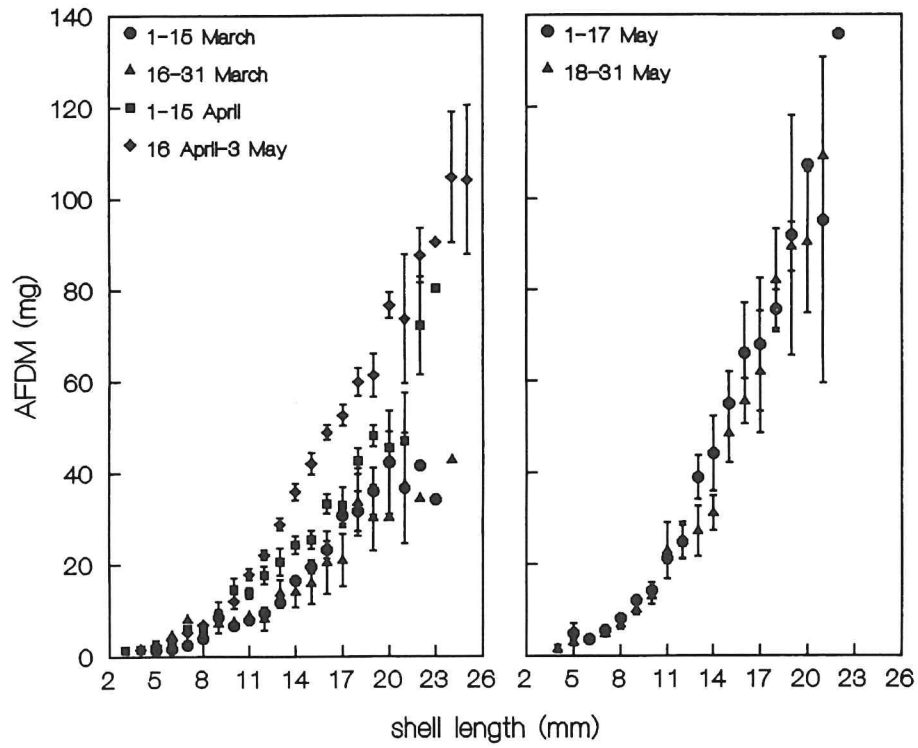

Fig.14. Relation between shell length and body mass (mg AFDM) in *Macoma balthica* in the different periods on Texel (a) and in Westerhever (b). The equations for the periods are resp.: 1-15 March: AFDM = 0.016·shell length$^{2.594}$ (n = 53, R^2 = 93.4), 16-31 March: AFDM = 0.121·shell length$^{1.845}$ (n = 30, R^2 = 69.7), 1-15 April: AFDM = 0.077·shell length$^{2.169}$ (n = 88, R^2 = 93.2), 16 April- 3 May: AFDM = 0.033·shell length$^{2.548}$ (n = 129, R^2 = 92.9), 7-17 May: AFDM = 0.035·shell length$^{2.659}$ (n = 54, R^2 = 93.0), 18-31 May: AFDM = 0.021·shell length$^{2.802}$ (n = 71, R^2 = 88.1). For all equations $p < 0.001$; AFDM was measured as an average of all individuals per size class, so n represents the combination of the number of size classes present in each sample and the number of sampled plots.

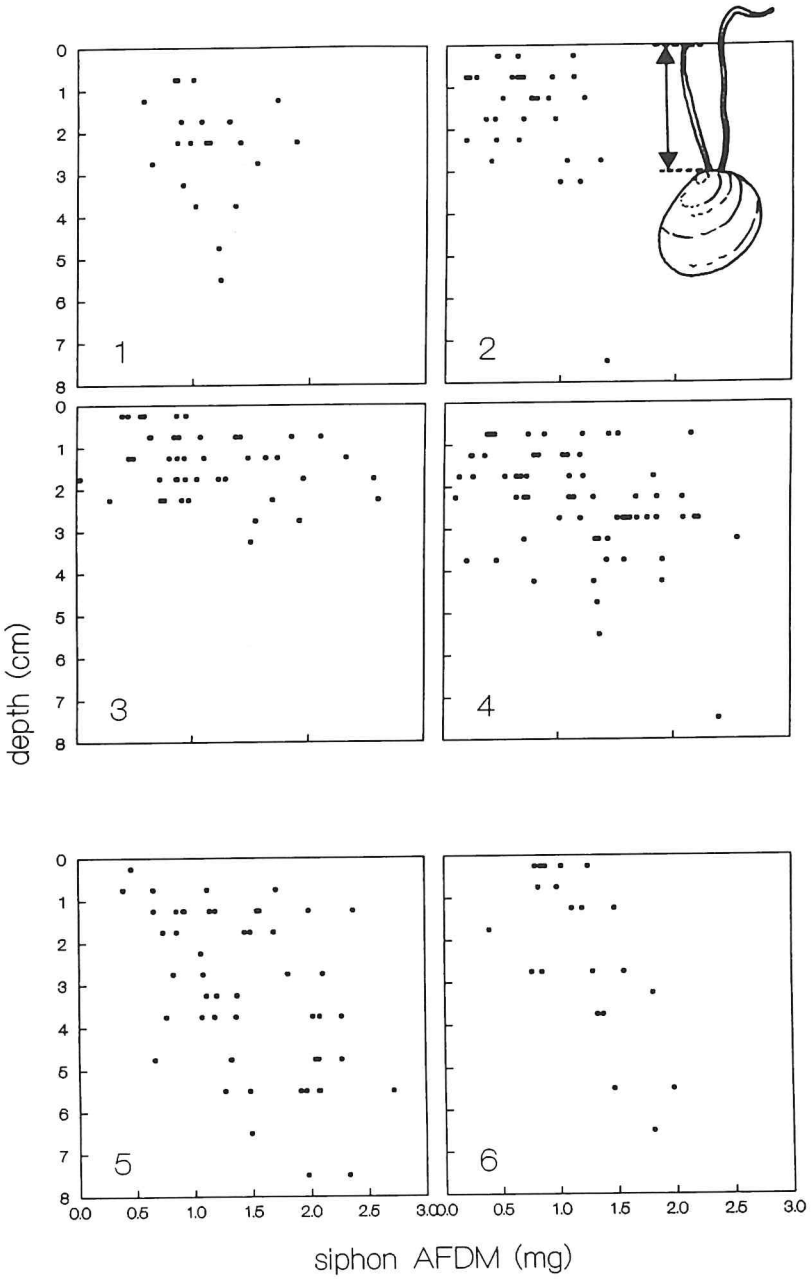

Fig.15. Relation between siphon AFDM and burying depth for the 17-19 mm size class of *Macoma balthica*. Numbers indicate the successive two-week periods in March, April and in May. At Texel on all, minus one, sampling days (3 days per period) a significant positive correlation between burying depht and siphon mass (adjusted for shell length) was found.

