Red Knots scavenging on large, dying cockles: opportunistic feeding by a sensory specialized mollusc-crushing shorebird

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Despite their specializations, shorebirds can be opportunistic foragers during the non-breeding season. We describe how a highly specialized probe-feeding shorebird, the Red Knot *Calidris canutus*, suddenly ignored its shallow buried hard-shelled mollusc prey and opportunistically shifted to an unusual prey type: dying and dead cockles of size classes larger than 25 mm that were lying with gaping shells on the mud surface. Such prey items are normally not available because they are too large to be swallowed and too hard to be crushed in the gizzard. In the last week of August 1990, thousands of Red Knots arrived near Schiermonnikoog in the eastern part of the Dutch Wadden Sea. These birds belonged to the subspecies *Calidris canutus islandica* that winters at intertidal wetlands in NW Europe. During the autumn study period, the diet of the approximately 20,000 birds in our study area consisted of small shallowly buried shellfish, comprising Edible Cockle *Cerastoderma edule* (44.8%), Baltic Tellin *Macoma balthica* (36.9%) and Mudsnail *Hydrobria ulvae* (18.3%). In the second week of October, the diet of the complete population present shifted to dying and dead cockles lying on the surface of the tidal mudflats in a restricted area, ranging in lengths from 25 mm to 35 mm. The death of the cockles was probably due to oxygen shortage caused by the decomposition of a bloom of *Noctiluca scintillans*. Sampling of benthic fauna showed that the Red Knots had to deal with a relatively low availability of small profitable shellfish, which diminished in the course of the autumn as *Macoma* buried deeper. After one week of foraging on the opportunistic food source, with also many thousands of birds of other species such as gulls *Larus* spp. and Eurasian Oystercatchers *Haematopus ostralegus* sharing the unexpected food bonanza, almost all Red Knots left the area because the source became depleted. Foraging by knots on the dying cockles may be explained by a combination of: (1) the seasonal decline in abundance of harvestable 'normal' prey; and (2) the superior profitably of dying cockles over the alternative hard-shelled food items. We discuss the repercussions of the diet shift from hard-shelled mollusc to soft-bodied food with respect to gizzard atrophy.

INTRODUCTION

Although migratory shorebirds are very specialized foragers with in general very restricted diets due to specific adaptations regarding bill shape, prey-detection capacity, leg length, and other features, it is known that they can be opportunist foragers during the non-breeding season, with several studies describing this behaviour for a wide range of species (Gochfeld & Burger 1980, Skagen & Oman 1996). The Red Knot *Calidris canutus* (henceforth called Knot) is a shorebird marked by a tapered bill with numerous minute tactile organs for specifically localizing hard-shelled prey buried in the soft wet sediments of intertidal flats. Particularly small bivalves are a major constituent of their diet and these molluscs are detected by a pressure sensory system while probing the bill into the sediment (Piersma *et al.* 1998). The molluscs are eaten whole and the shells are crushed in the specially adapted strong gizzard (Piersma *et al.* 1993a). Only a small fraction of the total biomass hidden in the sediment is actually harvestable by Knots, because most shellfish grow fast to a size too big to be swallowed and such large individuals tend to bury too deeply (Zwarts *et al.* 1992). When Knots are staging in the Dutch Wadden Sea, of all potential prey species the Baltic Tellin *Macoma balthica* is often the most profitable and highest-quality prey (van Gils *et al*. 2005a, Zwarts & Blomert 1992). Other shelled prey types taken by Knots in the Dutch Wadden Sea are the mudsnail *Hydrobia ulvae* and small specimens of the

