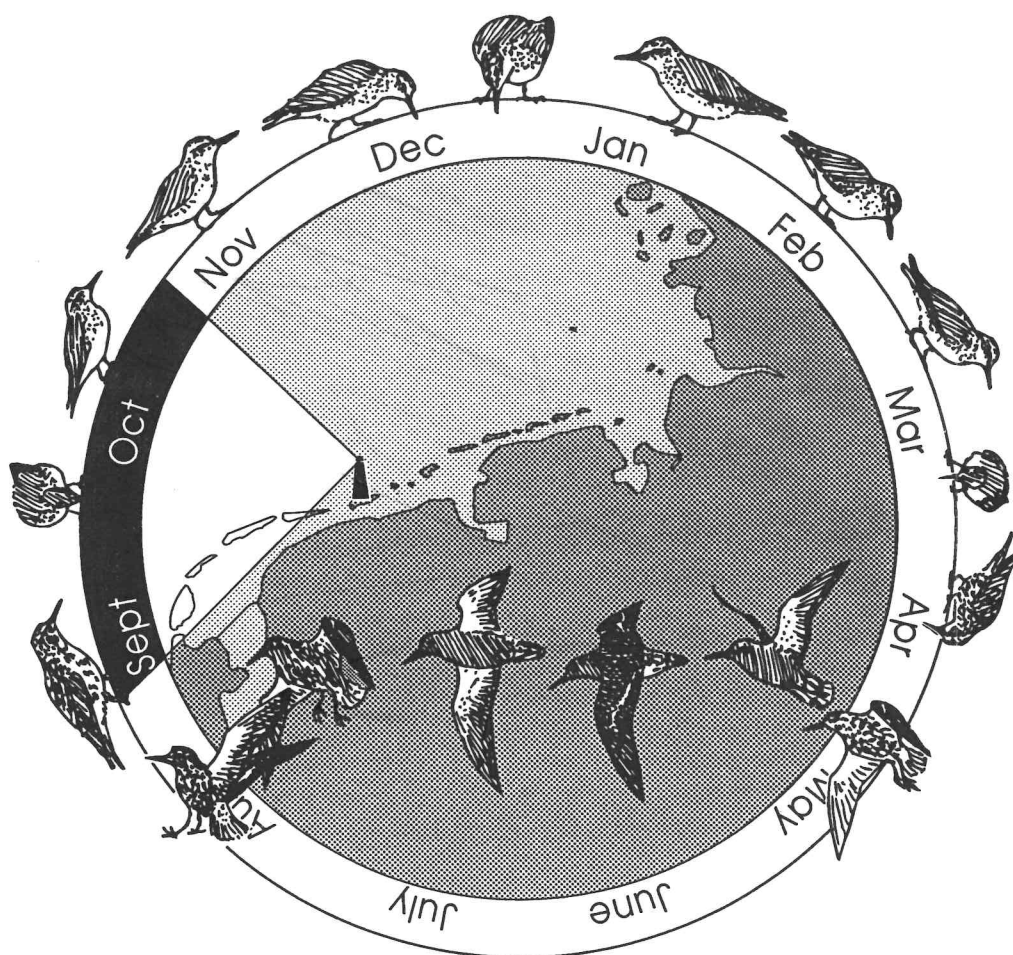


FEEDING ECOLOGY OF KNOTS AT SCHIERMONNIKOOG DURING AUTUMN 1990: DEEP *MACOMA* FORCE KNOTS' FORAGING EFFORT TO GREAT HEIGHTS

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MACOMA FORCE KNOTS' FORAGING EFFORTS TO GREAT HEIGHTS**

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ABSTRACT

Knots of the subspecies *Calidris canutus islandica* were studied while staging on the intertidal mudflats near Schiermonnikoog in the autumn of 1990. The question of this survey was whether Knots of the subspecies *C. c. islandica* wintering in the eastern part of the Dutch Wadden Sea are influenced in their foraging behaviour or even occurrence by the seasonally induced burying depth of their main prey *Macoma balthica* in the course of autumn. Do they get problems keeping a balance between energy intake (food) and expenditure (thermoregulation, activity) as a result of the deeper burying depth of *Macoma balthica*? From the end of August until the beginning of November time budgets and energy intake were determined. Moreover, prey sampling (both depth and density) took place at those places where Knots had been seen foraging. In this way food availability was estimated.

From the end of August about 20,000 Knots were present on the intertidal mudflats near Schiermonnikoog. This is 6 percent of the total population of the subspecies *Calidris canutus islandica*. The birds roosted on the island Schiermonnikoog, but for feeding the huge flocks flew to the intertidal mudflats in middle of the Wadden Sea. These areas turned out to be out of reach of the observers. Due to safety reasons the study area was restricted to the dead water area up to 2 kilometers south of the island. Within this range both observations of feeding behaviour of flocks up to a maximum of 1000 birds could be obtained as well as food availability assessments could be made.

In the study area the food availability of preferred size classes of Knots' main prey *Macoma balthica* turned out to be extremely low (0.5 g AFDM/m² or less). This low availability was mainly due to the burying depth of the *Macoma*. On average more than 85 percent of the AFDM of preferred size classes was out of the Knots' bill reach. In the course of autumn a significant decline in burying depth of *Macoma balthica* was found. Therefore, although the food availability was already low at the end of August, the Knots encountered a further decline in the food situation of *Macoma balthica* during the autumn of 1990. As a consequence, only 32 percent of the ingested AFDM was based upon *Macoma balthica*. Instead, the diet of Knots was dominated by small (< 13 mm) Cockles (*Cerastoderma edule*). On average 63 percent of ingested AFDM estimated from dropping analyses turned out to consist of *Cerastoderma edule*. The remainder 5 percent of the diet amounted to the mudsnail *Hydrobia ulvae*.

The Knots spent proportionally more time foraging during the low tide period in the course of the autumn. The most pronounced effect of increasing foraging time took place at the second part of the low tide period.

In the beginning of October Knots started to feed at dying/dead Cockles, which were lying in big quantities on the surface of the mudflats. During 2 weeks all 15,000 Knots present by that time were foraging on the mudflats in the dead water area and did not fly to the mudflats in the middle of the Wadden Sea anymore. Only small flocks were seen feeding in the ordinary probe-feeding manner. Feeding rate (prey/min) increased while feeding at this extraordinary, but temporarily prey type. Calculations of thermostatic costs revealed that Knots probably could not maintain a balance between energy expenditure and energy intake under the food conditions (*Macoma balthica* and small *Cerastoderma edule*) present on the intertidal mudflats near Schiermonnikoog. At the end of October, after two periods of low temperature and additive tailwinds, the Knots left the study area, probably for British estuaries.

INTRODUCTION

General introduction

Wader species *Charadrii* are well adapted to wet environments with many hidden prey types which are not detectable by eye. Most of the species, like the Knot *Calidris canutus*, are marked by a long bill with numerous minute tactile organs to localize prey in the soft soil and relatively long legs suitable for wading. The Knot is a long distance migrant which breeds in arctic regions. By breeding in the high north Knots take advantage of very short but enormous peaks in the food availability of adult *Diptera*. Especially the chicks are dependent on the emerging adult *Diptera*, because their bills are too short to thrust deep enough into the soil.

In order to escape from the severe arctic winter, when no food is available, Knots migrate south to temperate and tropical tidal ecosystems. These ecosystems are characterized by a high secondary production of benthic fauna, which means much food for Knots. Especially small bivalve molluscs belong to the main course of the diet. Knots detect such prey mainly by touch. The shells are eaten whole and thereafter crushed in the gizzard. One of the problems Knots have to deal with in these habitats is the fact that not all the food is available for them. For a probe-feeding wader such as the Knot, food availability is mainly determined by the burying depth of their prey. As adults, Knots again encounter the problem that their bills, although fully grown to 3.5 cm, can be too short to reach prey.

The concept of a long distance migrating wader results from a long process of natural selection. It is hypothesized that the common ancestors of the Knot lived during the Tertiary epochs, when the climate was much warmer without the real tundra regions (Van Rhijn 1984). During this period the ancestors of waders probably specialized in breeding in areas with a temporary but very high food availability in the form of *Diptera*-emerging peaks. These conditions can occur in swampy areas after seasonal river-floods or rainy periods. By the present climate these specific conditions occur in a large area of the arctic region. Nowadays, speaking in terms of evolutionary history, waders in general and Knots in special have to fly all over the world between habitats where is enough food to rear offspring and habitats where they can winter and are able to fuel enough energy reserves in such a rate that the breeding grounds can be reached within the limits of the annual time budget.

The Knot is an outstanding example of a bird species of which different subspecies meet different ecological pressures during their life cycle to maintain a balance between energy expenditure and energy intake. Kersten & Piersma (1989) have made clear that waders have to deal with high thermoregulation costs because they live in exposed and windy habitats. In comparison to other birds of the same weight, waders in general are energetically characterized by a much higher metabolic rate. In this way waders are able to counterbalance the larger loss of warmth due to the high conductances caused by the physical conditions encountered, while living on the intertidal mudflats and salt-marches. Remarkable fact is that of the different subspecies of Knots, *C.c. islandica* is the only subspecies which winters on temperate latitudes. All the others winter in tropical regions. Knots which winter in tropical areas avoid high thermoregulation costs, but on the other hand they pay a price for wintering in the tropics by a higher cost on migration. *C.c. islandica* which winter in temperate estuaries do have to cope with high thermoregulation costs (Piersma, Drent & Wiersma 1991). From this perspective it is interesting in order to

get insight in why different populations of Knots perform different migration strategies (temperate wintering versus wintering in tropical regions). A first step is to investigate the differences between the annual energy budgets of the different subspecies and to focus on the ecological and physiological factors which determine the limits of the annual energy and time budget. In this study we have focussed on the ecology of the *C.c. islandica* subspecies wintering on the intertidal mudflats in the eastern part of the Dutch Wadden Sea.

From above it follows that for the *C.c. islandica* subspecies food availability must be a very important ecological condition in order to accommodate a high energy expenditure by severe thermoregulatory demands and additional activity costs. Food availability could be so decisive for populations of the *C.c. islandica* subspecies that it restricts the possibility to winter at temperate intertidal mudflats. The Knot's main prey in the Dutch Wadden Sea, the bivalve *Macoma balthica*, shows a remarkable change of depth in the course of a yearly cycle. Especially during the periods when large flocks of Knots of the subspecies *C.c. islandica* are staging on the intertidal mudflats of the Dutch Wadden Sea *Macoma balthica* shows a decline or maximal depth (Zwarts & Blomert 1992, Piersma pers. comm.). Since organisms in general have to maintain a balance between energy expenditure and energy intake, we have investigated the effect of burying depth of *Macoma balthica* for the food intake and ultimately for the energy budget of Knots staying in the eastern part of the Dutch Wadden Sea near Schiermonnikoog. The study was carried out in the autumn of 1990.

The Knot

The Knot *Calidris canutus* is a wader of which at least five subspecies can be categorized all over the world. During the moulting and wintering season two subspecies of the Knot occur in the Dutch Wadden Sea, i.e. *C.c. islandica* and *C.c. canutus* (Roselaar 1983). The Knots that have been investigated for this survey belonged to the *C.c. islandica* subspecies. *C.c. islandica* originates from its breeding grounds in north-east Canada and Greenland and is present in western Europe from August until May. During this period large quantities of *C.c. islandica* can be present in the Dutch Wadden Sea. As already mentioned *C.c. islandica* is the only subspecies which winters on temperate latitudes. All the others winter in tropical regions.

Davidson and Wilson (1992) give an up-to-date review of the migration system of *C.c. islandica* wintering in Europe (see figure 1). Most important wintering areas for *C.c. islandica* are situated in Great Britain (e.g. the Wash). Probably all of the population reaches its moulting and wintering grounds in Britain, France and the Wadden Sea in autumn via staging areas in western Iceland (in late July-early August), where they pause to refuel for one or two weeks. According to Davidson and Wilson (1992) *C.c. islandica* only visits the Wadden Sea for moulting. After the moulting process has finished most Knots subsequently move to Britain and France to join others that have moulted there. Only a limited number of Knots actually winter in the Wadden Sea (Smit & Piersma 1989).

The other subspecies which visits the Dutch Wadden Sea is *Calidris canutus canutus*. *C.c. canutus* breeds in Siberia and migrates via western Europe to the wintering areas in Mauritania (Altenburg *et al.* 1983), Guinea-Bissau (Zwarts 1984) and South-Africa (Summers 1987). In the field no difference between *C.c. canutus* and *C.c. islandica* can be noticed. However, the Afro-Siberian subspecies has a somewhat longer bill and shorter wings as compared to the Canadian-European subspecies (Roselaar 1983). Moreover,

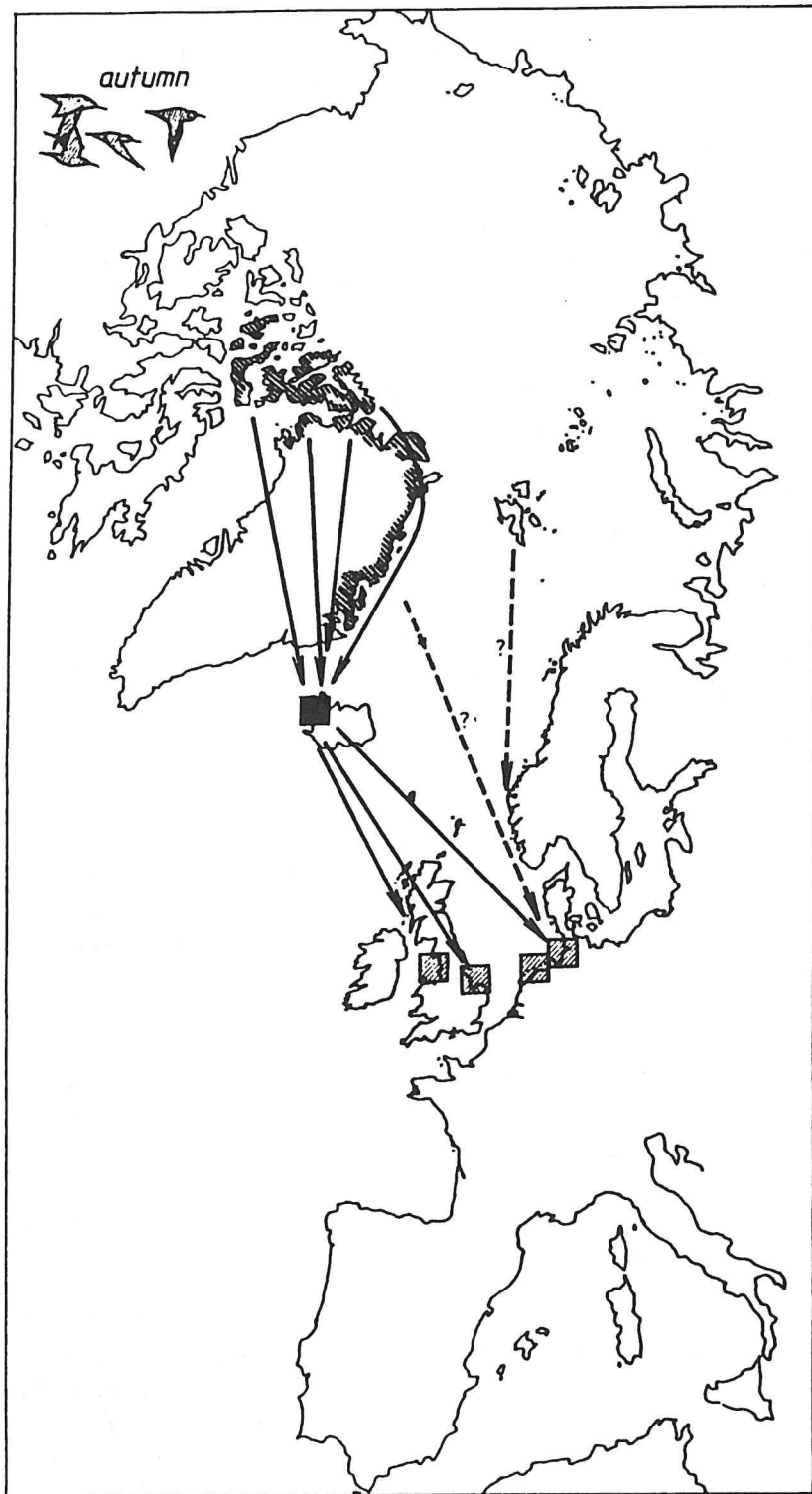


Figure 1. A summary of the autumn migration system of *C. c. islandica* given by Davidson & Wilson (1992). Breeding areas are shaded. The solid symbol indicates the main staging area, and the squares show according to Davidson & Wilson (1992) the main moulting areas.

recent research has hinted at differences in physiology between these two subspecies (Cadée 1992, Verboven 1992, and preliminary results of measurements of Basal Metabolic Rate from *C.c. canutus* wintering in Guinea-Bissau and South-Africa, pers. comm. T. Piersma, P. Wiersma & L. Bruinzeel 1993). *C.c. canutus* pass through western Europe for several weeks in late summer in July and August and in spring in April and May, taking a rest and fattening for their long way to Africa and breeding grounds in Siberia respectively. In these periods they can occur in the Tejo-estuary in Portugal (mainly spring), Vendée in France (ditto), Schleswig-Holstein in Germany (especially in spring) and in the Dutch Wadden Sea (both autumn and spring) (Dick *et al.* 1987).

The three remainder subspecies do not visit Europe. *C.c. rogersi* breeds in east Siberia and migrates to Australia and New-Zealand. *C.c. rufa* migrates from the breeding grounds in low arctic Canada to South-America. Another subspecies (*C.c. roselaari*) breeds on Wrangel Island (eastern Siberia) and in Alaska and migrates via the Pacific coast of North-America to as yet unknown wintering areas.