Prey harvestable to knots

The harvestable proportion of the prey present is defined as accessible prey (not too deep) of the right size (not too small or too big): in this case *Macoma* of 10-18 mm long and buried in the upper three cm of the substrate. Summarizing, the accessibility of *Macoma* increased during spring, and as a result the density of prey of suitable size classes changed (Fig.8 and 9). At first in spring, *Macoma* moved to the surface, but animals < 15 mm were already buried deeper in the last part of the staging period of

knots (Fig.11). Taken the suitability and accessibility of *Macoma* into account, we calculated the harvestable part for knot (Fig.16 and Fig.17). In Fig.16 average harvestable biomass of the plots frequently visited by knots are given. Because not all these plots were sampled in all periods we lumped plots that were sampled in the same periods in Fig.17. This figure also shows which part of the total biomass was actually harvestable. On plot 1 and 3, harvestable biomass of *Macoma* increased between 1 March and 15 April from less than 0.5 g AFDM m^{-2}, to more than 1 g AFDM m^{-2}. On plot 6 and 7 biomass increased from 0.5 g AFDM m^{-2} (16 March) to nearly 3 g AFDM m^{-2} (3 May). Since the accessible fraction decreased at the end of April, presumably part of the increase of harvestable biomass in the last period is caused by an increase in body mass of the individual *Macoma* (Fig.14). Although total biomass increased on plot 10-12 and 16, the harvestable fraction remained nearly equal (2 g AFDM m^{-2}) in period 3 and 4.

Table 6. Surface area occupied by the layer of *Cerastoderma edule* (m^2). Values are summarized for all size classes present; per size class πr^2 value was calculated and multiplied with the numbers per square meter. Asterisk indicate plots regularly visited by knots.

plot		surface area occupied by *Cerastoderma* (m^2)
20		0.00
21	*	0.22
22	*	0.14
23	*	0.16
24	*	0.37
25	*	0.49
26		0.00

In Westerhever the harvestable biomass of *Macoma* increased in the second half of May (from 0.7 g AFDM m^{-2} to 1.4 g AFDM m^{-2}),mainly due to the decreasing burying depth. But, in spite of this abundance of harvestable *Macoma*, this prey was hardly eaten (except on two days in May). We assume that the high densities of *Cerastoderma* were hindering knots to reach Macoma. None of the size classes of *Cerastoderma* present were ingestable for knots; *Cerastoderma* longer than 12 mm can not be ingested. And by forming dense cockle beds they hinder knots to reach the deeper layers of the bottom where *Macoma* live. On favourite foraging plots (21-25) the density of Cerastoderma ranged between 253 and 1191 n m^{-2}. Only on the plots 20 and 26, spots not very favourite to knots, low densities of *Cerastoderma*, 19 n m^{-2} and 8 n m^{-2}, were found. A *Cerastoderma* of 23.4 mm (the most abundant size in Westerhever) can cover a area of 4.3 cm^2. When 253 cockles (plot 21) are present in one square metre, they cover an area of 0.11 m^2, 1191 cockles (plot 24) cover even an area of 0.49 m^2 (Table 6). On a spot where cockles lay remarkably close together, the area is even larger, because then the mud surface in between the cockles is not available for probing. Assuming that in that case the surface a cockle covers is the square of its length (one cockle of 23.4 mm covers 5.48 cm^2), cockles can cover 0.65 m^2 on plot 25, and 0.47 m^2 on plot 24. Plot 24 and 25 are the only two sites where such dense cockle beds were observed. On Texel this problem did not occur because the densities of *Cerastoderma* were very low, the average density was 14.6 n m^{-2} (SD 19.3).

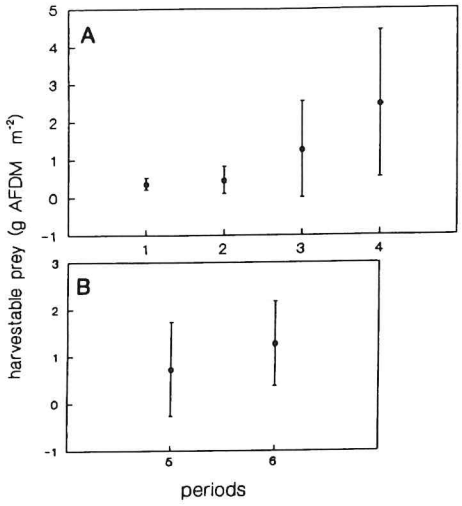

Fig.16. Harvestable *Macoma balthica* (g AFDM.m^{-2}) presented for the locations visited by knots and mentioned in Fig.17. (A: Texel, B: Westerhever).

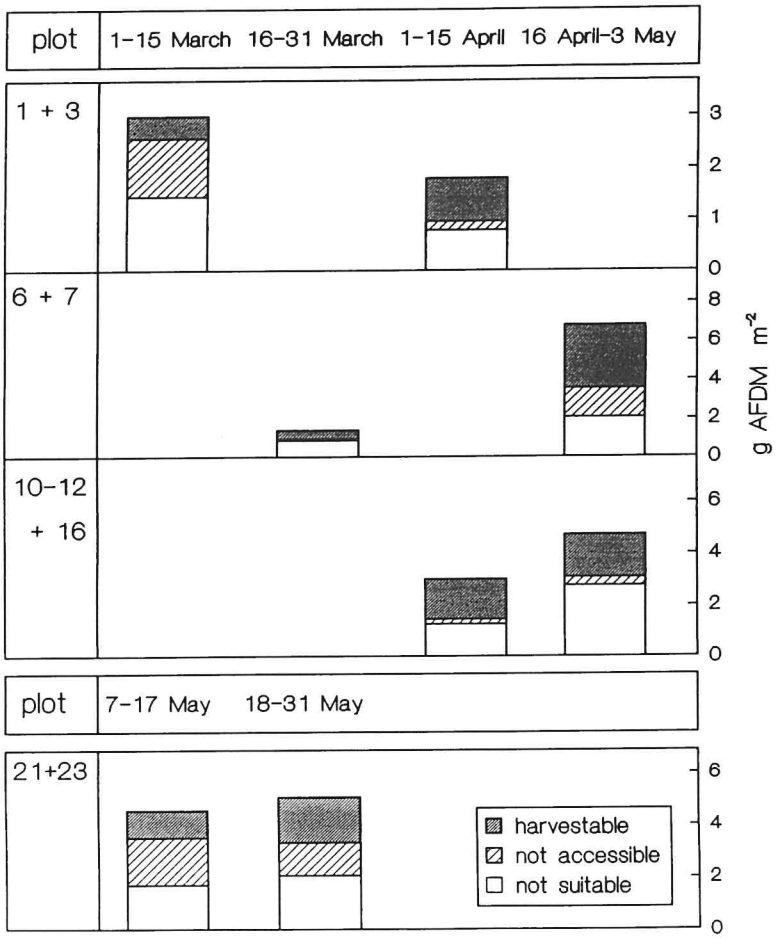

Fig.17. Total and harvestable *Macoma balthica* (g AFDM.m^{-2}) presented for the locations that were regularly visited by knots, and sampled twice in the course of spring. The hatched and shaded part together indicate AFDM·m^{-2} of suitable size classes (ingestable, not too big, and profitable, not too small). Note different y-scales.

Diet composition

The results of the calculations of biomass equivalents of faeces samples are given in Table 7. The total AFDM values are in the same order of magnitude as the values given by Dekinga & Piersma (1993) (range 32.5-37.2 g AFDM/dropping).