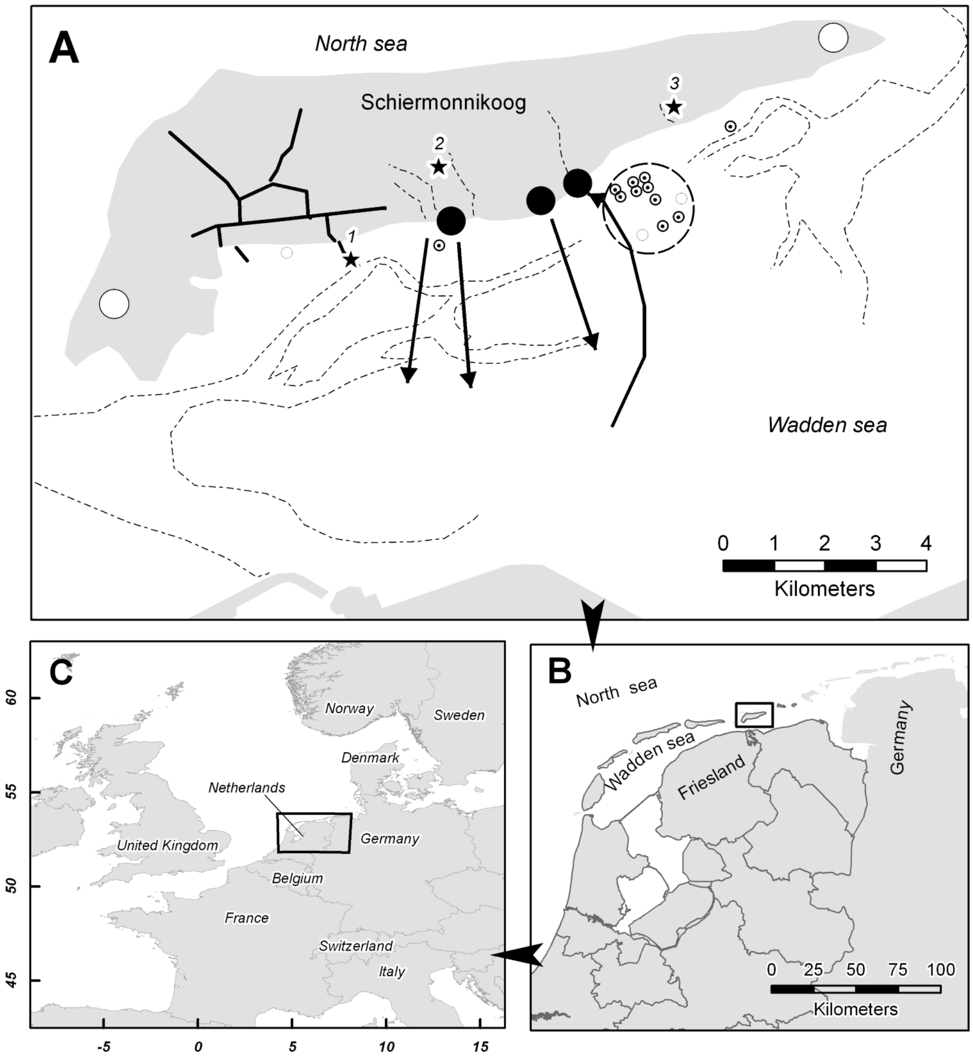

Fig. 1. Map of Schiermonnikoog as it was in 1990. Arrows indicate the flight movements to and from major feeding areas in the middle of the Wadden Sea, before all 15,000 Knots shifted to feed on dying or dead cockles in a restricted area indicated by the large dashed circle. The large closed dots indicate the frequently used high-tide roosts of the Knots. The two large open dots indicate alternative roosts used during severe storms with extreme high tides. The small circles with a central dot are the benthos stations where both density as well as the depth distribution of buried molluscs was determined. The small open dots indicate stations where only a density sample was taken. Reference points are indicated by asterisks: *1 is the ferry harbour; *2 is the beacon of Kobbeduinen; *3 is the beacon at Willemsduin.

Edible Cockle *Cerastoderma edule* (Piersma *et al.* 1993b, van Gils *et al.* 2003, Zwarts & Blomert 1992).

Burying depth of *Macoma balthica* shows a seasonal pattern, with shallow depths in spring and early summer, and greatest depths in autumn and winter, when large numbers of avian predators are present (de Goeij 2001, Kamermans 1992, Reading & McGrorty 1978, Zwarts & Wanink 1993). In autumn 1990, a study was conducted on the influence of the change in depth distribution of the Baltic Tellin on the foraging efforts and the energy budget of Knots wintering in the eastern part of the Dutch Wadden Sea (Poot & Roelen 1993). From the end of August until the end of October 1990 up to a maximum of 20,000 Knots of the *islandica* subspecies were present in the study area near the island Schiermonnikoog, in the eastern part of the Dutch Wadden Sea. At the time of the study this was an estimated 5% of the total population of this subspecies (Davidson & Wilson 1992, Wetlands International 2002).

Here we describe a case of this highly specialized probe-feeding shorebird shifting to an unusual prey type, namely dying cockles of size classes larger than 25 mm. This prey type is normally not harvestable by Knots because they are too large to swallow and the thick shell is too hard to crush. In order to explain the diet shift we have formulated two non-mutually exclusive hypotheses: Knots fed on the dying cockles (1) because the normal prey was not harvestable in large enough or decreasing quantities (the harvestable food hypothesis), or (2) because the dying cockles were a better prey type as the shellfish flesh was readily available without the necessity to crush protective shell material in the gizzard after swallowing (the profitable food hypothesis). In this paper we report on this remarkable event, building the story with observations on the behaviour and occurrence of the birds, reconstruct their diet and prey selection and further substantiate what happened with data on the food availability of alternative prey types normally preferred by Knots, in order to formulate arguments for the two hypothesis. In doing so, we also discuss the repercussions of the diet shift from hard-shelled mollusc to soft-bodied food with respect to gizzard atrophy (Dekinga *et al.* 2001, Piersma *et al.* 1993a, van Gils *et al.* 2003).