Zwarts and Blomert (1992) and Piersma (pers. comm.) have shown that in the Dutch Wadden Sea Knots are mostly specialized in feeding at the Baltic tellin *Macoma balthica*. Zwarts and Blomert (1992) calculated that from all the food present in the Dutch Wadden Sea *Macoma* from 10 to 17 mm are the most profitable prey items for Knots. Of all possible prey species, *Macoma balthica* is relatively the most profitable one, because of the combination of being lightly shelled (easily digestible), a high meat content (high yield per food item) and high densities (high encounter rate). When *Macoma* is not available Knots can be rather opportunistic in their food choice, feeding upon preys varying from Mussel *Mytilus edulis* to the polychaete worm *Nereis diversicolor* (Prater 1972; Goss-Custard *et al.* 1977; Reading and McGrorhy 1978; Evans 1979; Warner 1981; Summer and Smith 1981; Emms and Elston 1982; Davidson and Evans 1986; Crockford *et al.* 1986, Alerstam, Gudmundsson & Johannesson 1992) to even the eggs of the Horseshoe crab *Limulus polyphemus* by the *C.c. rufa* subspecies (Morrison & Harrington 1992). As a rule of thumb, probably the 'harvestable' species with the largest abundance in the feeding area is being eaten by Knots in case *Macoma* is not present abundantly. Where *Macoma* is available in large quantities this prey species is preferably being eaten by Knots (Prater 1972; Goss-Custard *et al.* 1977; Reading and McGrorhy 1978; Evans 1979; Warner 1981; Summer and Smith 1981; Emms and Elston 1982; Davidson and Evans 1986; Crockford *et al.* 1986, Zwarts & Blomert 1992, Dekinga & Piersma 1993).

The profitability of a prey is determined by the ability of Knots to detect and take up the shells out of the soil. Because Knots are searching for buried molluscs mainly by touch, Knots press their bill in a fast sewing machine manner up- and downwards in the soil. Therefore, the searching behaviour of Knots can be regarded as a random process of detecting and picking up prey items. According to the theory of the functional response (see Stephens & Krebs 1986) prey density and prey depth must determine the prey intake of Knots to a great extent in a passive way. Both Piersma, Van Gils & de Goeij (pers. comm.), using experimental obtained functional response curves, and Zwarts & Blomert (1992), using a theoretical model, have shown that food availability figures predict food intake of Knots in the field quite accurately. On the other hand, the rate at which food can be processed plays an important role in the profitability of molluscs as well. In comparison to *Macoma balthica* an alternative prey, the Cockle *Cerastoderma edule*, is characterized by a less favourable ratio between meat content and shell mass. This implies that the threshold to switch to this prey type by Knots will be at a higher level than expected on basis of density and depth only.

The Prey

Several studies on prey choice of the Knot in the Dutch Wadden Sea have already taken place. The results of these investigations suggest that in late summer the Knots mainly feed on *Macoma balthica*. *Macoma balthica* is a common species in the Dutch Wadden Sea. Of spat *Macoma*, many thousands can be present per square meter, of mature individuals several hundreds can be present per square meter. Large quantities of *Cerastoderma edule* are also present in the Dutch Wadden Sea, although distribution of this mollusc is rather clustered. Other abundant invertebrates are *Hydrobia ulvae* and the shrimp *Corophium volutator* (Beukema 1976; Zwarts 1988). During the autumn it has been shown that the diet of Knots can change from *Macoma balthica* to *Hydrobia ulvae* as most important prey item (Dekinga & Piersma 1993, Hoekstra 1989). This is probably due to the fact that the availability of *Macoma* decreases during autumn, since *Macoma* move deeper into the sediment in the course of the autumn. This has rather important implications for the proportion of *Macoma balthica* available (i.e. both detectable and accessible) for Knots. On the other hand, from the *Macoma*'s point of view; the deeper the burrow, the lower the risk of being taken by a predator.

The burying depth of the bivalves is partly dependent on their foraging methods. Generally, two kinds of foraging methods are being used: Suspension feeding and deposit feeding. Using suspension feeding, the mollusc extends its inhalant siphon to the surface. With this siphon water is being sucked in. After food particles have been filtered out the remaining water is excreted via the exhalant siphon. With deposit feeding the molluscs use part of their inhalant siphon to graze the surface around their burrow.

Cerastoderma edule uses only suspension feeding. Therefore the burying depth of *Cerastoderma edule* remains fairly constant throughout the whole year, i.e. 1-2 cm. There is an increase of depth with size and their burying depth in winter is larger than in summer, but these differences are marginal (Zwarts and Wanink 1989). The Cockles always remain within reach of the Knot's bill. Therefore it is not depth but strength and size which offers Cockles the best protection against the risk of predation by Knots. Because Knots swallow the molluscs as a whole they can only prey upon *Cerastoderma edule* < 14 mm. (Goss-Custard *et al.* 1977). The maximum size of *Cerastoderma edule* that can be swallowed by Knots is smaller than of *Macoma balthica*, because the width of the shell of *Cerastoderma edule* is wider than that of *Macoma balthica* (Zwarts & Blomert 1992).

Macoma balthica must be regarded as a deposit feeder, although the species can use suspension feeding too. *Macoma balthica* shows a large difference between summer and winter depth. During the spring when the production of benthic diatoms increases rapidly the feeding method of *Macoma balthica* changes from suspension to deposit feeding. Since deposit feeding requires a longer siphon, in order to extend the siphon out of the burrow, the burying depth decreases during this period. The *Macoma* is then more vulnerable to predators such as the Knot. In the course of the autumn the production of diatoms decreases forcing the *Macoma* to rechange to suspension feeding (Hummel 1985). Using suspension feeding the siphon does not have to extend out of the burrow. As a result the *Macoma* can move deeper into the substratum to avoid predation (Zwarts & Wanink 1989). Other factors which could influence the burying depth of *Macoma* are siphon cropping by flatfish, crabs and shrimps (in case of deposit feeding) and unfavourable physical conditions in the mud during the summer period due to oxygen shortage and high sulphur concentrations (pers. comm. P. de Goeij).

Aim of the study

Dekinga & Piersma (1993) and Hoekstra (1989) have shown that Knots of the subspecies *C.c. islandica* which stayed in the Dutch Wadden Sea in autumn and fed mainly on *Macoma balthica* encountered a deteriorating food availability, because in the course of autumn *Macoma balthica* buried deeper in the sediment, out of reach of Knots' bills. In this period the Knots switched to another prey type, the mudsnail *Hydrobia ulvae* (Gastropoda). Knots were probably forced to do so in order to maintain a balance in the energy budget.

From these findings the hypothesis has arisen that the burying behaviour of Knots' main prey *Macoma balthica* sets an important ecological limit in the wintering ecology of the *islandica* subspecies when staying in the Dutch Wadden Sea. To cope with the decline in the wintering situation the Knots have several opportunities. They can increase their foraging effort in order to increase intake rate, so more prey is eaten per time unit. Another way of dealing with the problem is an expanding of foraging time. The birds could spend less time resting and more time feeding during a low water period. But there are other opportunities as well, for instance a switch of prey type or just leave the area and find a better place to stay.

Thus, the hypothesis is stated whether Knots of the subspecies *C.c. Islandica* 'wintering' in the eastern part of the Dutch Wadden Sea are influenced in their foraging behaviour or even occurrence by the seasonally induced burying depth of their main prey *Macoma balthica* in the course of autumn. Do they get problems keeping a balance between energy intake (food) and expenditure (thermoregulation, activity) as a result of changing burying depth of *Macoma balthica*?

Plan of action

In order to investigate the hypothesis that the occurrence and the foraging behaviour of Knots at the Dutch intertidal mudflats is determined by the burying behaviour of their main prey *Macoma balthica*, the survey that has been conducted can be divided in three parts. A food availability sampling programme, observations of the behaviour of Knots at the same time and the transition of weather figures into energy expenditure figures according to the methods developed and described by Wiersma (1991).

The principle of this survey was to do observations of time-budgets and feeding rates of different groups of Knots to measure the energy intake. In combination with figures of digestion and food processing from experiments of Knots in captivity (Dekinga & Piersma 1993) energy intake figures could be obtained. At those sites where Knots had been observed food availability assessments were carried out in order to couple feeding rate measurements to food availability. Most of the time this sampling occurred one to three days after observations were made. In this way coupled samples of both behaviour and food availability from same sites were obtained in the course of autumn.

Measurement of available foraging time has been calculated from the exposure times of intertidal mudflats below + 25 cm N.A.P. These calculations have been carried out on basis of water level data obtained from Rijkswaterstaat. Field observations showed that Knots flew out from their roost when these sandy mudflats started to emerge.

To acquire figures of energy expenditure during the autumn period Knots have been observed. Weather data from the weather station at Schiermonnikoog (temperature and global radiation) and Lauwersoog (wind speed) have been used. According to the extended study of Wiersma (1991) with so-called heated taxidermic mounts, thermostatic costs for

C.c. islandica wintering near Schiermonnikoog could be calculated. Besides, the preliminary results of experiments with Knots feeding at artificial mudflats (Piersma & Poot in prep.) are used to estimate costs of foraging and other activities.

MATERIALS AND METHODS

Schiermonnikoog

The investigation took place at the intertidal flats south of the island Schiermonnikoog in the Dutch Wadden Sea ($53^{\circ} 28' \text{ N}$, $6^{\circ} 10' \text{ E}$). A little village is situated in the western part of the island. On the western and northern edge Schiermonnikoog is surrounded by sand dunes. The southeastern part of the island is a salt marsh traversed by several gullies. The salt marsh gradually passes into a large intertidal mudflat. For orientation three reference points were used: the ferry harbour, the beacon at Kobbeduinen and the beacon at Willemsduin (figure 2).

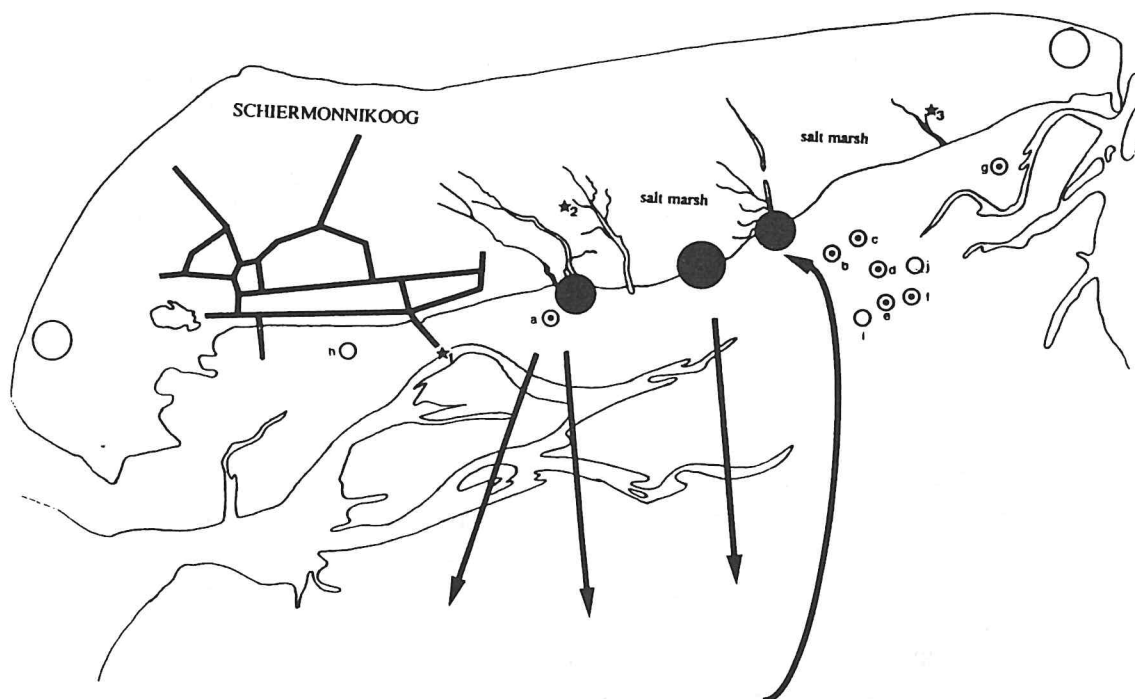


Figure 2. Map of Schiermonnikoog and the intertidal mudflats. The reference points are indicated by asterisks: *1 is the ferry harbour; *2 is the beacon at Kobbeduinen; *3 is the beacon at Willemsduin. Also the stations where density and depth samples were taken are indicated: ● both density and depth samples were taken; O only density samples were taken. The frequently used high tide roosts are indicated by closed circles. Open circles indicate the roosts during severe storms. Arrows indicate the flight movements to and from the feeding areas.

KNOTS

Observations

From the end of August until the beginning of November Knots of the subspecies *Calidris canutus islandica* were observed in 1990. Two different aspects of the feeding ecology were investigated: activity (time budgets) and feeding rate (number of ingested prey per time unit). Moreover, the average nearest neighbour distance in bird lengths was noted and regularly a plumage scan was made. The methods of observation of feeding behaviour are described below.

Observations took place with a 80-120x telescope (Questar) or with a 15-45x telescope (Bushnell). Nightly observations were trying to be made several times. This was done using a 500 mm light intensifier telescope (Olde Delft). Only observations in the twilight and in some moon light could be made with this light intensifier telescope.

The investigation period was subdivided into 4 three-weekly periods. Period 1 lasted from 28 August until 16 September (week 35, 36, 37), period 2 lasted from 17 September until 7 October (week 38, 39, 40), period 3 lasted from 8 until 28 October (week 41, 42, 43) and period 4 lasted from 29 October until 11 November (week 43, 44, 45). If possible the observations were started 3 hours before low tide and ended 3 hours after low tide. The low tide period was subdivided into 5 two-hourly periods. Period -2 lasted from 5 hours before actual low water until 3 hours before low water, period -1 lasted from 3 hours before until 1 hour before low water, period 0 lasted from 1 hour before until 1 hour after low water, period 1 lasted from 1 hour after until 3 hours after low water and period 2 lasted from 3 hours after until 5 hours after low water.

Activity and plumage scan

Of the flocks a representative part of birds was individually observed. The activity of the sampled individual was noted at the moment of watching. The following behaviours were distinguished: foraging (the bird was probing it's bill up and down in the soil or was pecking at the surface), preening (with it's bill the bird was probing at it's feathers), sleeping (the bird was standing on one or two legs with it's head turned backwards in the feathers of the back), walking (the bird was walking over the surface without pecking at the surface) and standing (the bird was standing on one or two legs with it's head kept forward). If the flock size was smaller than 400 birds the total group was scanned.

In the course of the observation period a plumage scan was made regularly. The following plumages were distinguished: summer plumage, 3/4 summer plumage, 1/2 summer plumage, 1/4 summer plumage, winter plumage and juvenile plumage. The summer plumage of the Knot can easily be identified with its brick-red underparts and brown upper parts. The 3/4 summer plumage is characterised as an almost completely summer plumage. However, in the upper parts some grey moulting feathers are already visible. Moreover, the red underparts of such birds contain some white moulting feathers which results in a rather pale appearance of the underparts. Birds that were the 1/2 summer plumage can be identified by the fact that half of the underpart feathers are already moulted into grey-white feathers. Hence the underpart seem blotching red and white. The upper part also contains many grey feathers. In the 1/4 summer plumage the moulting has almost been completed. Only few red summer plumage feathers are visible at the posterior end of the underpart (vent). The rest of the underpart feathers are grey-

white. In the upper part feathers almost no brown feathers are present. The winter plumage is characterized by grey-white underparts in which no red feathers are present any more. The upper part is completely grey without any brown feathers. The juvenile plumage resembles the winter adult, but the upper part feathers have strikingly black and white endings. Also, the breast tints to peachy.

Feeding rate

One bird of the group was individually followed during 5 minutes at most with a minimum of one minute. The plumage of the bird and the time at which a prey was captured was recorded. Of the 'captured' prey, type (bivalve or unknown small prey) and size were estimated.

MOLLUSCS

Prey sampling

At those places where feeding rates of Knots had been scored, the food availability was determined by prey sampling. Of the invertebrate species present in the soil the following species were sampled: *Macoma balthica*, *Cerastoderma edule* and the gastropod *Hydrobia ulvae*. Other bivalve species were found in too small quantities to be discussed in this report.

Density

A circular corer (185 cm² surface) was thrust 15 to 20 cm into the substrate. At each station 20 cores were taken out of the sediment. The samples were sieved on the spot over a 1 mm sieve. As *Hydrobia ulvae* is rather small, the sampling method for this species was somewhat different. At each station an additional 5 cores were taken out of the sediment. The upper 4 cm of these cores were sieved over a 0.5 mm sieve. The collected species were stored at -20 °C until processing.

Depth

Major fluctuations of depth could only be expected for *Macoma balthica*. Therefore, depth distribution was only determined for this species. The same corer was used as for density sampling. Before the core was taken a pin was pushed into the substratum. The pin had a horizontal metal plate which was pressed onto the surface of the soil. Then the core ($\pm$ 20 cm) was cut and placed on the mudflat. The original upper layer of the core, which was sometimes washed off by the above water, was marked by the metal plate of the pin. Thin vertical layers were scraped off carefully until a *Macoma* was found. The distance between the surface (metal plate) and the upper edge of the shell was measured. *Macoma* within 4 cm of the surface was collected in depth classes of 0.5 cm (0-0.5; 0.5-1.0; 1.0-1.5 etc.). Species deeper than 4 cm were gathered in depth classes of 1 cm (4-5; 5-6; 6-7 etc.).

Processing of the density samples

Of each station separately the density samples were processed. The length of each shell from every station was measured using vernier calipers (figure 3). Firstly the molluscs were divided into separate classes according to the species. The animals were then divided among size classes with a 1 mm difference (1,2,3,4 mm etc.). A valve was nominated 4 mm if its size was between 3.5 and 4.4 mm, a valve was nominated 5 mm if its size was between 4.5 and 5.4 mm etc.