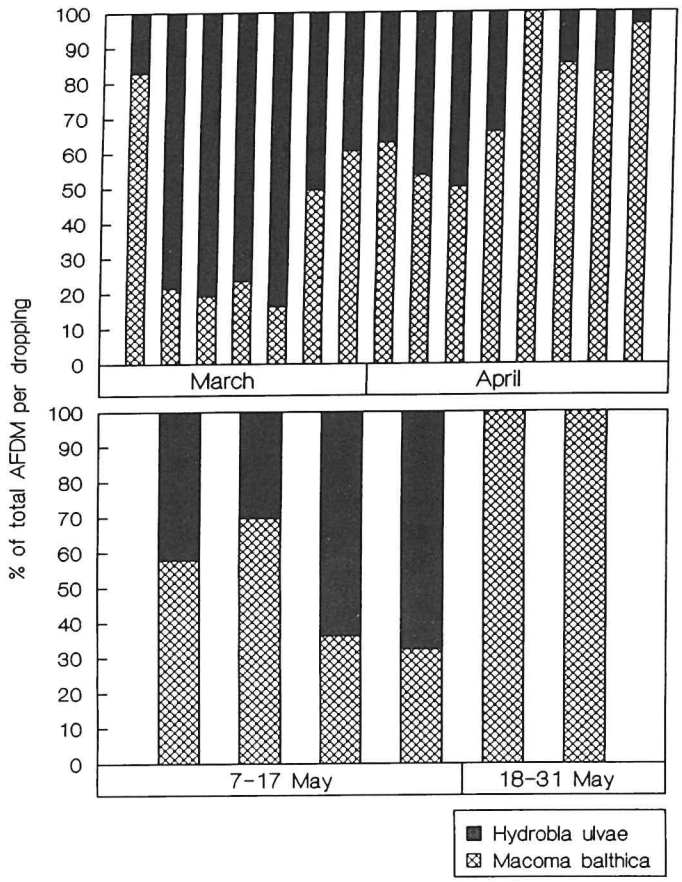

Fig.18. Proportional diet composition in the course of spring. Data are obtained from faecal analysis. The dates of the samples are ordered chronologically, but are not relative to the position on the x-axis. The exact dates are given in Table 7. When two samples per date were available, the mean value is presented in the figure.

We were surprised to find that *Hydrobia* made up such a large part of the knots diet (Fig.18) on Texel, since we hardly ever saw knots feeding on *Hydrobia*. This however is very difficult to see, even in cage experiments, where the distance between the knots and the observer was only a few meters (J. v. Gils, P. de Goeij, pers. comm.). The relative importance of *Hydrobia* is obvious also when the AFDM/dropping is split for the two prey species (Fig.19). This figure only presents results for Texel, since sample size for Westerhever was too small. The proportion of AFDM/dropping which is derived from *Macoma* gradually increased over the study period, which is the reversed pattern of the change in proportion of *Hydrobia*. The lowest panel presents the total biomass equivalents. This figure shows a slight increase in biomass equivalents. To test whether

the total AFDM per dropping decreased in course of spring, we carried out a regression of AFDM/dropping on date. The significant increase ($R^2=0.198$, $p<0.05$) in biomass equivalents of the droppings is what one would expect, if the knots had to increase their intake rate in order to gain mass prior to migration, if defaecation rate remains constant.

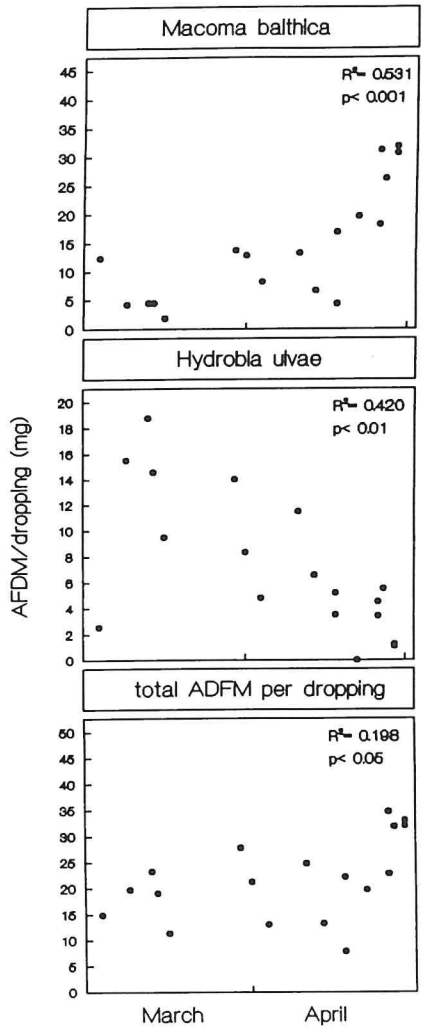

Fig.19. Biomass equivalents per dropping in the course of the premigratory period at Texel. The upper two panels present the biomass equivalents per dropping seperately for *Macoma balthica* and *Hydrobia ulvae*. The lowest panel shows the total biomass equivalents per dropping. In all three cases date and biomass equivalent are correlated. For Westerhever there is no significant increase or decrease in the biomass equivalents per dropping ($n=7$).

Of course measuring biomass equivalents of the droppings is not the complete story. To estimate actual intake rates, measurements on defaecation intervals and size of droppings are needed. Since we do not have these measurements we can only speculate about what possibly happened. One can imagine that different feeding rates (due to, for example, differences in prey density) can lead to subsequent different defaecation intervals.

In Westerhever biomass equivalents were lower compared to the Texel figures. Especially the two lowest values fall way out of range of the other measurements. Strikingly these two values refer to the same site (23). In Westerhever the diet consisted of both *Hydrobia* and *Macoma* during the first three weeks of May. The samples taken on 21 and 31 May consisted nearly solely of *Macoma*. On the latter of these two dates we could measure intake rates of knots for the first time, because knots were eating *Macoma* then. Nehls (1993) found, by analysing stomach contents and dropping observations, that knots predominantly ate *Hydrobia* in October til December and in March. Outside wintertime *Hydrobia* seemed of minor importance here, in favour of *Macoma* and *Cerastoderma*. We probably did not find any *Cerastoderma* fragments in the faeces samples, because the size classes present far exceded the knots gape width. Nehls (1993) recorded *Cerastoderma* as a major food source only from autumn 1987 to spring 1988, when small-sized *Cerastoderma* were abundant.

Table 7. Biomass equivalents per dropping. The location numbers correspond with the numbers of the sampling sites.