STUDY AREA AND METHODS

General set-up

From the end of August until the beginning of November 1990, on a weekly basis several types of observations were made on the intertidal flats south of the island of Schiermonnikoog in the Dutch Wadden Sea (53°28’N, 6°10’E) (Fig. 1). A small village is situated in the western part of the island. On its western and northern edge, Schiermonnikoog is surrounded by sand-dunes. The southeastern part of the island consists of a large saltmarsh traversed by several gullies. As GPS was not yet available in 1990, we oriented with compasses on the basis of three reference points (indicated in Fig. 1). For safety reasons (mobile phones did not exist yet, and a ship was not available), the study area was restricted to the intertidal areas up to 2.5 km south of the eastern part of the island. At those places where observations on foraging flocks of Knots were made and droppings were collected, samples of the benthos were taken within two days after the observations.

Total counts and behavioural observations

The total numbers of Knots were assessed on a weekly basis at the high-tide roosts (Fig. 1). Observations were made using an 80x120 telescope (Questar) and a 15x45 telescope (Bushnell). During different phases of the low-water period, activity-scans (n=86) were made of representative parts of flocks, with a maximum of 1,000 birds. If the flock size was <400 birds, the total group was scanned. For every individual bird its activity at the moment of observation was recorded. The following behaviours were distinguished: foraging, preening, sleeping, walking (the bird was walking over the surface without pecking at the surface) and standing. Also focal scans were made in which an individual Knot actively foraging was followed during one minute (n=217) in order to determine prey choice and rates of interaction. Since flocks moved so much, no hide was used, but a hide is not necessary as flocks of Knots can easily be approached to quite close distances.

Reconstructing the diet by prey remnants in the faeces

To describe the diet composition on the basis of faeces in this mollusc-eating shorebird, we followed the protocol of Dekinga & Piersma (1993). On the basis of their feeding experiments with Knots in captivity, the consumption by Knots in terms of the ash-free dry mass (AFDM) of different shell species can be reconstructed. The principle of the method is to compute ingested AFDM of meat out of the dry mass of sieved shell remnants. 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.

Shell lengths of the prey eaten by Knots were reconstructed on the basis of the length of hinges retrieved from the droppings, and for *Hydrobia* on the width of the last whorl of broken specimens in the droppings. Length hinge in *Macoma* and *Cerastoderma* and length whorl width relationships in *Hydrobia* were used from Dekinga & Piersma (1993).

In the field, when a group of Knots had been observed for longer than one hour and the birds had left, a sample of 50 droppings was gathered. Between week 35 and week 40, 21 samples of 50 droppings of Knots were collected on 11 different days. In week 38, bad weather prevented fieldwork. In week 41, >95% of all Knots present were scavenging on large dying and dead cockles with the faeces not containing any shell fragments. In weeks 42 and 43, most birds had left and the remaining birds were too few to allow collection of sufficient droppings.

Prey sampling and processing

In the course of the autumn, at places where foraging observations and activity scans of Knots had been made, the densities of bivalves as potential prey for Knots were determined by core sampling. This was done at 14 different stations on 14 different dates (Fig. 1). Of the invertebrate species present in the sediment, the following species were sampled: *Macoma balthica, Cerastoderma edule, Mya arenaria, Scrobicularia plana, Spisula subtruncata* and *Abra tenuis* – all bivalve species – and the gastropod *Hydrobia ulvae*. A 185 cm^2 corer was pushed 15–20 cm into the substrate. At each station, 20 randomly located cores were taken from the sediment. Samples were sieved on the spot over a 1-mm sieve. As *Hydrobia ulvae* is rather small, at each station an additional 5 cores of the upper 4 cm of the sediment were taken and were sieved over a 0.5 mm sieve. The collected specimens were stored at -20°C until processing.

For *Macoma* and *Cerastoderma* the length of each shell from every station was measured using callipers, and subsequently AFDM was determined per size class per species. For each separate size class, the molluscs were removed from their shells and the flesh of all animals was dried over a period of two to three days in a ventilated stove at 60°C. Then the dry mass (DM) per size class per species was determined. Values for AFDM were obtained by weighing the bodies again after incineration at 500°C for two hours. The ash-free dry mass per size class per species could then be calculated as the difference between dry mass and ash mass (AFDM = DM - AM). For *Hydrobia,* overall values of AFDM per individual were used from autumn 1988 near Griend (data from Piersma *et al.* 1993b).