Of each species (except *Hydrobia*) and each size class separately the molluscs were removed from their shells. The flesh of all animals was dried during 2 to 3 days in a ventilated stove at 60 °C. Hereafter, the dry mass (DM) was confined by weighing the dried individuals with an accuracy of 0.1 mg. Values for ash free dry mass (AFDM) were obtained by weighing the bodies again after incineration at 500 °C for 2 hours (after Klaassen 1984). The ash mass (AM) was determined with an accuracy of 0.1 mg. The ash free dry mass could then be calculated as the difference between the dry mass and the ash mass ($AFDM = DM - AM$). Figures of AFDM of *Hydrobia* were used from Dekinga & Piersma (1993). See further the paragraph about Faeces.

Processing of the depth samples

The length of each *Macoma* was measured using vernier calipers. Since *Macoma* was divided into classes according to the burying depth, the AFDM belonging to each depth could be calculated. However, using the depth sampling method, proportionally more small *Macoma* is overlooked than larger ones. Therefore, the results of the depth samples were only used in order to divide the assessed AFDM per square meter obtained by the density samples over the different depth classes. The AFDM belonging to each shell length was also known from the density samples. Hence, the total AFDM per square meter available for a Knot could be calculated.

DROPPING ANALYSIS

Reconstruction of the diet

On the basis of feeding experiments with Knots in captivity described by Dekinga and Piersma (1993) the consumption by Knots of AFDM of different shell species can be calculated. The principle of the methodology is to compute ingested AFDM of meat out of the dry mass of shell remnants retained on a 0.3 mm sieve. In combination with known length-specific ratios of AFDM/dry shell mass and a frequency distribution of ingested length classes total AFDM per dropping can be calculated.

In the field when a group of Knots had been observed for longer than one hour and the birds had left mostly 50 droppings were sampled. After drying at 60° C, the faeces sample was sieved over a 0.3 mm mesh to remove sand, organic material and the smallest shell fraction. Hereafter weight of the fraction was determined. Next step was to sieve the shell fragments over a 0.5 mm sieve in order to sort out the biggest fragments. In these samples most measurable items were found in order to arrive at a frequency distribution for the different prey types. Last task was to take sub-samples of the shell remnants in order to determine species-specific dry mass fractions.

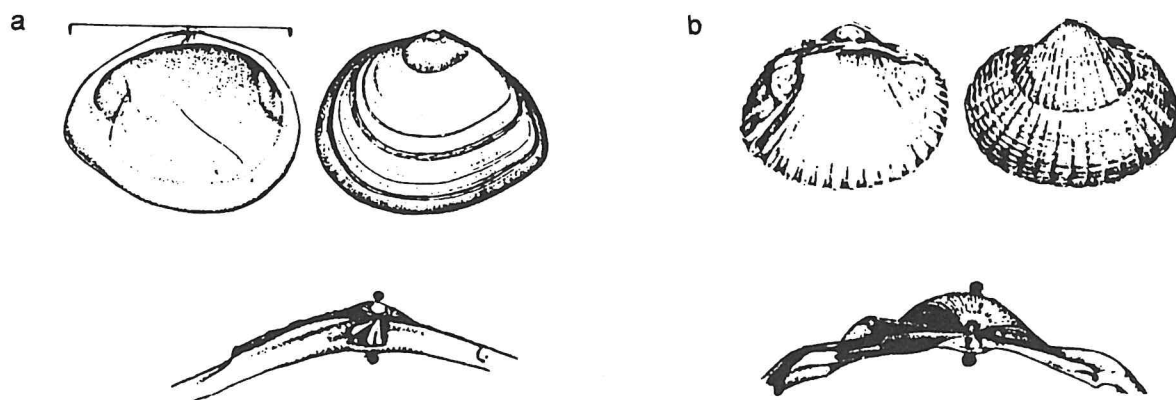


Figure 3. Indications of measurements of (A) *Macoma balthica* and (B) *Cerastoderma edule*. The measurements of the hinges are indicated by the closed dots.

In both *Macoma* and *Cerastoderma*, shell length is allometrically related to hinge and top height (see figure 3). In *Hydrobia* the width of the last whorl was measured to reconstruct ingested shells. However, in *Hydrobia* small shells are more likely to remain undamaged when passing the digestive tract of Knots than big ones. According to Dekinga and Piersma (1993) a correction for this has been executed. Measurements were done by using a binocular with an ocular micrometer. For more information we refer to Dekinga and Piersma (1993).

DATA HANDLING

Statistics

Statistical analysis were carried out using the Systat, Fastat and Statview software.

RESULTS

KNOTS

Numbers

The first Knots arrived at Schiermonnikoog in the afternoon 28 August. At the end of this week a total of 10,000 Knots was counted. The next week the number of Knots was doubled towards 20,000 individuals. The number gradually declined during the autumn but the major exodus took place from 15 to 21 October (week 42). Only 900 Knots were present in this week. A second departure took place between 29 October and 4 November (week 44). After 8 November no more Knots were seen in the study area (figure 4).

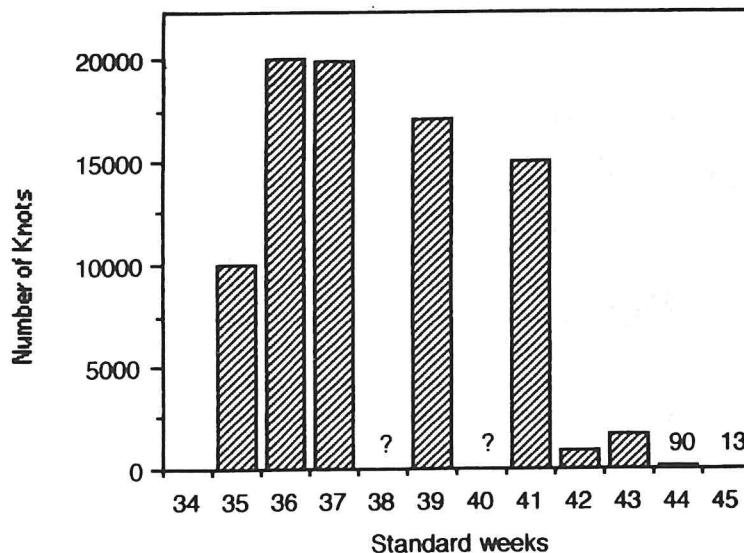


Figure 4. Number of Knots present at Schiermonnikoog during the investigation period. Per week the highest number of counted birds is plotted.

The main high-tide roosts of the Knots were between the third and the fourth gully on the borderline between salt-march and mudflat. However, occasionally during spring-tide in combination with stormy weather the regular roosting sites were flooded and could therefore not be used. The Knots were then forced to roost somewhere else. In these situations the Knots usually roosted on the east point of the island (de Balg). On 4 September 1990 the Knots were even compelled to roost on the east side of the North Sea beach due to severe storms (figure 1).

For safety reasons the study area was restricted to the dead water area up to 2 kilometers south of the island. Within this range both observations of feeding behaviour of

flocks up to a maximum of 1000 birds could be obtained as well as food availability assessments could be made. Foraging took place only during low tides. During these low tides the birds flew in groups varying from ± 30 to 2000 individuals towards the feeding areas. Unfortunately, the vast majority of the Knots flew in south-eastern direction to the mudflats in the middle of the Wadden Sea. This distance was far too big to bridge over by feet. As a result, activity scans and intake rates could not be obtained at those places.

Observations at night

During two nightly trips groups of Knots were heard at the intertidal mudflats. In those nights the birds had the opportunity to fly out from their high tide roost when daylight was still available. At 1 October a large flock was encountered during the night at the intertidal mudflats. With the use of the light intensifier, the birds were actually seen foraging. At this particular night the onset of exposure was far beyond sunset, so the birds must have fled out in darkness. Our survey has been concentrated on the behaviour of Knots during the daytime. See the discussion for more about nightly foraging.

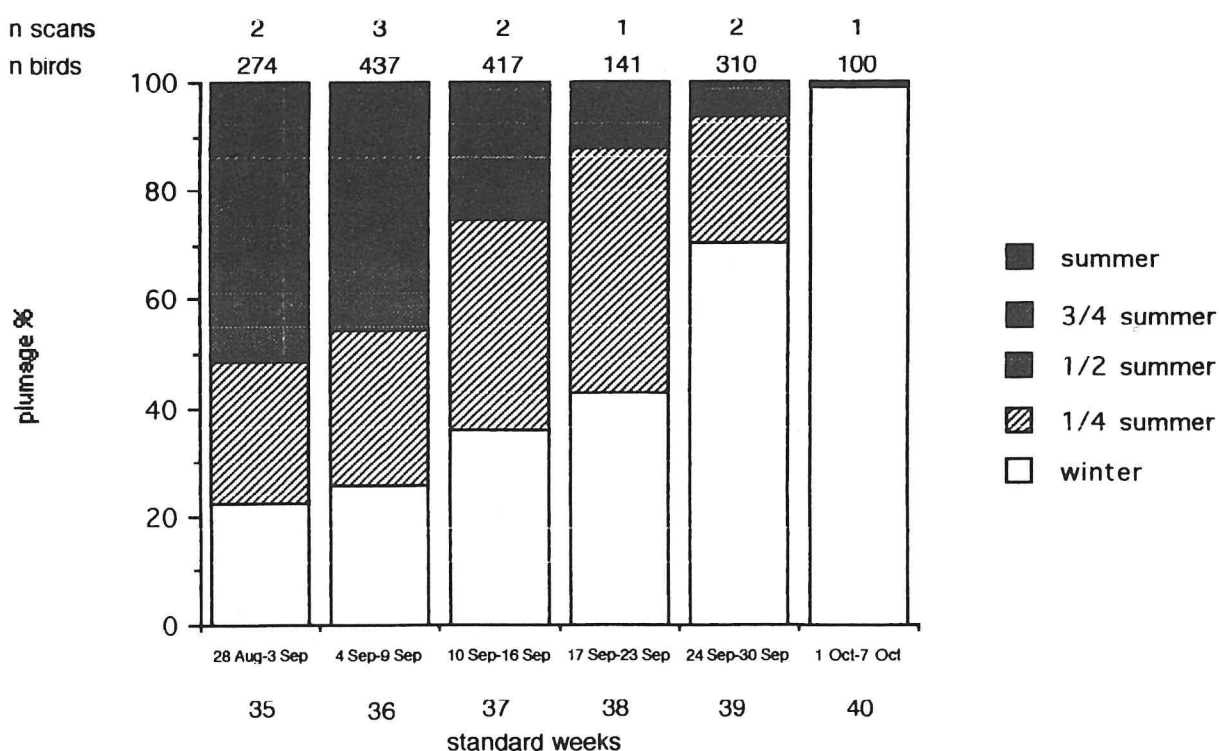


Figure 5. Plumage scan scores over a period of 6 weeks. Percentages of Knots in summer, 3/4 summer, 1/2 summer, 1/4 summer and winter plumages are indicated per standard week. A total of 12 scans was made.

Moulting of plumage

At the time the first Knots arrived at Schiermonnikoog only a small percentage of the birds was still in full summer plumage. Approximately 30 % had already moulted towards the 1/2 summer plumage, whereas about 20 % even were in full winter plumage. The

percentages of birds in summer, 3/4 summer and 1/2 summer plumage decreased gradually from there on. From the 4th of September until the 23th of September proportionally more birds moulted towards the 1/4 summer and winter plumage. However, from the 24th of September the percentage of 1/4 summer plumage birds decreased drastically as a result of moulting towards the winter plumage. From the first of October almost all birds had completed their moulting and were in winter plumage, although occasionally a 1/4 - or 1/2 summer individual was seen (figure 5). Only very occasionally (< 10 times) a juvenile bird, recognizable by a dark stripe along the feather edge, was seen.

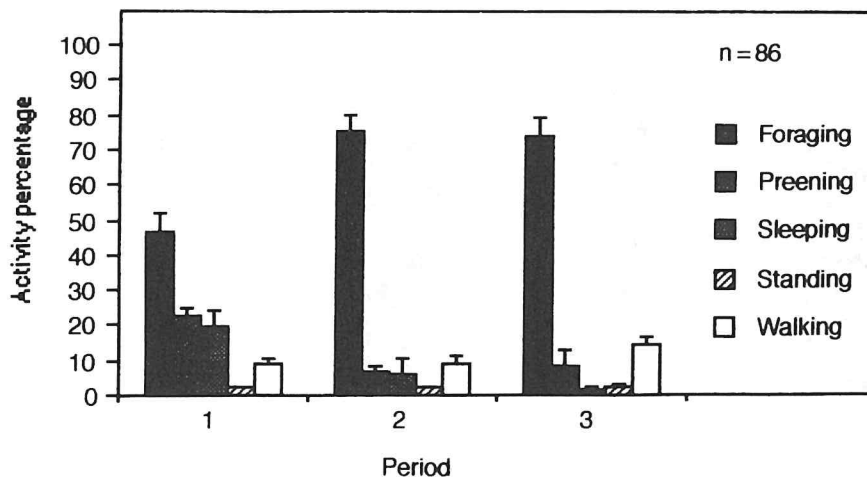


Figure 6. Changes in time budgets of Knots. From the results of the activity scans (n=86) the percentages of birds foraging, preening, sleeping, standing and walking were calculated. The percentages are presented in 3 periods of 3 standard weeks each.

Activity in the course of autumn

Activity scans have been used to calculate time budgets. The results are presented in figure 6. It can be concluded from this figure that Knots spent proportionally more time foraging during the low tide period in the course of autumn. This conclusion was confirmed by an analysis of variance of arcsin-transformed foraging percentages in relation to autumn period: (F-ratio: 14.342, $p < 0.001$, R^2 : 0.262). A following contrast test for verifying a positive trend in the data gave a significant difference as well (F-ratio: 26.121, $p < 0.001$, R^2 : 0.242).

Preening, sleeping and standing were significantly less performed in the course of time during the presence of Knots at the intertidal mudflats (Kendall Rank correlation test $p < 0.001$). Although the decline in the proportion of preening in the time budget can be a result of the ending of the moulting process, the decrease in the percentages time spent sleeping and standing is a strong indication that Knots indeed reserve more time for foraging in the course of autumn.

Interesting is that a slight increase in the proportion of walking in the activity scans

was found (Kendall Rank correlation test $p = 0.20$). Although the figure is not statistically significant, this finding can be considered as a trend. This result could indicate that Knots met an increasing difficulty in locating prey in the course of autumn. An alternative explanation is that the chance to scan walking behaviour have increased proportionally due to the increased foraging activity.

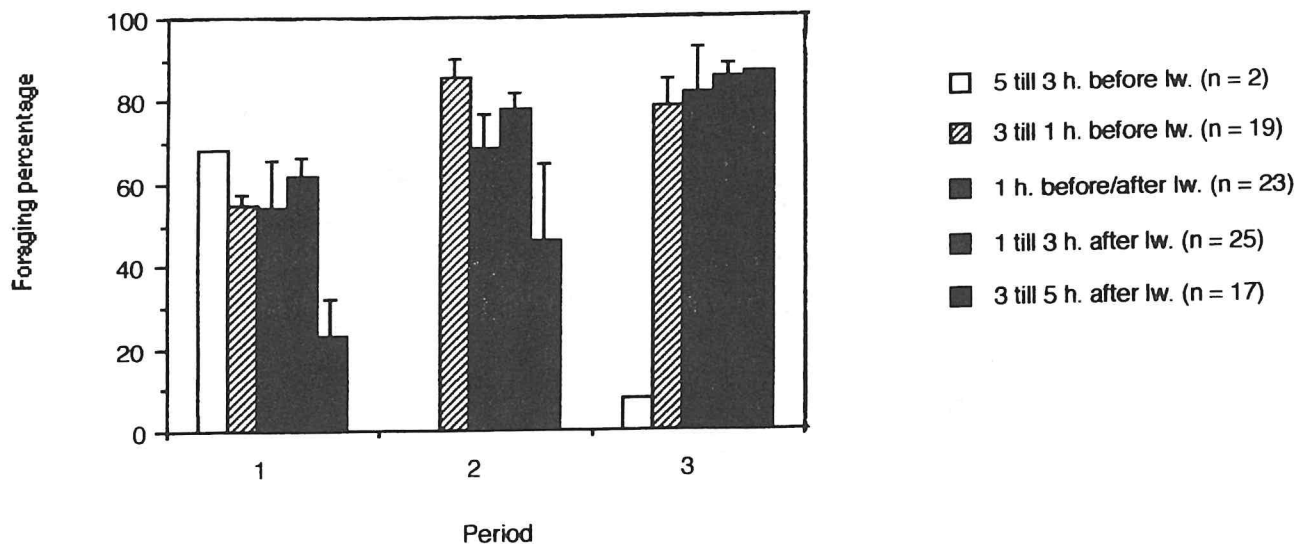


Figure 7. Foraging percentages (+ standard errors) during the low water period, presented per autumn period.

Activity patterns within the tidal cycle in the course of autumn

In figure 7 one can see how Knots change their time budget during the low water period in the course of autumn. In this figure the foraging percentages found by the activity scans are subdivided per 5 periods of 2 hours during the low water period, presented per period during the autumn. More time is spent foraging at the end of the low water period later in the autumn. Sleeping, standing and preening, behaviours which can be categorized as 'marking time', seem to be more and more restricted to the time spent at the high water roosts, when the intertidal mudflats are not exposed.