Area	Location	Date		Number of droppings	Dry mass (g) *Macoma*	Dry mass (g) *Hydrobia*	Ingested AFDM (mg AFDM/dropping) *Macoma*	Ingested AFDM (mg AFDM/dropping) *Hydrobia*	Ingested AFDM (mg AFDM/dropping) Total
Texel	5	March	3	50	8.68	0.75	12.37	2.54	14.92
	3		8	50	2.99	4.56	4.26	15.50	19.76
	3		12	100	6.30	11.04	4.49	18.76	23.25
	7		13	100	6.29	8.56	4.49	14.56	19.05
	3		15	100	2.61	5.57	1.86	9.48	11.34
	10		28	50	9.83	4.12	13.76	14.00	27.76
	10		30	100	18.39	4.90	12.87	8.34	21.21
	3	April	2	100	7.16	2.83	8.20	4.80	13.00
	15		9	100	11.58	6.75	13.27	11.48	24.75
	5		12	100	5.79	3.86	6.64	6.57	13.21
	5		16	100	2.78	2.06	4.34	3.50	7.84
	3		16	100	10.84	3.04	16.93	5.18	22.11
	8		20	75	9.45	0.00	19.68	0.00	19.69
	7		24	100	20.01	2.00	31.25	3.40	34.66
	3		24	100	11.69	2.64	18.25	4.50	22.76
	7		25	100	11.84	3.24	26.03	5.51	31.82
	7		27	100	19.67	0.72	30.73	1.23	31.95
	6		27	50	10.21	0.32	31.89	1.08	32.97
Westerhever	21	May	8	50	2.23	1.87	8.72	6.35	15.07
	24		9	150	4.31	4.14	5.62	4.70	10.31
	23		9	100	1.35	0.27	2.64	0.47	3.11
	21		10	100	1.52	3.08	2.97	5.23	8.20
	24		15	100	1.46	3.52	2.85	5.99	8.84
	23		21	122	4.31	0.00	5.98	0.00	5.98
	20		31	100	30.64	0.02	51.78	0.03	51.81

Feeding activity

In order to find out if knots gain body mass prior to migration by increasing their working day and therefore their daily energy intake, we made activity budgets. The length of the effective working day can either be increased by working longer, limited only by the length of the exposure time of the mudflats, or by increasingly use suboptimal feeding time (for instance feed at night), as recorded by Zwarts *et al.* 1990. To investigate the latter effect observations on nighttime foraging are necessary. Since we did not have the right equipment we have no data on nocturnal foraging. On a few clear days though, we were able to carry out our observations till long after sunset. The behaviour of the birds on those days did not give any reason to assume that knots behaved differently at night (Fig.20).

The proportions of birds engaged in feeding activity throughout the tidal cycle are presented in Fig.21. The percentage of the day that knots spent feeding, depends on the time per day birds spend feeding and on the percentage of birds that is actually feeding during that period. Unfortunately we have not enough data in the begin and the end of low tide periods to say something about the length of the feeding time. The observations in the middle period (-2hrs to 2hrs) allowed us to compare the different periods in respect of the proportion of birds that was actually foraging. The result of a oneway ANOVA showed no difference in % feeding in the four periods on Texel

(p = 0.357, n = 87). Nor was there any difference between the two periods in Westerhever (p = 0.104, n = 53), or between all four periods on Texel and both periods at Westerhever (p = 0.095, n = 140).

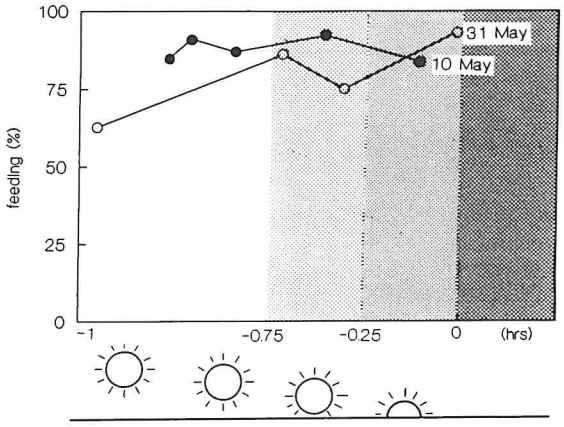

Fig.20. Percentage of birds feeding throughout two twilight periods recorded on 10 May and 31 May. A dot represents one activity scan of at least 100 birds.

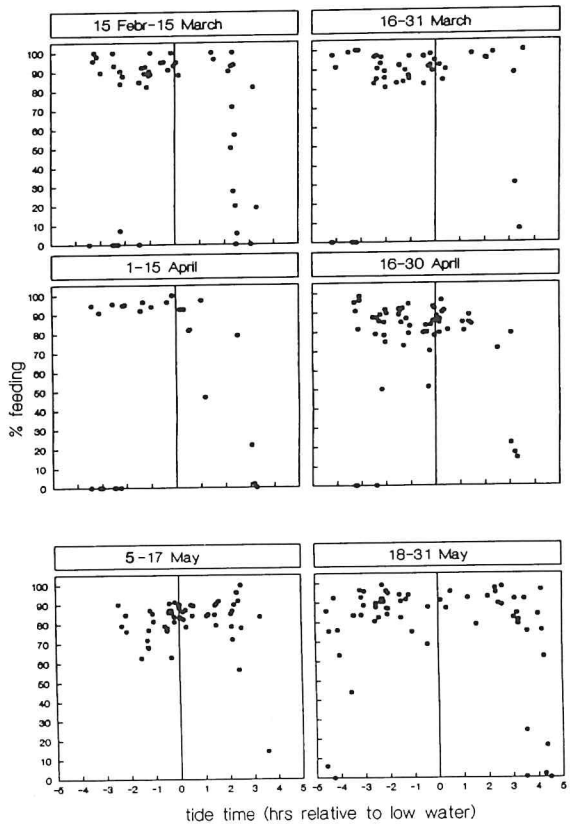

Fig.21. Feeding activity during the low tide period at Texel, and in Westerhever (lower two panels). Each dot represents one activity scan of ±100 birds. No distinction is made between scans recorded on spring or on neap tides.

Intake rates

Based on the continuous observations, we calculated intake rates. During these observations we distinguished a few categories in describing prey that was eaten: *Macoma*, small *Macoma* (< 10 mm), big *Macoma*(≥ 10 mm), small prey, worm (size estimated relative to bill length). The eating of worms occurred on two days (13 and 14 March) when after a period of cold weather, temperatures suddenly increased. In this case knots were apparently feeding by sight. The sudden higher temperatures might have induced higher activity of the worms and therefore facilitated the locating of the worms (probably *Nereis diversicolor* and *Nephthys hombergi*) by knots. According to Esselink & Zwarts (1989) the surface activity of *Nereis* in spring is high because of the bloom in benthic algae and at the same time density of food in the water is still low, which makes filterfeeding unprofitable. Ens (1982) recorded high feeding rates of Oystercatcher (*Haematopus ostralegus*) on *Nereis* during sunny periods in spring.
To estimate intake rates we used the frequency distribution of eaten *Macoma* (from the faeces analysis) to specify the recorded shell lengths. Biomass values, obtained from the benthic sampling in the different periods were used to estimate the biomass equivalents of eaten prey. For each observed bird a mean intake rate per second was calculated. The calculated intake rates as given in Table 8, are average values of all birds observed within a period. Assuming that prey intake could only be recorded when birds were feeding on *Macoma* and intake of *Hydrobia* could not be identified, we corrected the obtained value for the percentage of *Hydrobia* that was found in the faeces analysis. We could not calculate a value for period 5, since in this period knots were predominantly feeding on *Hydrobia*, which is too small prey to actually observe being eaten. To analyse if intake rates in the different periods differed we carried out an ANOVA with period as variable. When all five periods are included intake rates do differ significantly ($p < 0.008$). Scheffé tests showed that the difference was due to period 2 and 6 ($p = 0.050$). If only the four Texel periods are included in the analysis, the intake rates in period 1 and 2 are different (ANOVA: $p = 0.017$, Scheffé test for difference between subsets of periods: period 1 and 2, $p = 0.027$).

Table 8. Average intake rates in the different periods. n represents the number of observation minutes. No intake rates could be measured in period 5, since knots largely foraged on *Hydrobia ulvae*.