Arcsinus-transformed foraging percentages of different tide periods were tested by an analysis of variance in relation to autumn period. Period -2 and 2 are excluded from the analysis because too few or none observations in one or more autumn periods were obtained. Both during the period of 3 till 1 hour before and 1 till 3 hours after actual low water significant differences in foraging activity between different autumn periods were found (table 1). When executing the Kendall Rank correlation test the highest correlation coefficient was found for the period of 1 till 3 hours after actual low water (table 2). Apparently the most gradual effect of expanding foraging time occurred in the second part of the low tide period.

Table 1. Analysis of variance of foraging activities in different tides in relation to autumn period

Period during low tide	F-ratio	P	N
-1	8.413	0.005	16
0	1.508	0.245	23
1	6.028	0.008	26

Table 2. Kendall Tau Coefficients of foraging activities per tide period in relation to date

Period during low tide	Kendall Tau	P	N
-1	0.272	0.135	16
0	0.363	0.015	23
1	0.522	0.000	26

Remarkable in respect to the general foraging activity pattern during a low tide period is that during the period of actual low water no difference in foraging activity was found. The proportion of birds sleeping was found to be highest at the end of the low tide period and at low water. Moreover, the highest preening activity was observed at low water as well (figure 8). In Oystercatchers it has been shown that birds do not economize on the time spending on plumage maintainance (Leopold, Swennen & de Bruijn 1989). The pattern found in preening activity during the tidal cycle could be explained by the hypothesis that since the onset of exposure the birds' first aim is to satisfy their intake needs and that just after some time the birds start to spend time on other important behaviours like preening.

An additive effect which could occur during foraging is that the intake rate during the low tide periods can be higher than the rate of digestion, especially when feeding upon such 'hard to digest' prey as bivalves. As a result breaks in foraging bouts could be necessary to process the content of the stomach. This has been referred to as hidden feeding time. As a side effect these pauses create the opportunity for feather maintainance activities.

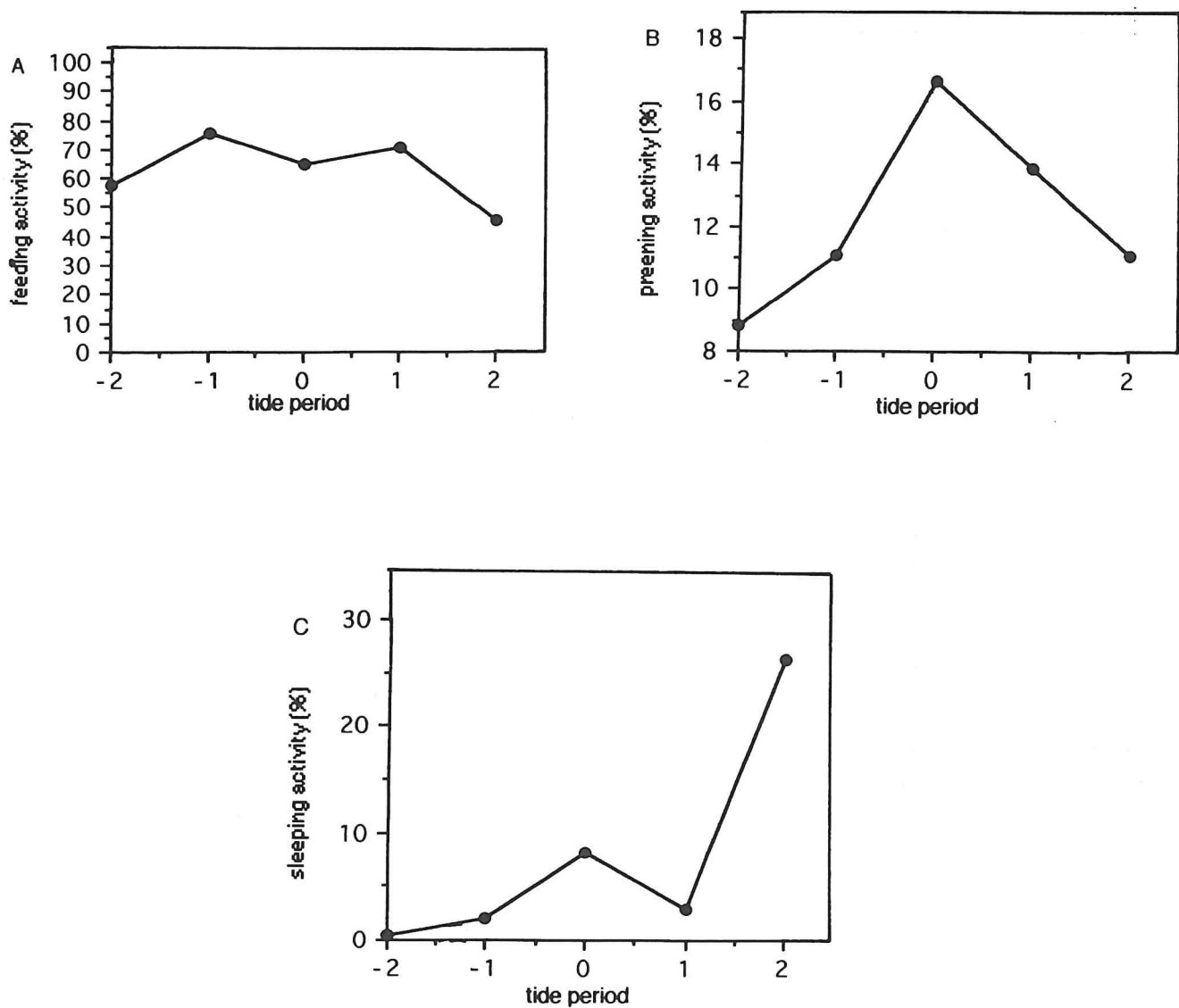


Figure 8. Activity changes within the tidal cycle. The proportion of Knots performing the activity is plotted against the low tide period. All activity scans of the entire investigation period ($n = 86$) were used. (A) Feeding activity, (B) preening activity, (C) sleeping activity.

Feeding rate in the course of autumn

Feeding rate was determined by observing one bird individually usually for five minutes but with a minimum of one minute. The numbers of prey eaten by the observed bird were noted. Only complete focal scans of exactly one minute have been analysed. We have

assumed that no bird effect exists and therefore have treated all obtained focal minutes as independent measurements of foraging success of 'the average Knot'. At some days no species of taken prey could be distinguished, so the feeding rate implies intake of both *Cerastoderma* as and *Macoma*. From the analysis of droppings it is known that a substantial part of the diet consisted of small *Cerastoderma*. The average feeding rate of Knots foraging on small bivalves (*Macoma* and small *Cerastoderma*) was about 0.4 prey per minute (figure 9).

When analyzing the feeding rate data per autumn period it turned out to be that the observed frequency distributions of numbers of prey per minute strongly followed Poisson distributions (Kolmogorov Smirnov one sample tests for all 3 autumn periods each $p > 0.995$, see table 3). Because of the data were distributed Poisson, the figures were transformed in square roots before executing an Anova to find any seasonal tendency of expected changes in feeding rates. No statistically significant differences in the feeding rate was found between the different autumn periods (F-ratio: 0.735, P: 0.471).

Table 3. Feeding rate (bivalve per minute) per autumn period.
Test of randomness.

Autumn period	Prey/min	Observed	Expected	G-test P
Period 1	0	37	39.54	0.995
	1	21	16.49	
	2	2	3.48	
	3	0	0.48	
Period 2	0	96	94.66	0.995
	1	34	35.68	
	2	6	6.73	
	3	2	0.85	
Period 3	0	30	32.2	0.995
	1	18	14.17	
	2	2	3.12	
	3	0	0.46	

Unfortunately, problems arose in determining prey intake due to unexpected opportunistic feeding behaviour of the Knots. From week 39 (period 2) onwards many dead Cockles were present on the surface of the tidal mudflats. Remarkably, these dead Cockles were all of lengths bigger than 25 mm up to 35 mm. Normally, these Cockles can

not be eaten by Knots because of their size, and thick and strong shells. But now dying, the Cockles had opened their shells and therefore the flesh was available. The cause of death of the Cockles is unknown but was probably due to oxygen shortage caused by the decomposition of a bloom of *Noctiluca scintillans* (Cadée 1990), which occurred massively during the investigation period (own observations).

Especially Oystercatchers *Haematopus ostralegus* and Herring gulls *Larus argentatus* were feeding upon the dead Cockles but also Knots changed their feeding habits to forage on these easy preys. In period 2 still some flocks of a few hundred Knots could be observed foraging in the ordinary probe feeding manner. In period 3, however, the Knots went massively over to feeding upon dead Cockles. Most of the time all 15,000 birds which were present around Schiermonnikoog were then foraging in the dead water zone south of the island, where most dead/dying Cockles were lying. After the food supply of dead Cockles had diminished, the huge flocks did not change from feeding area anymore. At the end of October, after two periods of low temperature and additive tailwinds, the Knots left the study area, probably for British estuaries.

Knots could be seen which spent several minutes on a dead Cockle, constantly pecking at it and tearing pieces of flesh from it. Regretfully, it became harder to score the feeding rate, for it was difficult to distinguish whether a bird had only pecked at a dead Cockle, or actually eaten some of the flesh. When Knots were feeding on dead/dying Cockles prey intake was scored when the Knot visibly tore a piece of flesh from the Cockle and ingested it. By using this criterium the feeding rate increased towards almost 1 prey per minute (figure 9).

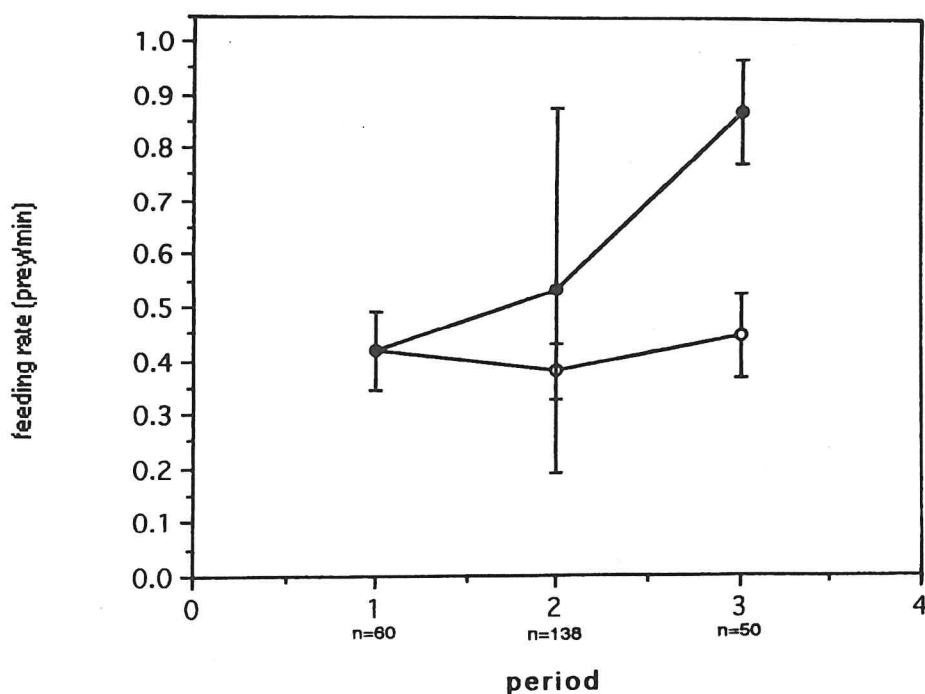


Figure 9. The average feeding rate in prey per minute ($\pm$ standard error) by each three weekly period. The heavily open dots indicate the feeding upon small bivalves i.e. *Macoma balthica* and *Cerastoderma edule*. The closed dots indicate the additional feeding rate which arose due to foraging on dead Cockles. In this behaviour 'prey-intake' was scored when the Knot visibly tore a piece of flesh from the dead Cockle and ingested it. The data are calculated from a total of 248 one-minute protocols.

Interactions

During the focal scans, in which a Knot was observed individually during several minutes, it was sometimes seen that the observed Knot drove away another Knot of the flock or vice versa. The interactions never lasted long and consisted mostly of a small peck towards the other bird or a little chase. Every interaction seen during the focal scans was noted. Although the total observation time was not the same for each period (61.8 minutes in period 1; 77.4 minutes in period 2; 79.3 minutes in period 3) a comparison of the number of interactions per minute is made between the periods. Of every period, the total number of interactions seen was divided by the total observation time of that period.

The number of interactions per minute between Knots gradually declined from period 1 to 3 (figure 10). As the Knots went over foraging on the dead Cockles, the distribution of the birds partly became dependent on the distribution of these Cockles. Since the Cockles were spread rather sparsely the distance between the Knots increased while foraging on the Cockles. The average nearest neighbour distance per period is depicted in figure 11. Although the increase from period 1 to 3 is not significant at 5%, it may be called a trend (t-test, $p = 0.06$). This increase in distance could explain the decrease of aggressive interactions between Knots.

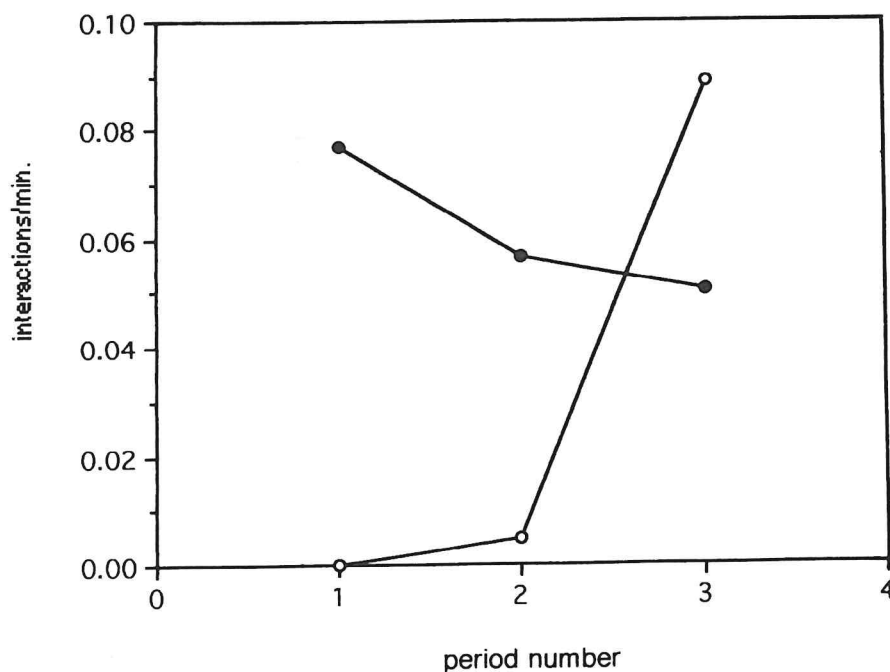


Figure 10. Change in average number of inter-and intraspecific interactions per minute during the investigation period. For each period separately the focal animal observations in seconds, obtained while scoring intake rate, were added and the average number of interactions was calculated. Closed dots indicate interactions between Knots exclusively, open dots indicate interactions with Oystercatchers and Dunlins.

At the moment the Knots begun feeding upon the dead Cockles aggressive interactions with Oystercatchers and Dunlins were observed. The Knots had become competitors of the Oystercatchers and were therefore sometimes chased away by the Oystercatcher, and occasionally by a Dunlin. Only one time it was seen that a Knot became aggressive against another wader species (Dunlin).

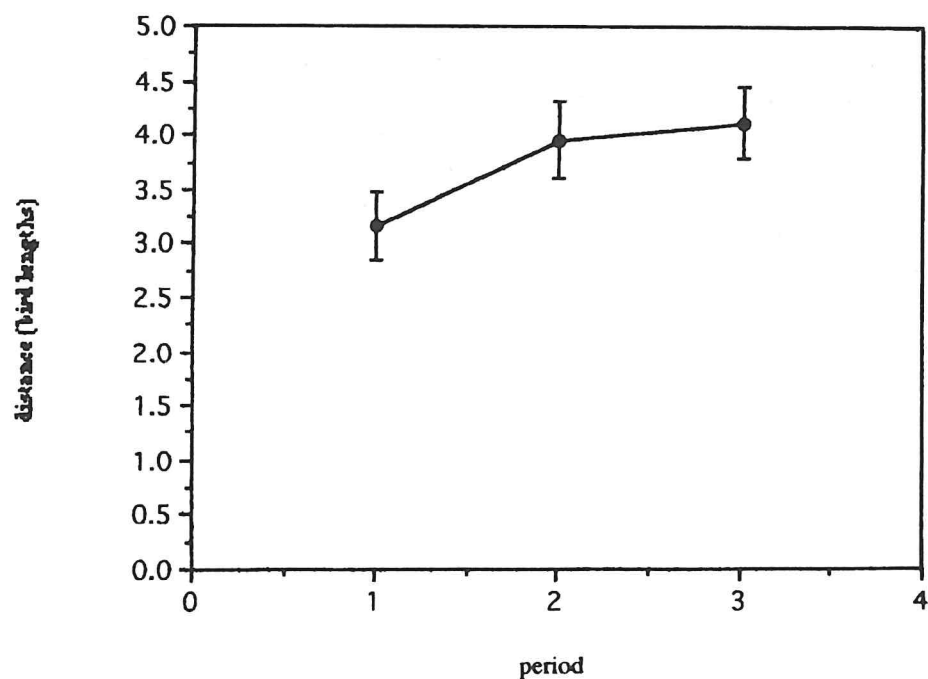


Figure 11. The average distance (in bird lengths) between Knots in a flock during the investigation period. data were scored during 31, 25 and 21 activity scans in period 1, 2 and 3 respectively. Bars indicate standard errors.

MOLLUSCS

Density distribution

Depth and density samples were taken at various places (stations) on the intertidal mudflats (figure 2). At most stations (a-g) both density and depth samples were taken. At the stations b and c respectively 2 and 4 combined depth and density samples were taken during the investigation period. The stations h, i and j were only sampled for density.

As can be seen from figure 12a the number of *Macoma* per square meter varied enormously between the different stations (51 at station j and 1262 at station c). This variance is mainly caused by the presence/absence of first year *Macomas*. Spat seemed to be most abundant at the highest parts of the mudflats. Edible Cockles were less abundant than *Macomas* although reasonable numbers were present (figure 12b). In figure 12c the total number of *Hydrobia* per square meter is depicted. This distribution is also rather scattered. Most remarkable is the absence of *Hydrobia* within the dead water zone.

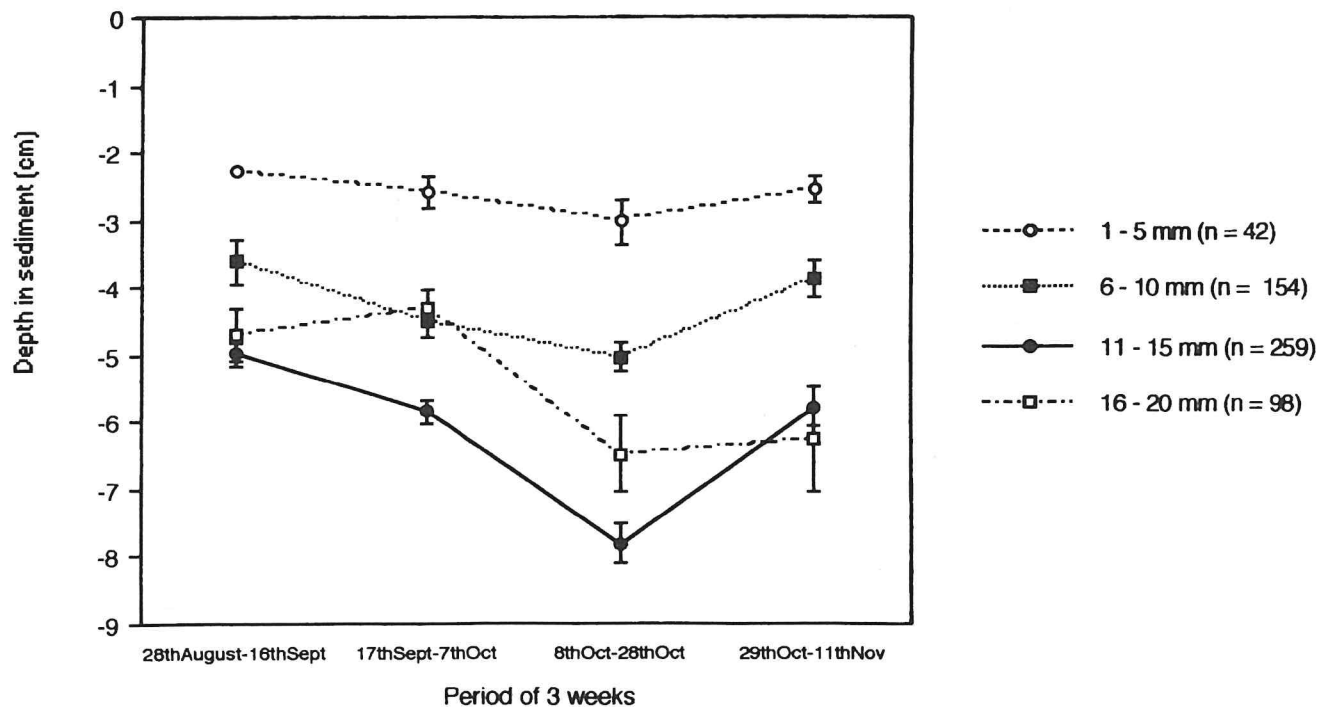


Figure 13. Change in depth distribution of four length classes of *Macoma balthica* during the autumn periods.

Burying depth of *Macoma* in the course of autumn

It is known that the burying of *Macoma* varies throughout the season. Usually, the depth in spring is less than the depth in winter. In order to describe the depth distribution of

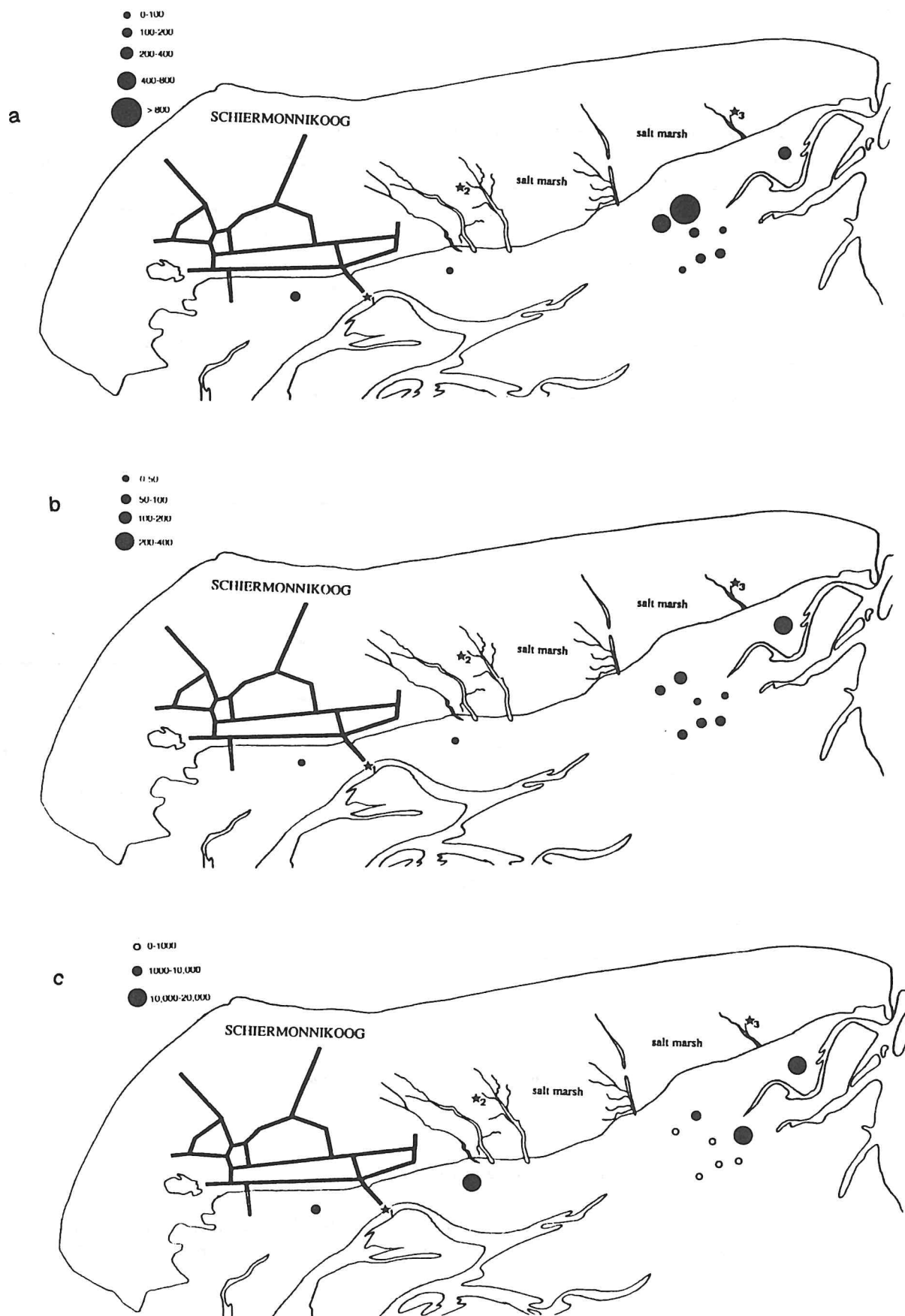


Figure 12. Number of molluscs per square meter at the stations where density distribution was determined. Densities at station b and c are the mean values of 2 and 4 sampling days respectively. (A) number of *Macoma balthica* per square meter, (B) number of *Cerastoderma edule* per square meter, (C) number of *Hydrobia ulvae* per square meter.

Macoma in the course of the investigation period the *Macoma* were grouped into four length classes of 5 mm each. The average depth of each size class per period is determined. The results are depicted in figure 13. All size classes, except those of 1-5 mm length, show a significant decline in depth from period 1 to 3 (table 4). However, in period 4 the *Macoma* had moved back closer to the surface. As a result the depth in period 4 is approximately equal to the depth in period 1.

Table 4. Analysis of variance of depth distribution for different size classes of *Macoma* in relation to autumn period

Size class	F-ratio	P	N
1-5 mm	0.414	0.744	42
6-10 mm	5.961	0.000	154
11-15 mm	25.727	0.000	259
16-20 mm	6.578	0.000	98

On average most profitable size classes of *Macoma* turned out to be already too deep for Knots in period 1. Which proportion is available for Knots will be further analysed in the discussion. Only *Macoma* of 1-5 mm were on average within the depth range in which they could be predated upon by Knots. The change in depth for this size class was not sufficient to move out of the reach of Knots. During the entire investigation period *Macoma* of 1-5 mm were available for Knots.

AFDM content in the course of autumn

The specimens of *Macoma* and *Cerastoderma* obtained by the density samples were used to define the mean AFDM per length class. Since a possible decrease in AFDM could occur in the course of the autumn as described for *Macoma* and *Cerastoderma* (Beukema & de Bruin 1977, Zwarts 1992) the study period was divided into 4 periods of 3 weeks each. The mean AFDM per length class was calculated for each period separately. The AFDM of both mollusc species is proportionate to shell length.

In order to test any decline in AFDM of *Macoma* a covariance analysis was employed. However, testing similarity between slopes of log-transformed figures of AFDM and shell length already gave significant differences. Since equal slopes are required to test covariance further testing of difference between intercepts was not allowed.

Eventually, regression equations of AFDM in relation to shell length have been calculated for the four 3-weekly periods. These equations have been used to make an assessment of the decline in AFDM content of *Macoma* of different shell length. The results of this treatment is presented in figure 14. A slight decline in AFDM can be seen from August till November. Although this decline can not be tested statistically the

conclusion can be drawn that the AFDM content already was at a low level in comparison with figures from Beukema and de Bruin (1977) and Zwarts (1992) from other years. Possibly a small decrease in AFDM has taken place in the course of the investigation period. According to the figures obtained by the above estimation method the decrease in AFDM during the investigation period could have been around 8 % at most for a 17 mm *Macoma*, the largest length class eaten by Knots.

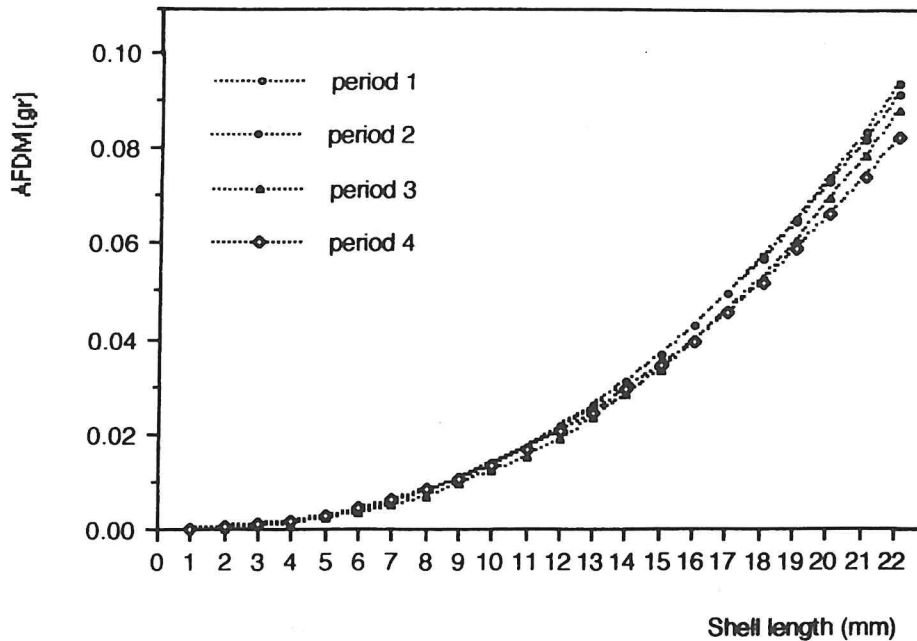


Figure 14. Shell length of *Macoma balthica* in relation to AFDM plotted separately for the autumn periods. For details of calculation see text.

Figures of AFDM content of Cockles during autumn showed a large variation in slopes between log AFDM in relation to log shell length was found. Thus, again no covariance analysis could be practised. In Cockles there exists a big variation in the occurrence of different length classes between the density samples of different stations. Actually, regressions of AFDM in relation to shell length for the four 3-weekly periods revealed a far from uniform tendency in AFDM change. The numbers found in the density samples are probably too scattered over the different length classes to find any trend which points in the direction the expected decrease in AFDM. Extrapolation from a few length classes will give rise to a big chance in variation between slopes of regression equations of AFDM in relation to shell length. Therefore, for further calculations all figures have been pooled in order to determine average AFDM numbers per length class.

Nothing can be said about an eventual seasonal change in AFDM of *Hydrobia* since these AFDMs were not determined. To our knowledge nothing is known about seasonal fluctuations in AFDM of *Hydrobia*.

FOOD INTAKE BY KNOTS

Prey selection

The *Macoma* present in the intertidal flats near Schiermonnikoog can be roughly distributed in two size (year) classes. The median length of the first size class is 5 mm, the main size of the second group is about 12 mm. However, the frequency distribution of *Macoma* eaten by Knots shows a different distribution (figure 15). *Macoma* of 11-17 mm were the most preferred sizes, with the 15 mm *Macoma* being the absolute favourite. *Macoma* with a shell smaller than 11 mm were rarely taken, and shell sizes smaller than 7 mm, although very abundant in the sediment, were never found to be present in the Knot's faeces.

No shift in length class selection of ingested *Macoma* could be found. The mean length of ingested *Macoma* for the compared periods (period 1 and 2 together and period 3 and 4 together) were almost similar, 14.4 mm and 14.6 mm respectively. An unpaired t-test on data of ingested length classes of *Macoma* for the two autumn periods revealed a non-significant probability of $p > 0.10$.

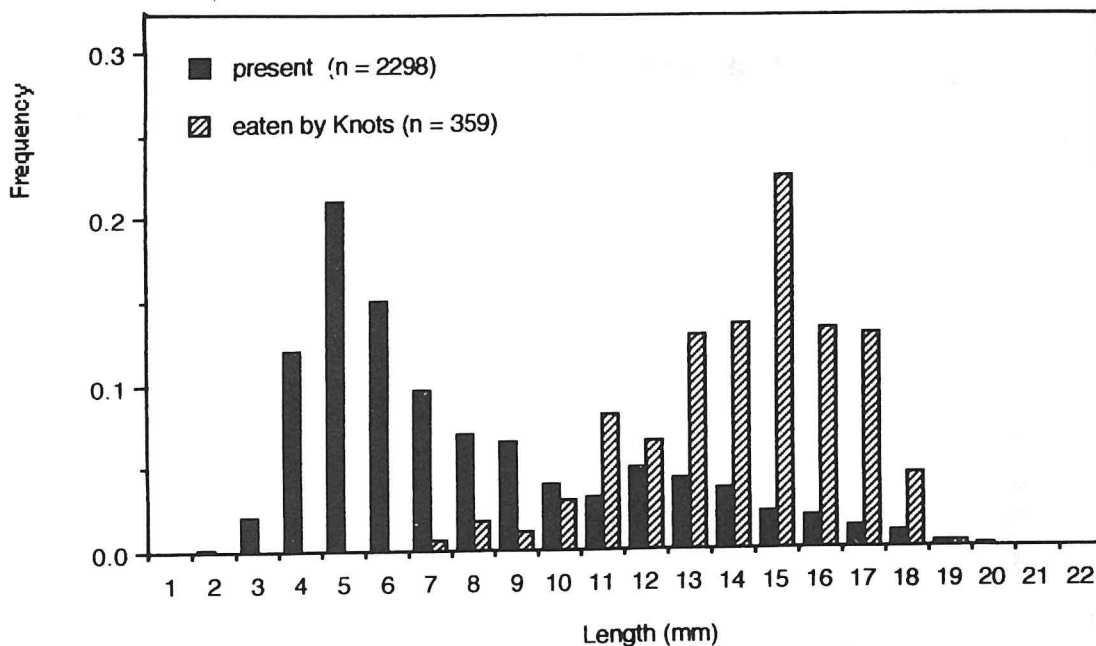


Figure 15. Frequency distribution of length classes of *Macoma balthica* in benthic (black bars; $n = 2298$) and eaten by Knots (shaded bars; $n = 359$). The shell length of macomas eaten by Knots were reconstructed on the basis of the heights of hinges retrieved from the droppings.

The size distribution of Cockles present in the study area showed a more complex pattern. Numerous Cockles were present in the range of 4-13 mm, probably first year specimens. Other high numbers were found in the size classes between 20-22 and 29-31 mm. But Cockles bigger than 15 mm can not be eaten by Knots because the shells are too big to be swallowed. Therefore, the sizes eaten by Knots as revealed by the faecal analysis were all between 4 and 13 mm.