Location	Period	Intake rate (mg AFDM s^{-1})	95% confidence limits	n
Texel	1	0.378	0.102	120
	2	0.187	0.049	177
	3	0.200	0.156	83
	4	0.305	0.070	231
Westerhever	6	0.407	0.120	81

DISCUSSION

Repercussions of changes in prey harvestability on prey size selection

During March and April, knots on Texel gradually took larger Macoma, the upper size threshold changed from 16 unto 18-19 mm long (Fig.8). In Westerhever no growth of *Macoma* was observed and the size selection did not change in May (Fig.10). Our results show that this change in selection is more likely to be the result of changes in burying depth than of an increase in shell length of *Macoma* in spring. Shell growth of *Macoma* is largest in May and June (Beukema & De Bruin 1977); in March and April *Macoma* can grow at the most 2 or 3 mm per month (Zwarts 1991). The total densities of suitable size classes did not change remarkably during the staging period of knots on Texel. However, not all size classes had an equal burying depth during March and April. Late March all individuals moved closer to the surface, but later in April only smaller ones (< 15 mm) buried deeper again (Fig.10). Larger *Macoma* stayed buried more superficially in late April, and therefore the accessible part of larger size classes (15 mm or larger) increased in the same period. In this period *Macoma* of 15-19 mm long were better accessible (Fig.8). The preference for these size classes might also be due to a better detectability. The touch area of a 19 mm *Macoma* is 5-fold the touch area of a 10 mm *Macoma* (Zwarts & Blomert 1992), thus the encounter rate of these large *Macoma* is much higher than that of smaller ones. In spite of this, Zwarts & Blomert (1992) argued that the upper size threshold for *Macoma* is 16 mm, since they found that *Macoma* of this size were refused half of the time. Larger prey are less profitable to ingest: knots use catch and throw movements to transport the food up the bill and for larger prey more of such movements are needed. This increases the handling time and reduces the profitability of the prey. Prater (1972) and Goss-Gustard (1977a) also found that 16 mm was the upper size threshold. So this selection of large *Macoma* by knots on Texel and in Westerhever seems rather remarkable.

On Texel and in Westerhever we also collected rejected *Macoma* (picked up by a knot and after several unsuccessful swallow efforts rejected and left on the mud surface) (Fig.22). The rejected prey items on Texel were as large or larger than the upper treshhold of the selected size classes. In Westerhever, knots also refused suitable size classes. Of all these rejected prey items the bodymass was lower than the average values obtained from the sampling data. Hulscher (1982) showed that Oystercatcher rejected *Macoma* infected with trematodes. But these *Macoma* were not infected and due to the weight of the trematodes infected *Macoma* do not have a lower body mass (Zwarts 1991). We can not be sure on what basis knots rejected these inferior prey items, possibly they can distinct them somehow.

We assumed that the maximal probing depth of knots was 3 cm. Our calculations on the harvestable prey are based on this assumption. Since knots have a bill of 35 mm, and they need 5 mm to purchase a shell of 10 mm, the upper 3 cm of the mud can only be fully exploited when knots always probe to the base of the bill (Zwarts & Blomert 1992). The upper 2 cm of the sediment are thus more thoroughly probed by knots than the sediment below 2 cm. If knots probed more superficially than we assumed before, then a large proportion of *Macoma* buried between 2 and 3 cm was missed by knots. In that case in April only *Macoma* larger than 14 mm were accessible (Fig.11) and knots were forced to eat these larger size classes. This also means that the harvestable proportion is presumably an overestimation for superficially probing knots. However, the knots we observed made very deep probes, regularly even until eye depth. So we feel that the estimation of harvestable *Macoma* biomass made in the

result is an accurate estimation.

In the course of spring on Texel, *Macoma* formed an increasing part of the diet (Fig.18 and 19). In the same time the harvestable proportion of *Macoma* increased

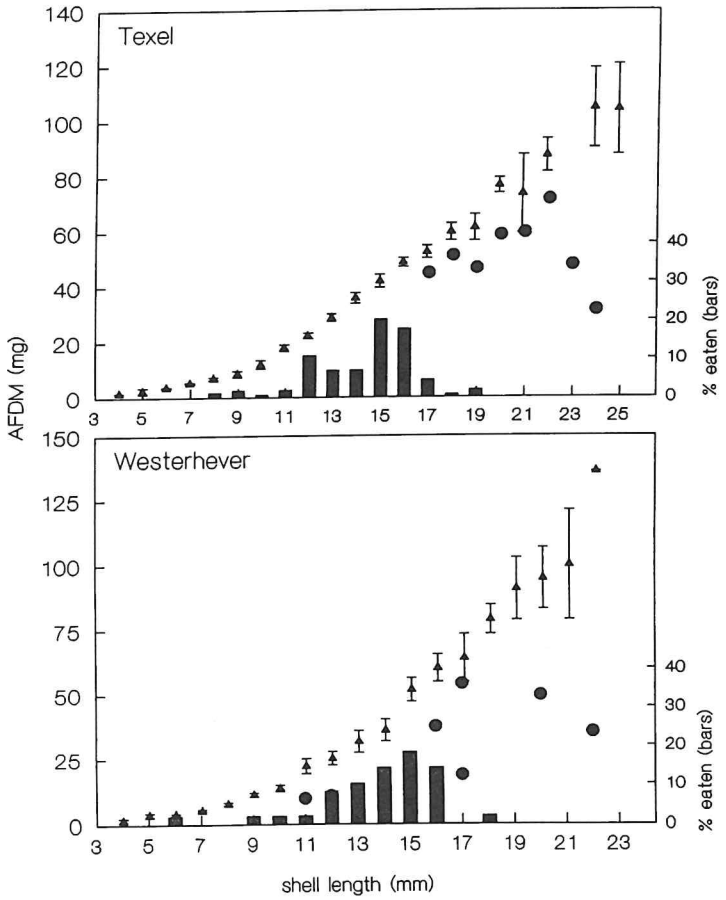

Fig.22. Biomass values of rejected *Macoma balthica* (dots) compared to average biomass values (triangles) per size class. The bars indicate the size class frequency distribution of eaten *Macoma balthica* (obtained from faeces analysis).

(Fig.16). When the proportion of this prey in the diet is plotted against the harvestable biomass (Fig.23) it is evident that knots only started feeding on *Macoma* (making up >50% of the diet), when the density of harvestable *Macoma* was at least 1 g AFDM m^{-2}. The same change in diet composition was apparent in Westerhever. At first *Hydrobia* and *Macoma* were both important prey (Fig.18), which is contrary to the situation in previous years (Nehls 1993). He found that *Hydrobia* was of minor importance outside wintertime in Westerhever. In 1990 however, the mudflats in Westerhever contained high densities of large *Cerastoderma* (Table 6), which might have prevented free access to the *Macoma* living underneath this layer. Therefore knots had to take the one alternative prey left: *Hydrobia*. Later in May, *Macoma* moved to the surface and became more accessible to knots. This decrease in burying depth might have made up for the hinder of the layer of *Cerastoderma*.

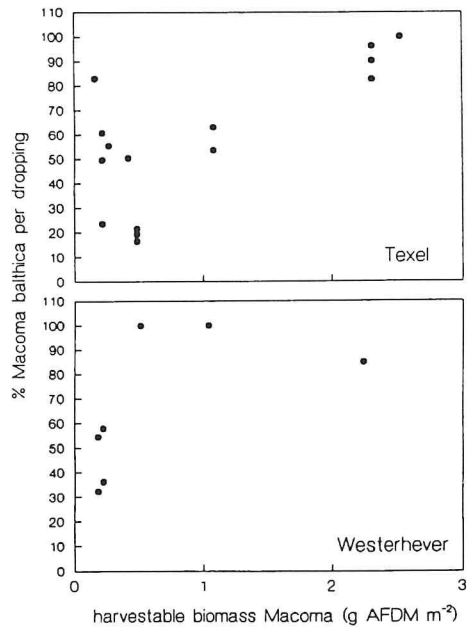

Fig.23. Proportion *Macoma balthica* of the diet as a function of the harvestable biomass of *Macoma*.

The variation in knot densities does not allow us to make an estimation of the predation pressure imposed on the harvestable biomass by knots like Prater (1972) did). We did observe though that certain cohorts disappeared. Fig.8 shows that small sized *Macoma* (10 mm or smaller) present in early March disappeared in April. Since *Macoma* grow just 2 or 3 mm in this period (Zwarts 1991), the larger ones of this large quantity of small *Macoma* should appear within the range of suitable size classes of knots in April. Knots might have depleted these growing *Macoma*, which could explain the sudden disappearance of this size class. But, since burying depth is very small in the second half March, these small *Macoma* can also be fed upon by little fish or other predators selecting small prey.

Comparison of feeding behaviour between the two subspecies of Knot

In this report we have presented results on food and feeding of the nearctic (*C.c. islandica*) and the palearctic (*C.c.canutus*) knot. When comparing the two subspecies we have to keep in mind that observations were carried out at different sites and in different periods. The actual comparison can not be made between the different subspecies as such, but only between the subspecies in their respective areas during the respective time spans. Therefore we can only discuss the differences in feeding habits and not whether these are related to the difference in subspecies, location or period. The period which would be useful for direct comparisons, when both subspecies were present in the German Wadden sea, was very short. Furthermore, both species were in a different stage of the premigratory period at this time (early May): *islandica* knots well fed and about to leave, *canutus* knots just arriving from their African wintering grounds and building up new fat stores.

In both areas the local benthic fauna held the same possible prey species for knots (*Macoma*, *Hydrobia* and *Cerastoderma*) and the prey species composition of the respective diets was similar. In March on Texel knots ate mainly *Hydrobia* and switched to a mixed diet, with an increasing proportion of *Macoma*, later in April (Fig.18). In Westerhever birds were also predominantly feeding on *Hydrobia* at first but in late May suddenly switched to a uniform *Macoma* diet. In both cases the harvestable proportion of *Macoma* increased during the study period, while the alternative prey *Hydrobia* was available all the time and locally extremely abundant in Westerhever. While *Cerastoderma* was present in both places, knots did not feed on them, probably because the size classes present were too large to be swallowed. Apparently both knot species preferred *Macoma*, when there were alternatives at choice (i.e. when increasing numbers of the bivalve prey became harvestable). In view of the more favorable ratio between shell mass and organic matter of *Macoma*, this is not surprising (Zwarts &

Blomert 1992; knots preferred *Macoma* when they could choose between *Macoma*, *Hydrobia* and *Cerastoderma* in cage experiments, Borsje, pers. comm.).

When knots on Texel left their roosts after high tide and started foraging again they moved from one spot to the other until the water receded from the mudflats in the east (Fig.6). Possibly they favoured the areas far east to feeding spots just offshore, because there they were further from the dyke and human disturbance. Following the water's edge can be advantageous because prey items are more active and therefore more easily to find just after the water has receded, an explanation that Kersten & Piersma (1984) used to explain high intake rates of Grey Plovers *Pluvialis squatarola*. In Westerhever the foraging flocks hardly moved from a relatively small area lying just offshore. Compared to Texel, the area was far less frequently visited by people, who could cause disturbance to the birds.

Because the staging times of the two subspecies in the Wadden Sea are not synchronised (until late April and the month May for *C.c.islandica* and *C.c.canutus* respectively), the *canutus* knots experience longer daylight periods. Assuming that nocturnal foraging is less efficient than feeding in the daylight, knots might benefit from longer daylight periods. The difference in lattitude between the two areas did not compensate for this. As shown before, there is no difference in feeding activity during the middle part of the low tide period. But the working day seems longer in the last period of May than in the other periods. This effect can be caused by increasing day light periods. However the results are incomplete because of very little observations at the beginning and end of the low tides in the other periods.

When comparing intake rates between the two subspecies, the *canutus* knots seem to have a much higher intake rate. The values obtained on Texel (Table 8) are in fact relatively low, compared to the value of 0.63 mg AFDM s^{-1} found by Zwarts & Blomert (1992) and even compared to the value of 0.37 mg AFDM s^{-1} found by Zwarts *et al.*(1990a) in Mauritania. This is surprising, since waders wintering in this tropical area have the benefit of relatively low thermostatic costs (Piersma *et al.*1991a) and can therefore gain body mass with less food intake than their conspecifics wintering in more temperate areas.

Striking the balance: how do knots manage to gain mass?

In Fig.1 the various factors, that can cause increase of body mass in course of the premigratory period, were presented. In our study we wanted to quantify the changes in several of these factors, contributing to an increase in net daily energy gain. Finally we will evaluate (as far as possible) if factors changed and if so, in what way they changed. Result of this evaluation is shown in Fig.24. The most obvious changes occurred in the food situation. In both areas burying depth decreased, especially of the bigger (15-18 mm) *Macoma*. This change and the increase in biomass per individual *Macoma* caused an increase of the total harvestable prey biomass.

The question whether or not the body mass gain of knots is due to the increase in daily energy intake should be illustrated by changes in intake rates and length of working days. Intake rates did not increase, but as stated above, a large proportion of the small items being swallowed was probably missed during the focal observations and therefore values are underestimates. The biomass equivalents of droppings (Table 7), as a measure of intake rates show a significant increase in course of the period on Texel. But since we do not have measurements on defaecation intervals and sizes of droppings, no conclusions about actual intake rates can be drawn. Intake rate depends

also on the foraging effort of the birds. Foraging effort as such, can not be measured in the field. Foraging success depends on food abundance, so measuring changes in foraging effort is only a fair measure in situations with exactly the same food supply (in an experimental setup).