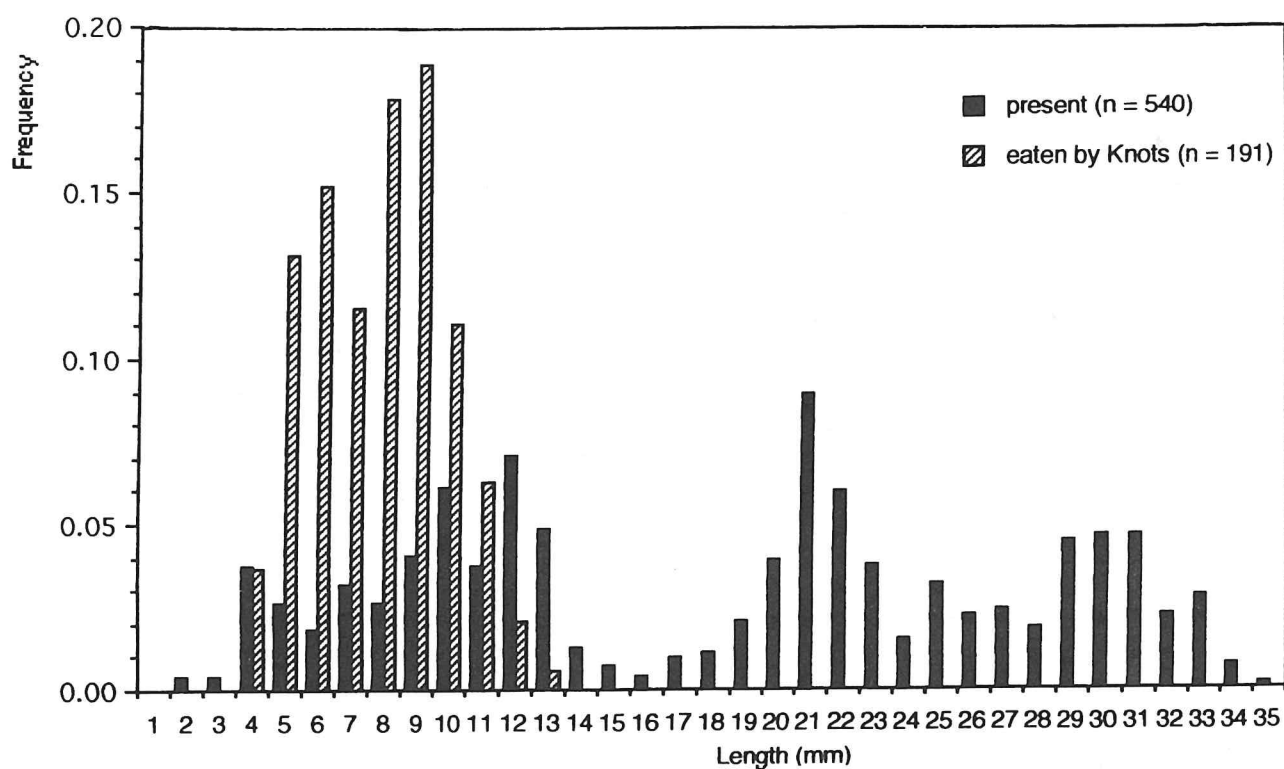


Figure 16. Frequency distribution of length classes of *Cerastoderma edule* in benthic (black bars; $n = 540$) and eaten by Knots (shaded bars; $n = 359$). The shell lengths of *Cerastoderma edule* eaten by Knots were reconstructed on the basis of the lengths of hinges retrieved from the droppings.

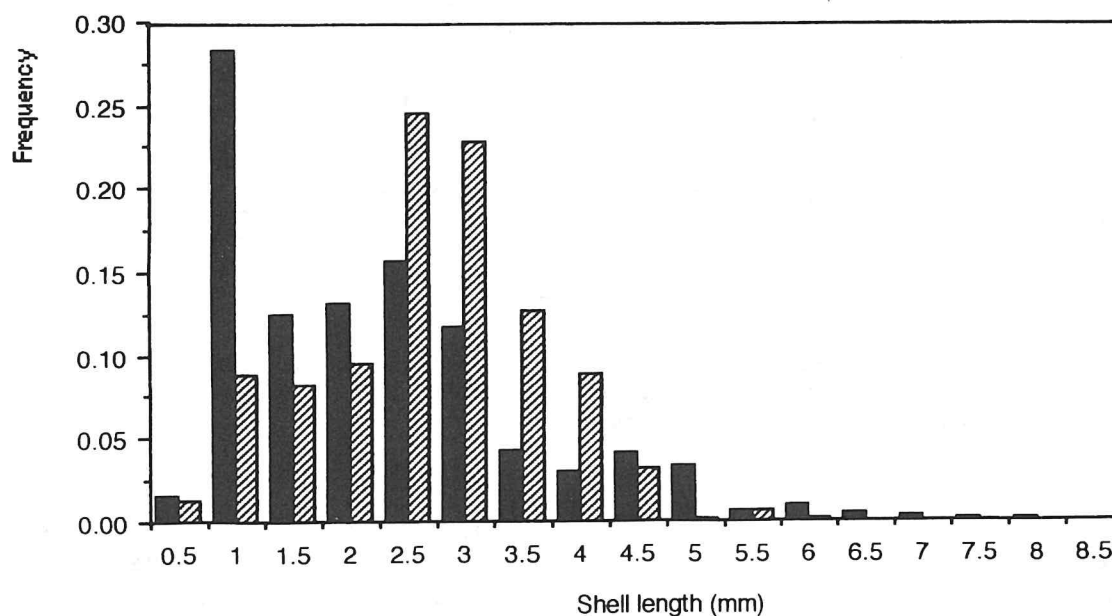


Figure 17. Frequency distribution of length classes of *Hydrobia ulvae* in benthic (black bars; $n = 4940$) and eaten by Knots (shaded bars; $n = 359$). The heights of *Hydrobia* eaten by Knots were calculated by measuring the width of the last whorl of broken *Hydrobias* in the droppings (height = $1.729 \cdot \text{width}^{1.729}$; Dekinga and Piersma in press).

The frequency distribution of *Hydrobia* present in the sediment and in the faeces of Knots is depicted in figure 17. The heights of *Hydrobia* eaten by Knots were reconstructed from the widths of broken *Hydrobia* found in the Knot's droppings. Knots preferred *Hydrobia* of 2.5-3.5 mm. *Hydrobia* smaller than 2.5 mm were also eaten, although less than would be expected on account of the distribution in the sediment.

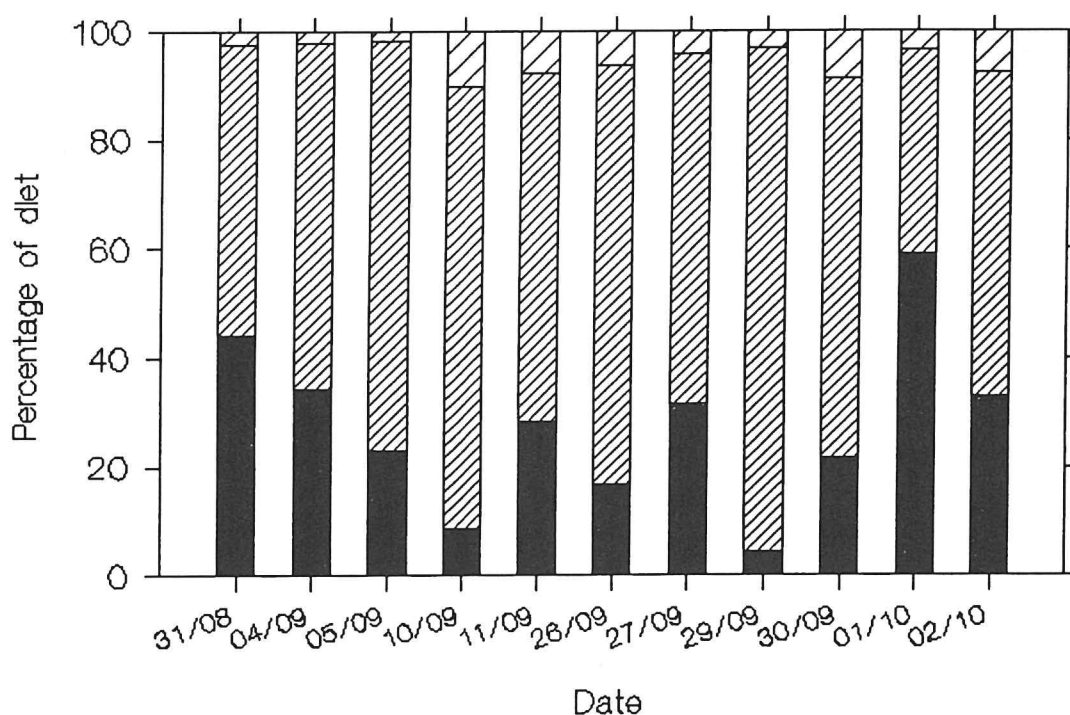


Figure 18. Knots' diet composition on 11 different dates. Lightly striped bars indicate *Hydrobia ulvae*, heavily striped bars indicate *Cerastoderma edule* and black bars indicate *Macoma balthica*.

Diet composition

The methods described by Dekinga & Piersma (1993) have been used to calculate ingested mg AFDM of different food types per dropping. By weighing shell remnants found in the droppings the diet of Knots could be reconstructed. Already at the start of the study period a big proportion of the diet (62.54 percent) consisted of small *Cerastoderma edule*, even in that extent that the surprising conclusion must be drawn that *Macoma* was not the main prey for Knots staging near Schiermonnikoog in the autumn of 1990. On average only 32.08 percent of the diet consisted of *Macoma*. There seems to be a tendency of a proportional decrease of consumed AFDM of *Macoma* in the beginning of the observation period and later on an increase again (see figure 18). Only a small proportion of the diet consisted of *Hydrobia* (5.38 %). No big changes in the total amount of ingested AFDM equivalents were found in the course of the autumn, although a substantial variation exists between the ingested mg AFDM equivalents of droppings collected on different days (see figure 19).

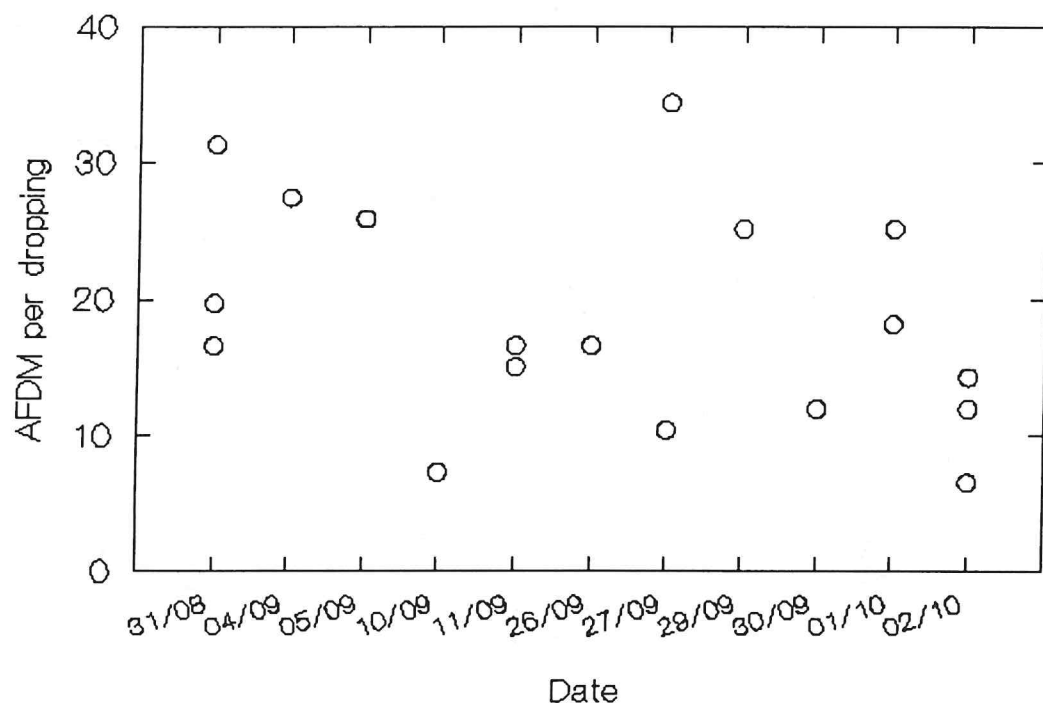


Figure 19. Mg AFDM equivalents of droppings in the course of autumn.

DISCUSSION

Why did Knots forage so far from their roost?

Although the intertidal flats near Schiermonnikoog are rich feeding grounds the dependence on particular size classes of small bivalves as food restricts the number of sites at which Knots are able to find enough food to counterbalance their energy expenditure (Evans and Davidson 1990). The food availability of *Macoma* and small *Cerastoderma* of the intertidal flats near Schiermonnikoog in general was very low (see further). Possibly the densities of small bivalves were more profitable on the feeding areas chosen by the majority of the Knots, the intertidal flats in the middle of the Wadden Sea. Unfortunately, due to the large distance, it turned out to be impossible for the observers to reach these feeding areas. Therefore no depth and density distribution of the benthic prey was determined at those patches.

For safety reasons the study area had to be restricted to the dead water area up to 2 kilometers south of the island. The questions arise how different the food availability in the study area was in comparison to the feeding grounds where the bulk of Knots were feeding during the first part of the observation period. Although the food availability in the study area was low still flocks of Knots of considerable numbers foraged on the intertidal mudflats south of Schiermonnikoog during the low water period. Question is whether the flocks of Knots we have studied were the losers of a mega-scale contest competition about favourable feeding sites or can we regard these birds as equal with the massive numbers feeding on the intertidal mudflats in the middle of the Wadden Sea? Did the birds feeding in the studied area encounter the same feeding conditions as the birds feeding on the intertidal mudflats in the middle of the Wadden Sea? We can only speculate about this, but it is likely that the areas near the mainland must have had a higher food availability than found in the study area. Zwarts & Blomert (1992) have shown that on the intertidal mudflats near the coast of Groningen Knots only fed at those spots with the highest food availability, which differed from year to year. Since all Knots present on the roosts at Schiermonnikoog started to feed on the dead Cockles within the studied area south of the island, we believe that we have monitored the decrease in ecological conditions for the whole population present.

Foraging activity in the course of the autumn

The question is whether Knots have increased their foraging time in response to the deteriorating climatic and food situation? Expanding foraging time is a way to increase energy intake on a medium time scale like a day to respond in behavioral sense on a negative energy balance. A negative energy balance could be the result of increased energy expenditure relatively to energy income per time unit. An increased energy expenditure can be caused by increased thermoregulatory demands due to harsher weather conditions in the course of autumn. A first execution was to investigate whether there is any seasonal correlation concerning the foraging activity with increased thermostatic costs. Also a comparison was made between correlation coefficients of alternative independent factors which could possibly determine the foraging behaviour of Knots as well (see table 7).

In table 5 figures of thermostatic costs are presented. These figures are calculated on

weather data from the weather station at Schiermonnikoog (temperature and global radiation) and Lauwersoog (wind speed) according to formulas of Wiersma (1991). When executing a analysis of variance of thermostatic costs in relation to autumn period a statistically significant effect was obtained (F-ratio: 5.826, P: 0.001, R²: 0.193). In addition, a regression of thermostatic costs in relation to the advancing days was carried out, which revealed a possitive correlation as well (F-ratio: 26.121, P: 0.000, R²: 0.242). These results agree with the idea that Knots have increased their foraging activity in response to the deteriorating climatic conditions in the course of autumn.

Table 5. Thermostatic costs in relation to autumn period

Autumn period	Mean	Minimum	Maximum	Std.dev.	N
1	1.826	1.317	2.349	0.346	17
2	2.292	1.871	3.353	0.412	21
3	2.226	1.478	3.075	0.472	21
4	2.311	1.670	2.825	0.313	18

However, another way Knots can build up a negative energy balance is to be restrained to go out foraging because the intertidal mudflats do not expose or expose very shortly due to the combination of the lunar cycle and strong wind effects. In this way Knots do not get the opportunity to acquire sufficient energy reserves to overcome the high tide period without using body reserves. It can be expected that when this situation arise Knots try to compensate during the following tide, so longer foraging times can be expected during tides following a short one.

In table 6 the results of linear regressions of arcsinus-transformed foraging percentages are presented in relation to the duration of the tide during which the observations were done and of one tide before. In this table the data of the independent factors have been standardized in order to be able to compare the correlation coefficients. No relation was found between foraging activity and the duration of the tide before, but in fact a positive correlation was found in relation to the duration of the tide the birds were actually foraging in. However, the variance explained by this regression is less than the result of the regression of thermostatic cost on date (see table 7). Moreover, the strongest correlation was found between foraging activity and thermostatic costs (see table 6). Therefore we think that increasing thermostatic costs is the most likely factor which explains the increase of foraging activity in the course of the autumn.

Still the occurance of short tides can not be ignored as an effect explaining the pattern of increased foraging activity. This is confirmed by the possitive relationships between both the duration of the same tide and the duration of one tide before and thermostatic costs (see table 8). The standardized coefficients for both regressions are of almost of the same magnitude. Moreover, for both the duration of the same tide as well as the duration of one tide before a statistically significant correlation exists. Therefore the conclusion

must be drawn that the duration of the tide is an additive effect explaining increased foraging activity caused by the simultaneous occurrence of short tides and high thermostatic costs on the same days. Apparently Knots compensate immediately within the same tide in case they experience a short exposure of the intertidal mudflats. The occurrence of a late onset of exposure of the intertidal mudflats could be a signal for Knots to forage at a higher activity level during the same tide.

Table 6. Regression of arcsinus-transformed foraging percentages in relation to standardized independent variables

Variable	Std.Coef.	F-ratio	P	R ²
Thermostatic costs	0.575	40.565	0.000	0.331
Date	0.492	26.121	0.000	0.242
Duration same tide	-0.523	30.794	0.000	0.273
Duration tide before	-0.128	1.368	0.246	0.016

Table 7. Regression of different dependent variables in relation to date

Dependent variable	Std.Coef.	F-ratio	P	R ²
Thermostatic costs	0.609	48.339	0.000	0.371
Duration same tide	-0.614	29.074	0.000	0.262
Duration tide before	-0.162	2.219	0.000	0.026

Table 8. Regression of the duration of tides in relation to thermostatic costs on the same day.