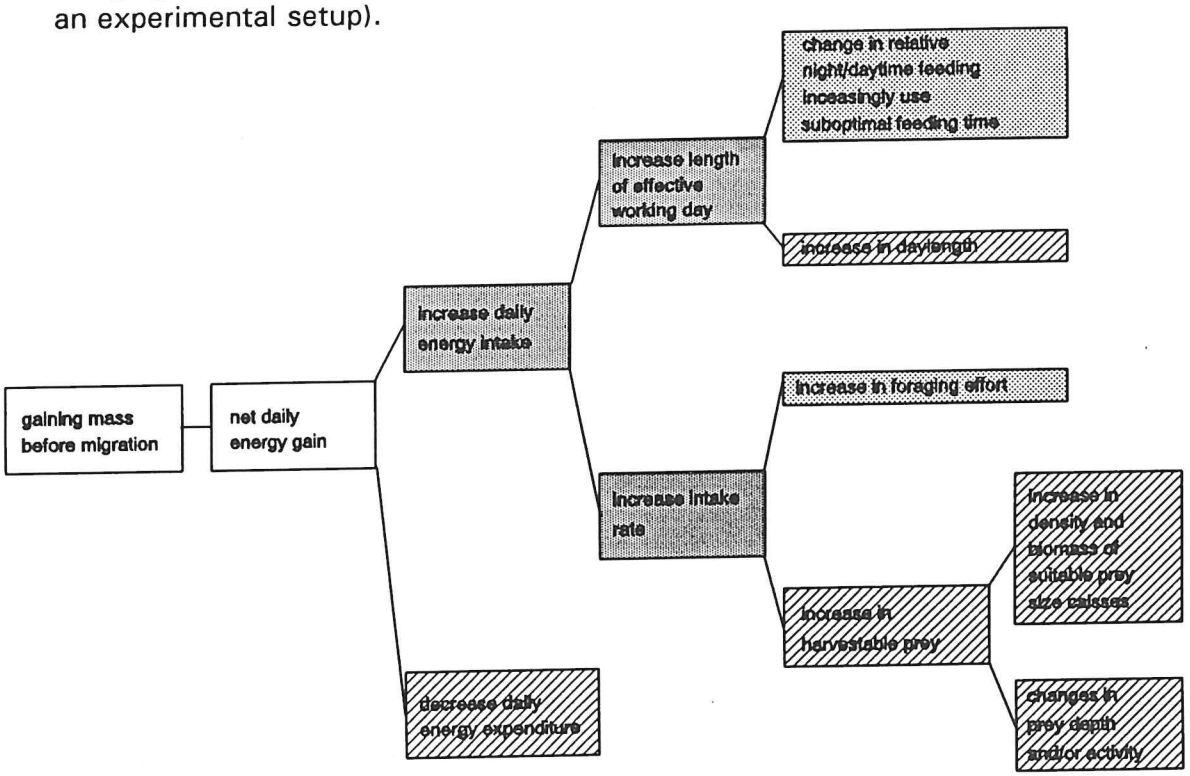

Fig.24. Scheme of possible pathways leading to mass gain in the period prior to migration. Hatched boxes indicate factors that contribute positively to the increase in net energy gain. Factors of which the effect is still not known are indicated in the heavily shaded boxes. Shaded boxes represent factors that were not measured.

The length of the effective working day could be increased by either feeding longer during low water periods or using suboptimal feeding time, which would both result in more foraging hours per day. During feeding periods mostly about 70-90 % of the birds were foraging (Fig.21). As shown before, there was no increase in percentage of birds that were foraging during the middle four hours of the low tide. Maybe a higher proportion is not possible because the processing rate of the food might be limited by the capacity of the gut to digest the food. Alternating bouts of feeding and other behaviour might be necessary to create digestive pauses (Zwarts & Blomert 1992). On the basis of the collected data we can not conclude whether there was any change in length of feeding time. As shown in Fig.25 most of the activity scans were made in the middle part of the low tide period. Besides this there is a wide range in waterlevel (and also of exposed mudflat area) within each tide time class (result of lumping the activity scans carried out on neap and on spring tides). Because of this, a distinction should be made between observations carried out at different tidal levels. Had we done this in our data analysis, we had ended up with very small sample sizes per tidal level per period. The effect that daylight period increased and so a relative larger proportion of low tide periods occurred during daylight in the course of the premigratory season, might have made it easier for knots to increase their working day.

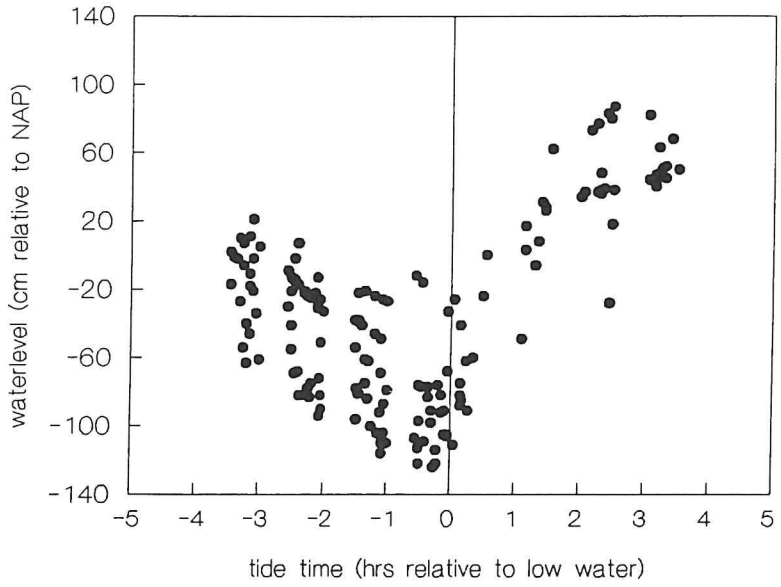

Fig.25. Tidal variation on de Vlakte van Kerken (Texel). Dots present water level relative to the tide time at the instants on which activity scans were made.

An exact value of the change in daily energy intake of knots can not be given for the reasons mentioned above. Nevertheless their expenses on account of thermoregulation probably decrease when temperatures rise in course of spring (Wiersma & Piersma 1993), which can decrease the cost of living considerably. According to the method outlined by Wiersma & Piersma (1993) it is possible to calculate thermoregulation costs with the use of data on air temperature, solar radiation and wind speed. As shown in Fig.26 the thermostatic costs (plus 1.5 W for activity costs, Piersma *et al.* 1991a) decrease rapidly in the course of the spring. It turns out that in February knots need all their energy uptake for thermostatic and activity costs. Only early March there is some possibility to start building up energy stores. To be able to reach the maximum metabolisable energy intake (Kirkwood 1983) of 4,5 BMR (BMR in knots equals 0.95, Piersma *et al.* 1991a) an intake rate of 0.63 mg s^{-1}, during 12 feeding hours of which 80% is actually spent foraging, is required. This intake rate is calculated from maximum metabolisable energy intake assuming that the energetic value of 1 g AFDM is 22 kJ, Beukema & de Bruin (1985) and the assimilation efficiency amounts 0.75, Castro *et al.* (1989).

Mass gain per day can be calculated, assuming that the knots use all the space the decrease of thermostatic costs leaves open, for energy storage. The mass gain per day can be calculated using the formula:

$$\text{daily mass gain} = \frac{\text{DEI-DEE}}{\text{EV}} \times \text{deposition efficiency}$$

Here DEI represents daily energy intake, DEE daily energy expenditure and EV the energetic value of 1 g store tissue which is assumed to consist of 80% fat and 20% protein (Lindström & Piersma 1992). For fat and protein deposition efficiency the values of 0.88 and 0.75 are used respectively (Kersten & Piersma 1987, Castro *et al.* 1989) If these calculated mass gains per day are summed over the whole period both Knot subspecies are present, they could end up with a mass gain of 78 g in the case of

islandica and 68 g in the case of *canutus*. Regarding that the lowest winter body mass of *islandica* is 135 g (Johnson 1985) and the body mass of *canutus* upon arrival in the German Wadden Sea is 150 g (Prokosch unpubl.), the calculated mass gain would be more than sufficient to reach the optimal departure body mass of ca. 200-210 g (Davidson & Wilson 1992, Piersma *et al.* 1992.). To reach these body masses they would not even have to hold on to this high intake level.