Dependent variable	Std.Coef.	F-ratio	P	R ²
Duration same tide	-0.614	49.703	0.000	0.377
Duration tide before	-0.402	15.806	0.000	0.162

Foraging at night

Our observations have shown that Knots indeed forage at night, a behaviour which can be expected from a mainly touch-feeding shorebird. During the daytime we have found a significant increase in foraging time. The question is whether a similar change has occurred during the night. From Curlews *Numenius arquata* staging in the Dutch Wadden Sea it is known that they do not forage at night in late summer, but later on in autumn they indeed start to do so. Probably Curlews start to forage at night in response to increased thermostatic demands (Zwarts et al. unpubl., in Zwarts et al. 1990). A similar pattern was found in wintering Knots *C. c. canutus* at the Banc d'Arguin in Mauritania. During the winter months no nightly foraging was observed, but in spring time during the pre-migratory fattening period the Knots exceeded their foraging time not only during the day, but also started to feed at night, even up to 50 percent of the exposure time (Zwarts et al. 1990). These results suggest that during the night Knots could have increased their foraging time even in a more extent than during the day. Unfortunately no observations can confirm this hypothesis.

During the period that Knots foraged at night it must be doubted whether the total amount of time spent at night at the intertidal mudflats is similar to the time spent during the day. Probably birds do not forage at nights with bad weather and/or bad light conditions. Finding spots with favourable food availability might be impossible in these circumstances. The functional response curve of captive Knots (Piersma, Van Gils & de Goeij pers. comm.) has showed that the choice of a feeding site could have important implications for the intake rate. Moreover, foraging at night could bring some risks, not only at night with bad weather and/or bad light conditions. This could be the reason why shorebirds do not feed at night in periods when no strong demands are imposed on them.

When conditions are good nightly foraging could be as efficient as daily foraging. However, Sutherland (1982) found that Oystercatchers selected smaller Cockles in the night than during the day. This difference can be explained by the fact that in daylight large Cockles are mainly detected by eye, while feeding at night Oystercatchers are fully dependent on the probing technique mostly seen in Knots. Sutherland (1982) calculated that due to this passive selection of smaller prey Oystercatchers could only reach 3/8 of the intake rate as observed during the day. Since we assume that Knots do rely on visual cues (see below), nightly foraging could also for Knots be less rewarding than foraging during the daylight period.

Prey selection

The size selection of ingested bivalve molluscs by Knots is set by the hard limit of the width of their bill nape. A few times we observed Knots having serious problems in swallowing a large bivalve. More regularly Knots were observed rejecting large bivalves by throwing them away after a single swallowing attempt. On the other hand the size selection of ingested *Macoma* and *Cerastoderma* probably occur mainly through passive prey selection. The surface of a small sized bivalve exposed to a foraging Knot, the so-called effective touch area (Zwarts & Blomert 1992), is relatively smaller than that of a larger bivalve. In other words, if a Knot is probing into the soil at random the chance of detecting a large bivalve is biggest, provided that equal numbers of all sizes are present. Therefore, the size of captured prey will passively shift to the larger ones compared to the distribution in the sediment.

In addition, Knots could actively select for the larger bivalves. A Knot has to decide whether not to select at all, to select the larger bivalves (more energy, easily detected, but most of the time less abundant than small bivalves) or the smaller bivalves (less energy, less easily detected but at some places in some years very abundant). The time spent searching (depending on density and depth), the handling time after selection (depending on size and depth) and energy content of the prey (depending on prey species and size) have to be weight on against each other to select the most profitable *Macoma* and *Cerastoderma* size. We assume that natural selection has shaped Knots to be able to make such an assessment on basis of the success of their foraging efforts. Since the highest intake rate ('the optimal intake rate') does not have to be the 'best' intake rate, we suppose that Knots make the 'right' selection in order to arrive at the 'right' intake rate possible under the prevalent food availability conditions. As Piersma (1991) has presented Knots wintering in tropical regions take smaller bivalves than expected on basis of optimal foraging theory. When energy demands are low Knots probably avoid high intake rates in order to minimize the risk of physical injury by swallowing large bivalves. Also in Oystercatchers 'suboptimal' food intake was found under less energetic stressing circumstances. Birds in captivity feeding on natural prey (Cockles) took smaller bivalves in summer, probably in order to minimize the relevant risk of bill breakage (Swennen, de Bruijn & Leopold 1991). It is likely that the Knots staying in the Dutch Wadden Sea during autumn and winter go for the 'optimal food intake'.

Only a small proportion of the diet consisted of *Hydrobia*. In the course of the autumn 1990 no shift was found in the diet towards this benthic prey species as was expected (Dekinga & Piersma 1993). Although Zwarts and Blomert (1992) and Dekinga and Piersma (1993) have shown that small *Hydrobia* pass the digestive tract of Knots more undamaged than larger *Hydrobia*, Dekinga and Piersma (1993) found that of ingested *Hydrobia* only up to 23 percent remain intact when passing the digestive organs of Knots. Since a proportion of about 70 percent intact *Hydrobia* was found in the droppings the idea came about that the high proportion of intact *Hydrobia* could be due to accidentally sampling of benthic *Hydrobia*. When droppings are collected some sand from the surface is taken as well. Because no correlation was found between the amount of sand sampled with the faeces and the total numbers of *Hydrobia* in the droppings (F-ratio: 0.234, p: 0.6) we do not believe that a part of the *Hydrobia* in the droppings came from accidentally sampling. Zwarts and Blomert (1992) calculated that *Hydrobia* smaller than 2 mm is not profitable for Knots because it's energy content is too low in relation to the handling time. Preliminary results of video analysis (Van Gils in prep.) has shown that peck rates and handling time are higher than used by Zwarts & Blomert (1992) in their calculations

(Gerritsen (1983)). This means that when only small *Hydrobia* is available Knots can forage profitably on *Hydrobia* smaller than 2 mm. The same holds for Knots foraging on small *Macoma*. Food availability assessments and dropping analyses of Knots of the autumn 1991 near Griend have revealed that Knots indeed take spat of *Macoma*, when no alternative prey is available (Piersma pers. comm.).

Food availability

Food availability is in case of Knots feeding on *Macoma* and small *Cerastoderma* a result of density and depth of prey. For a probe feeding wader like the Knot being successful in finding a prey can be regarded as a random process of detecting shells in the mud in case Knots mainly feed by touch. However, it is not exactly known to what extent Knots use other cues to find their prey. According to our own observations we presume Knots use visual cues to find prey as well. Indeed birds were observed slowly walking at a constant speed while moving the bill like the needle of a sewing machine halfway into the mud. In this way Knots probably are not searching for prey at great depths and feed by this method mainly by touch (and taste?). On the contrary, in other instances Knots were seen walking around a lot, stopping at certain spots and pressing the bill and even a part of the head completely into the mud and picking up *Macoma*. In these occasions Knots probably detected the *Macoma* at first instance by sight and were feeding deeper than the 2.5 cm described by Zwarts & Blomert (1992). Also Knots feeding on an alternative prey as *Nereis diversicolor* clearly detected the prey by eye (pers. comm. Tulp, Verkuil & Piersma).

We believe that the way prey is detected is not only in direct response to the occurrence of the prey type Knots are feeding on, but it is also determined by the density and depth distribution of the prey which is preyed upon. On basis of above mentioned observations we hypothesize that in case a high food availability of shallow buried *Macoma* is present, Knots will in accordance with optimal foraging theory adapt their searching strategy in order to detect prey in the most efficient way (Stephens & Krebs 1986). In case of a high food availability Knots can increase the rate of energy intake by feeding at a shallower depth and mainly feed by touch. In this way the findability of the prey is hardly influenced (perhaps even in a positive way) while the handling time can be minimized. When the food availability of *Macoma* is low, it is most profitable for Knots to select suitable micro spots by visual cues first and then find the shells by touch or taste in second instance. A cue which could point at a buried *Macoma* could be the hole of a siphon or a siphon itself. During the period when *C.c. islandica* visits the intertidal mudflats of the Dutch Wadden Sea, not only the burying depth of *Macoma* change, but probably also the activity of *Macoma*. This could imply that in case of a vast population of inactive and therefore inaccessible prey the best foraging method is by feeding by the few marks of siphons at the surface of the mudflats, which do point at certainly available *Macoma*. We suppose that for a foraging Knot it is the best to go for these marks in a world of unavailable and inactive *Macoma*. In these conditions it is not profitable to forage mainly by touch anymore, because most *Macoma* are buried too deep to be detected and/or captured.

Finally, when calculating the food availability of *Macoma balthica* for Knots the question arises up to what depth Knots are able to detect and to pick up *Macoma* from the sediment. Zwarts and Blomert (1992) argue that if Knots have to take up shells from the substratum they need to be capable of enclosing the prey. Because bills of Knots are of an average length of approximately 35 mm Zwarts and Blomert (1992) think that Knots can

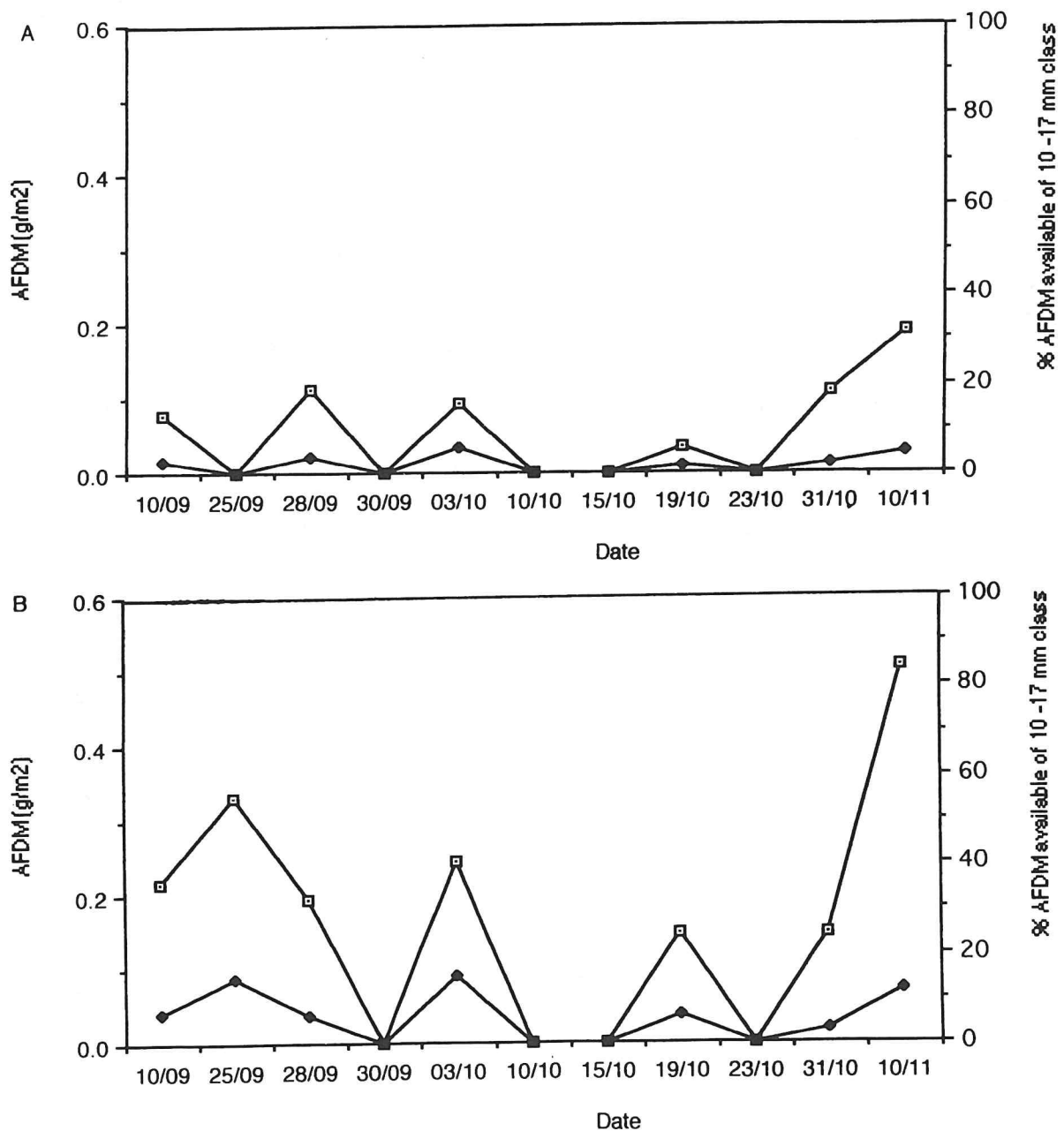


Figure 20. Food availability during autumn. (A) Profitable *Macoma* of 10-17 mm within bill reach of 2.5 cm. (B) Profitable *Macoma* of 10-17 mm within bill reach of 3.5 cm. Open squares indicate AFDM in gram per square meter (left Y-axis), closed squares indicate the percentage of available AFDM (right y-axis).

only forage efficiently at their most preferred *Macoma* of length classes around 15 mm when these shells are buried at a depth of 2.5 cm or less. However, they investigated migratory flocks of the subspecies *C.c. canutus* which visit the intertidal mudflats of the Dutch Wadden Sea during the late summer for just a few weeks. In this limited time period these birds store large amounts of body reserves for their flight towards their wintering sites in tropical Africa. By that time the food availability for Knots is much better than

during the autumn due to the shallower burying depth of *Macoma Balthica*. This could be the reason why Zwarts & Blomert (1992) observed a much shallower foraging depth than observed by us.

Because we observed that Knots fed deeper than 2.5 cm we have executed two calculations of food availability, one of 10 to 17 mm *Macoma* up to 2.5 cm depth and one of the same length classes within bill reach of 3.5 cm. According to Zwarts and Blomert (1992) the most profitable prey are *Macoma* of 10 to 16 mm length. Since we have found a substantial proportion hinges of 17 mm *Macoma*, we have also included these length classes into the calculations of total food availability at the sampled monster stations. The results are presented in figure 20. When comparing the figures of 2.5 cm and 3.5 cm detectable depths the conclusion must be drawn that most *Macoma* were indeed out of reach for Knots' bills. However, 1 cm detectable depth more made a lot of difference in the food availability of the bigger, preferred *Macoma* of 10 to 17 mm length. By this exercise considerable differences concerning available AFDM are obtained between 50 up to 100 percent for different stations. But still these figures point at a very low food availability of *Macoma balthica* in comparison to other studies. Zwarts and Blomert (1992) have shown that when Knots are specialized in feeding at *Macoma balthica* they mostly feed at mudflats with a food availability of more than 10 gram per square meter.

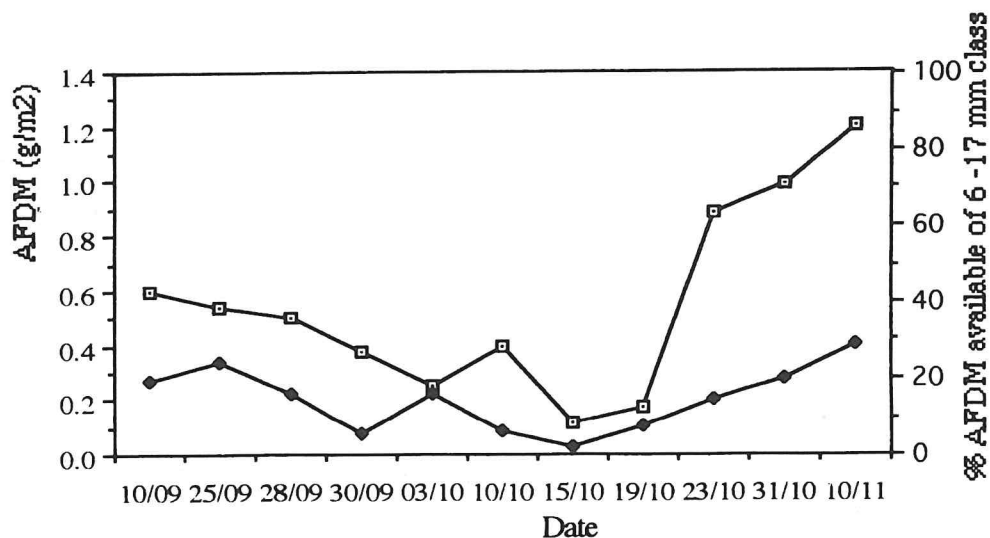


Figure 21. Food availability during autumn. Profitable *Macoma* of 6-17 mm within bill reach of 3.5 cm. Open squares indicate AFDM in gram per square meter (left Y-axis), closed squares indicate the percentage of available AFDM (right y-axis).

Highest food availability figure determined at a station on the intertidal mudflats near Schiermonnikoog in the autumn of 1990 amounted to little more than 0.4 gram AFDM per square meter with a bill reach of 3.5 cm. Although the food availability figures come from different stations we believe on basis of earlier surveys on depth changes in *Macoma balthica* (Dekinga & Piersma in press, Hoekstra 1989 and Zwarts 1992) that the results presented in figure 21 describe the actual changes in food availability of *Macoma balthica*.

in the course of autumn. The results in this figure show that a decrease of total food availability was found in the sample order of the stations. After 19 October the food availability increased again both absolutely as proportionally.

SYNTHESIS

Balancing Knot's energy budget in the Dutch Wadden Sea during their autumn stay in 1990

Time budgets calculated from the results of activity scans suggested that more time is spent foraging in the course of autumn. This finding is in accordance with the hypothesis that Knots have to compensate in reaction to the deteriorating wintering conditions at their late autumn staging grounds. It turned out to be that at the time of arrival Knots already encountered a low food availability of *Macoma balthica* in comparison to other studies (Zwarts & Blomert 1992, Piersma pers. comm.). In the course of autumn the conditions kept becoming worse because of deteriorating climatic conditions and the increased burying depth of *Macoma*. Calculations on basis of weather data have shown that Knots must have encountered increasing thermostatic costs in the course of autumn.

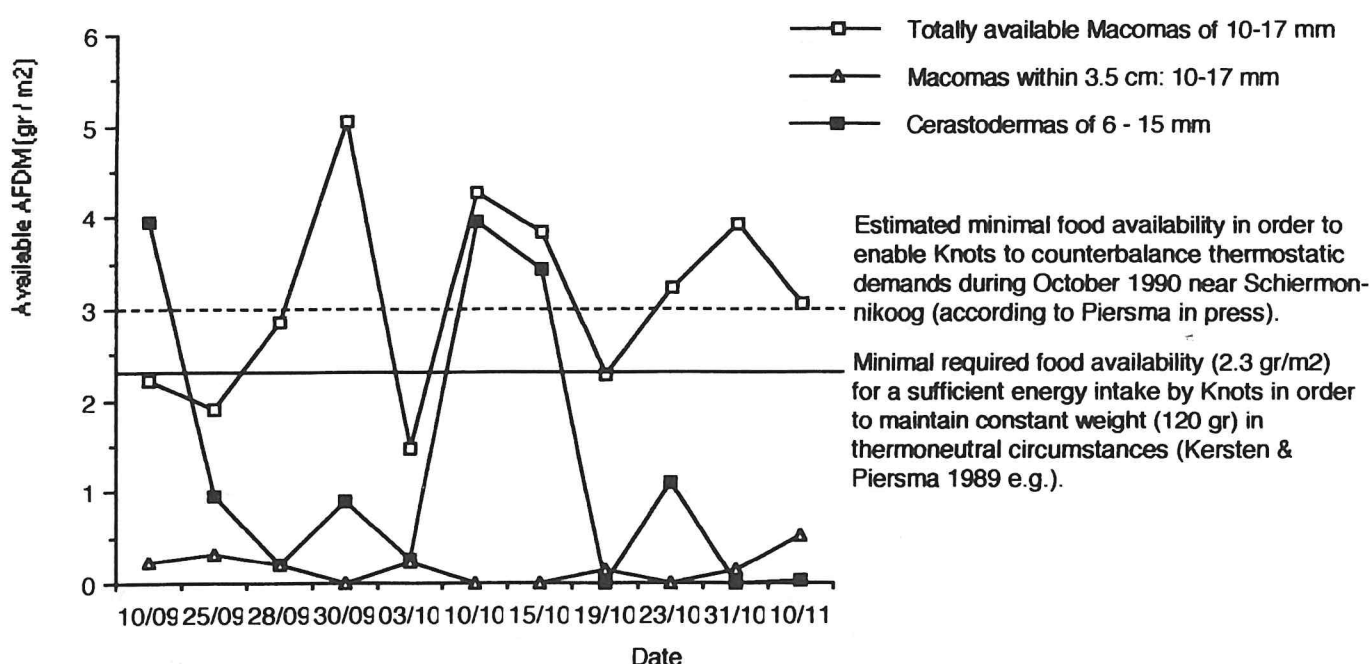


Figure 22. Food availability of preferred prey types at stations where Knots have been observed foraging.

Due to the developed models of thermoregulation and digestion we are able to quantify the consequences of the burying depth of *Macoma balthica* for the energy budget of Knots at their staging grounds in the eastern part of the Dutch Wadden Sea. Although we have not been able to execute such an extended sampling program in order to couple all observations of foraging towards food availability figures, we can make a first analysis to find any indication that the burying depth indeed could set a limit in the possibility of Knots to compensate for the harsh winter conditions at the intertidal mudflats near

Schiermonnikoog. These indications are found when we compare the figures of available AFDM irrespectively of the depth effect (figure 22). When we consider the food availability of *Macoma balthica* only, from the 11 stations only 2 contained (a little) less than 2 gram per square meter. Four stations within the studied area showed a food availability of at least 4 gram per square meter. According to the functional response curve empirically determined at a Knot in captivity (Piersma in prep.) this figure should enable Knots to reach an intake of at least 0.25 mg per second on *Macoma* of 10 to 17 mm only. Food availability of preferred size classes of *Macoma balthica* turned out to be extremely low (0.5 g/m² or less). On average more than 85 percent of the AFDM of preferred *Macoma balthica* length classes was out of reach of Knots' bills. Therefore, the burying depth of *Macoma balthica* seems to play a crucial role in the ecology of wintering Knots in the Dutch Wadden Sea.

Table 9. Calculation of intake rate.

	Macoma	Cerastoderma
Proportion of diet of ingested bivalves	0.34	0.66
Mean size (mm) of ingested bivalve	14.5	7.9
Mean AFDM (mg)	33.5	13.55
Feeding rate	0.40 prey/min	
Calculated intake	0.14 mg AFDM/s	

On the basis of our determination of feeding rates we have calculated an intake rate of 0.14 mg AFDM/s (see table 9). This figure is in the same order of magnitude as the minimal intake rate a Knot has to reach in order to sustain at the same weight in thermoneutral conditions (0.23 mg AFDM/s: Piersma in prep.). However, this figure is still far too low to counterbalance the energetic demands in October (which at least lies at 0.30 mg AFDM/s) (Kersten and Piersma 1987, Wiersma 1991). Moreover, Knots' energy budget consists of a substantial part of activity costs, which has to be counterbalanced as well. Experiments with the double-labelled-water technique on Knots foraging in an almost natural situation have revealed an activity cost of at least 2 Watt (Piersma & Poot in prep.) Combining this figure with the results of the time budgets (75 % foraging activity during the low tide periods) and the results of the calculations of thermostatic costs in October according to Wiersma (1991) results in an energy expenditure figure of about 4 Watt in October. This figure could have increased a little due to the energy spent during the limited periods of flying. Moreover, Knots wintering at temperate latitudes show an increase in body weight in the course of autumn (Piersma in prep.). The birds store energy reserves in

order to overcome periods of harsh winter conditions, in case energy intake can not counterbalance the energy expenditure. Moreover, especially in the situation of wintering at the intertidal mudflats of the eastern part of the Dutch Wadden Sea it is important to have sufficient energy reserves to leave the area and reach other estuaries in proper body condition. Thus, Knots even need some extra energy intake on top of the necessary 0.30 mg/s we have estimated in order to build up energy reserves.

The rather low figure of 0.14 mg AFDM/s could be explained by the possibility of missing prey intake during focal sampling. The first reason for the low intake figure is that ingestion of very small prey by Knots is very hard to observe. Because no hinges of small *Macoma* were found in the droppings, only the contribution of small *Hydrobia* must be accounted for the intake figure. When we assume a diet contribution of 5.38 percent of *Hydrobia*, the intake figure increases only to 0.17 mg AFDM/s. Still we think that a substantial part of the intake has been missed in the field. Missing the intake of a bivalve during an focal protocol could have rather important implications for the final intake figure. Since we could not carry out our focal sampling from a hide from close distance (as Zwarts & Blomert (1992) have done) we now believe that we have missed a part of the prey intake. We probably only have seen intake of the largest bivalves. Since we found unequivocal determinations of poisson distributions in the feeding success we think our failure to see all the intake must have been proportional to the total prey intake. Therefore we believe that the conclusion still holds that no significant change in prey intake occurred during autumn. The reason that no change in feeding rate could be observed during autumn was because the Knots were mainly feeding on small *Cerastoderma*. Since the change in burying depth in *Cerastoderma* occur within bill reach of Knots no decrease in foraging success can be expected in case Knots mainly feed on this prey species. According to the functional response on *Macoma balthica* the food availability figures of *Cerastoderma edule* exceeds the minimal intake threshold for keeping an equal weight under the climatic conditions in October at a few stations (figure 22). Although no functional response curve of *Cerastoderma edule* is available this comparison probably points that Knots were able to reach a sufficient intake in order to counterbalance the energy expenditure when feeding on small *Cerastoderma*. The results of the dropping analysis show that at the most places sufficient densities must have been present because the largest proportion of the diet consisted of *Cerastoderma edule*.

When visiting the Dutch Wadden Sea Knots normally are specialized in feeding at *Macoma balthica*. We have shown that the food availability of *Macoma balthica* was very low in the studied area. Consequently the diet consisted just partly of *Macoma*. When choosing an alternative prey Knot's main alternatives at the intertidal mudflats near Schiermonnikoog could have been *Hydrobia ulvae* and *Cerastoderma edule*. Other bivalve species were present in very low density or were too big (*Mytilus edulis*) and/or too deep to be predated by Knots (*Scrobicularia plana*, *Mya arenaria*). *Cerastoderma edule* spat fall mostly occurs in very spatial restricted patches, resulting in so-called banks (Zwarts 1988), which could explain the absence of confirmation of high densities of preferred *Cerastoderma* length classes. The same applies to *Hydrobia ulvae*, although the spatial distribution can even be more scattered because of large losses due to storms (Zwarts 1988).

The alternative to counterbalance the energy demands in autumn 1990 was by feeding at the huge amount of dead Cockles. In the beginning of October Knots started to feed at dying/dead Cockles, which were lying in big quantities on the surface of the mudflats. During 2 weeks all 15,000 Knots present by that time were foraging on the mudflats in the dead water area and did not fly to the mudflats in the middle of the

Wadden Sea anymore. In this way Knots probably were able to ensure a sufficient intake rate. Calculations of thermostatic costs revealed that Knots probably could not maintain a balance between energy expenditure and energy intake under the food conditions (*Macoma balthica* and small *Cerastoderma edule*) present on the intertidal mudflats near Schiermonnikoog. Apparently neither the food availability of the mudflats in the middle of the Wadden Sea were sufficient to accommodate the demands, because after the food supply of dead Cockles had diminished, the huge flocks did not change from feeding area anymore. At the end of October, after two periods of low temperature and additive tailwinds, the Knots left the study area, probably for British estuaries.

A play with the risk of starvation

According to monthly counts by Zwarts and Zegers (pers. comm.) Knots of the *C.c. islandica* subspecies visit the intertidal mudflats near Schiermonnikoog every year. Around the end of August between 10,000 and 25,000 Knots arrive near Schiermonnikoog and stay until October, after which most birds leave the area completely. Only in mild winters a maximum of 7,000 Knots stayed the whole winter period. Our results fit very well in this general picture.

Because the total population of the *C.c. islandica* subspecies amounts roughly 345,000 individuals (Davidson & Wilson 1992) it is interesting why approximately 6 percent of the total population visits the eastern part of the Dutch Wadden Sea very temporarily during autumn, since later on they abandon this area to move to other estuaries, probably in Britain. Most important wintering grounds for Knots of the *C.c. islandica* subspecies are formed by the British estuaries (see figure 23), of which the Wash is the most important (Davidson & Wilson 1992). Together with these areas, the intertidal mudflats near Schiermonnikoog are one of the northernmost wintering grounds for Knots. However, the climate in the eastern part of the Dutch Wadden Sea has to be considered as the most severe of the wintering grounds for Knots in western Europe. In normal winters, periods with very low temperatures in combination with strong winds are not uncommon in the Dutch Wadden Sea. In severe winters the intertidal mudflats can be covered with snow and ice, situations which are rare in British estuaries. Probably due to bad weather conditions elsewhere in Europe, up to 100,000 Knots can be present in the Wash in January. Thus, an interesting question is why do Knots staging in the Dutch Wadden Sea not migrate immediately towards British estuaries.

From several wader species it is known that individuals are faithful, from year to year, to the area where they settled successfully as juveniles (e.g. Ketterson and Nolan 1990). This behaviour is consistent with a model that assumes genetic control of a minimum distance (time) of travel from the breeding grounds, followed in some instances by competition for a place on a potential non-breeding site. This pattern was nicely found in Grey Plovers *Pluvialis squatarola*. Of marked juveniles from the same breeding area individuals with a smaller body size (wing length) moved further south than larger individuals (Evans and Townshend 1989). In this general picture of migration strategies of waders Knots may be regarded as an exception. Marked individual Knots have been recorded on different western European estuaries in the same month in different years. Moreover, Dugan (1981) presents figures of Knots moving around within the same winter. The dependence on particular size classes of small bivalves as food restricts the number of sites at which Knots are able to find enough food to counterbalance their energy expenditure (Evans and Davidson 1990).

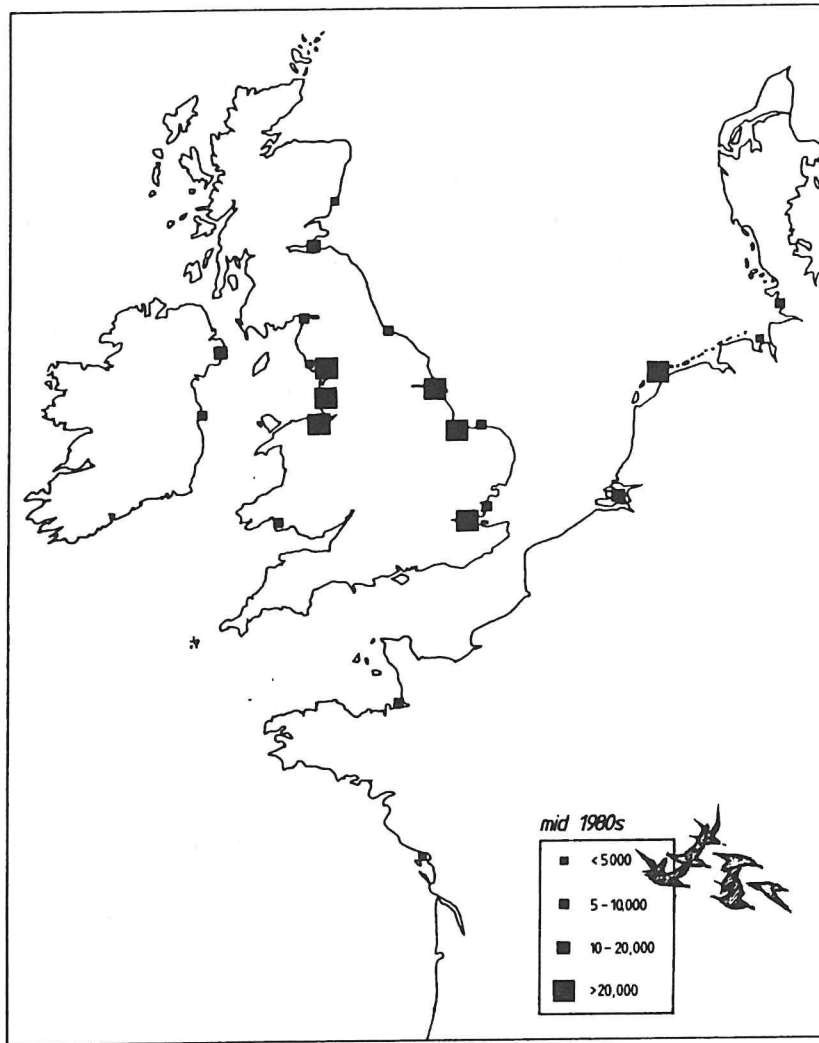


Figure 23. Winter distribution of *C. c. islandica* during the mid-1980s (from Smit & Piersma 1989 in Davidson & Wilson 1992)

We hypothesize that this is also the reason why Knots do show up at the intertidal mudflats near Schiermonnikoog every year, despite the prospect that thermostatic demands will overbalance the energy budget in this area in the course of autumn. The occurrence of particular size classes of small bivalves as *Macoma balthica* at certain sites is highly variable from year to year. Most species where Knots prey upon show year to year fluctuations in abundance (*Macoma balthica*, *Cerastoderma edule*, *Mytilus edulis* etc.). Some years with massive outburst are followed by decreasing densities of preferred prey for a number of reasons. In the course of years, after an outburst, food availability mainly diminishes due to loss of individuals being washed out by storms and mortality due to age. An important effect which decreases food availability, especially for Knots, is that subsequently the prey grows bigger than bill nape and therefore becomes too big to swallow [about the role of predation itself the debate is still running (Piersma 1987)]. Because Knots are mainly dependent on these small bivalves, different sites will be

favourable in different years. This implies that the Knots need to be very flexible in their migratory performance to be able to find proper areas to stay for an amount of time. It is most likely that by visiting the intertidal mudflats of the Wadden Sea the Knots profite from the high food availability when present in order to built up body reserves for the winter. When the food availability is favourable and the weather conditions are mild Knots are even able to winter in the Dutch Wadden Sea. Therefore the interpretation that Knots of the subspecies *C.c. islandica* only use the Wadden Sea as a functional moulting place given by Davidson & Wilson (1992) must be nuanced. When conditions are favourable Knots do winter in the Dutch Wadden Sea. It is the combination of food availability and weather conditions which ultimately determine the wintering distribution in Western Europe.

Up to what extent former experiences play a role in the decisions to stay or leave is an open question. When we assume that a part of the population of Knots has experience and knowledge of different staging grounds in western Europe, we can imagine how different subpopulations of the same subspecies could fly to different staging grounds under the limited number of tidal wintering grounds in concern. If body conditions are sufficient, the Knot are able to roam along some western Europe's tidal systems to encounter spacely and temporarily distributed favourable feeding conditions. About the proximate mechanisms involved in the decisions to leave or stay a lot remains unsolved (Piersma & Poot 1993). In future this could be cleared up by experimental design in standardized feeding conditions. We hypothesize that Knots respond in behavioral terms according to rules of thump towards energy intake in relation to body condition and energy expenditure. Although we are performing *ad hoc* explanations, field observations, including our own, have shown that Knots are very flexible in the way they respond to bad food conditions. The decision to stay or to leave probably depends on the remaining body reserves (Hulscher 1989). Leaving for another estuary means choosing for usage of body reserves. The question is whether better conditions are present in the new estuary. The final conclusion may be that the Knot's wintering performance seems to be a play with the risk of starvation.

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