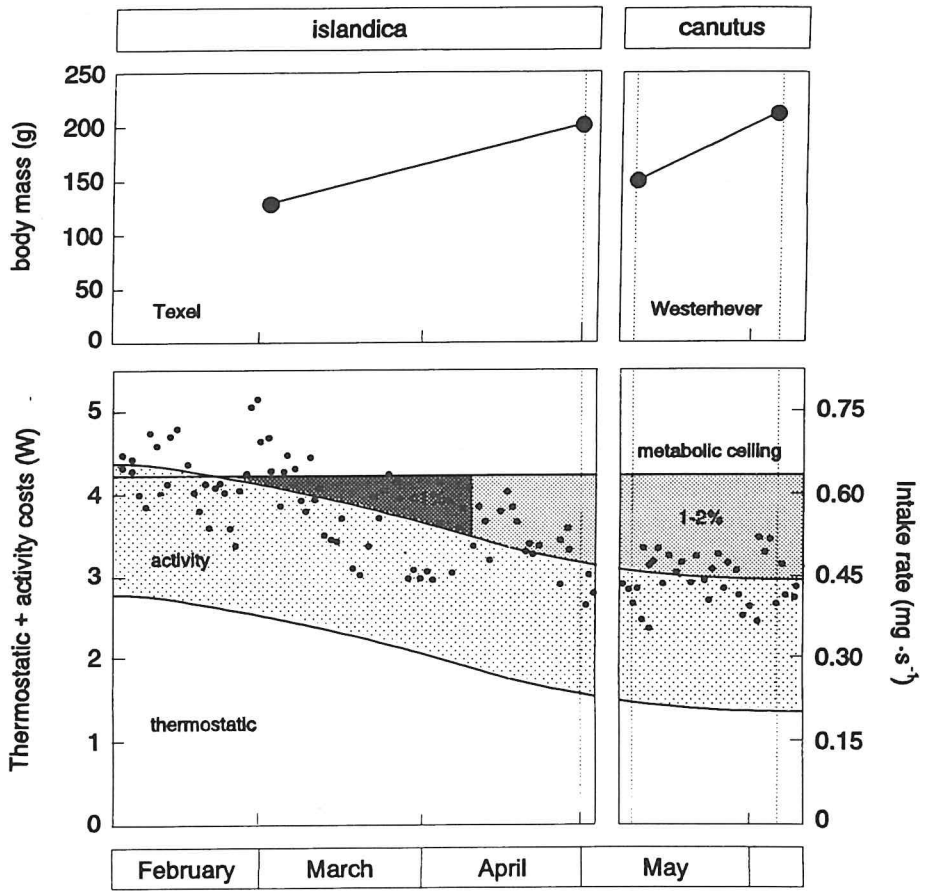

Fig.26. Lower panels: thermostatic costs (dots) in the course of the premigratory period for *islandica* on Texel (left panel) and *canutus* at Westerhever (right panel) calculated using the method outlined by Wiersma & Piersma (1992). The horizontal line indicates the maximum metabolisable energy intake as given by Kirkwood (1983), which is 4-5 BMR (3.8-4.75 W). Upper panels: body mass increase of *islandica* in the Dutch Wadden Sea and of *canutus* in the German Wadden Sea (Davidson & Wilson 1992, Piersma et al. 1992). Dashed lines indicate mean date of departure and/or arrival (in the case of *canutus*).

In Fig.26 also daily mass gain levels (expressed as % of lowest winter body mass, 135 g for *islandica*, Johnson (1985), 119 g for *canutus*, Zwarts *et al.* (1990b)) are shown. Compared to values given by Zwarts *et al.* (1990b) a mass gain of 1-2% is reasonable. But on the other hand, intake rates as calculated from visual observations (Table 8) are hardly enough to cover the thermostatic plus activity costs, let alone they can provide a surplus to spend on energy storage. Therefore we can not regard the calculated values

as absolute measures, since with these intake rates the birds would lose weight. The values of harvestable biomass (Fig.16 and 17) are plotted in a functional response curve (J.v. Gils, L.Zwarts & A-M. Blomert, pers.comm), which shows what intake rate can be achieved when knots are feeding in an area with a certain harvestable biomass. The required intake rate value of 0.63 mg s^{-1} can be achieved in period 3 and 4 on Texel and in period 6 at Westerhever, when knots solely feed on *Macoma* (Fig.27). In the other periods this intake rate value can not be achieved on the basis of *Macoma* alone. But keeping in mind that the average harvestable *Hydrobia* biomass amounts to 1.5 g m^{-2} knots can probably meet their requirements by completing their diet with *Hydrobia*.

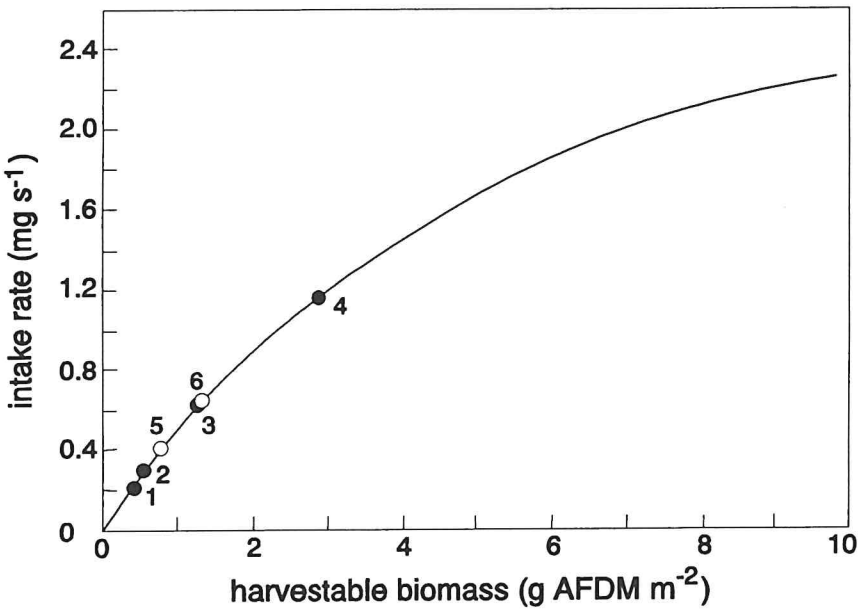

Fig.27. Functional response of knots feeding on *Macoma*. Closed dots indicate harvestable biomass of *Macoma* on Texel, open dots indicate harvestable biomass of *Macoma* at Westerhever. Numbers present the different periods. Note that intake rates are not the observed intake rates, the dots are plotted on the line to show attainable intake rates at certain levels of harvestable biomass.

Conclusions about whether the knots' premigratory mass gain is (partly) due to their own effort can not be drawn on the basis of the results presented. The increasingly better food situation apparently can, at least partly, fulfill the knots' premigratory needs. As shown above the decrease in thermostatic cost would create enough space for the knots to increase their body mass up to the required level. Therefore we believe that the most critical period is not the period just prior to migration, but the winter period during which the knots use up all the energy they are taking up for thermostatic and activity costs. Any unexpected cold spell demands payment in the form of grams body mass loss. The condition the birds are in at the end of the winter determines whether they will reach the required departure mass to be able to make the flight to Iceland or Siberia.

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