Among potential Knot prey in the study area, *Macoma balthica* is notable for a tendency to change its depth in the substrate, with many burying deeper than the reach of a Knot’s bill (Reading & McGrorty 1978, Zwarts & Wanink 1993). At 12 of the 14 stations, the depth distribution of this species was determined using the same corer as the one used for density sampling. A core of ~20 cm was cut and placed horizontally on the mudflat, and a metal plate was used to mark the original upper surface. Subsequently, thin layers were carefully scraped off vertically, starting from the original surface, until a *Macoma* was found and the distance between the surface (metal plate) and the nearest edge of the shell measured. *Macoma* within 4 cm of the surface were counted in depth classes of 0.5 cm, specimens deeper than 4 cm in classes of 1 cm, and the length of each shell measured using callipers.

In order to describe the change in depth distribution of *Macoma* in the course of the study period, the percentage of preferred 7–19 mm *Macoma* in the upper 3.5 cm of the mud was determined. Subsequently, based on length-specific ash-free dry mass, the total harvestable biomass was calculated per station. This was done for the three species, *Cerastoderma, Hydrobia* and *Macoma*, based on the preferred length classes reconstructed from the measureable parts

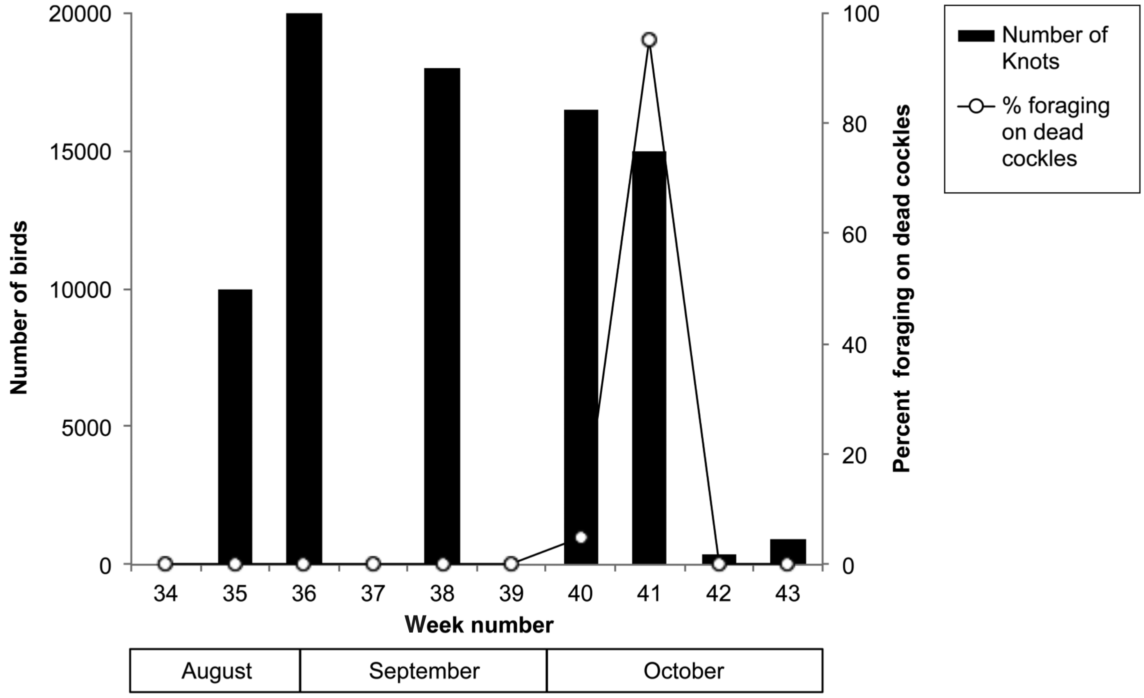

Fig. 2. Numbers of Knots present in the eastern part of the Dutch Wadden Sea near Schiermonnikoog in autumn 1990 and the proportion of the population feeding on large dying cockles. Total numbers were assessed at the high tide roosts (Fig. 1). In week 37 and 39 no complete counts could be made. In week 34 no birds were yet present.

retrieved from the droppings, as described earlier, and for *Macoma* taking into account the fraction in the upper 3.5 cm of the mud (*Cerastoderma* and *Hydrobia* occur in the upper layer and are always within reach of a Knot's bill).

RESULTS

Numbers and general behaviour of Knots

In the last week of August 1990 the first 10,000 Knots arrived at Schiermonnikoog (Fig. 2). The following week the number of Knots doubled to about 20,000 and remained at this level during September and the first part of October, with a gradual decline to about 15,000 in mid October. After this, a major exodus took place, coinciding with a drop in temperature and easterly winds. Only 900 Knots were recorded in the study area in late October and very few remained into November (Fig. 2).

The Knots roosted mostly on the edge of the saltmarsh at the southeastern part of the island. For feeding, the majority flew south to the intertidal mudflats in the middle of the Wadden Sea and areas closer to the Frisian coast (Fig. 1). Only during the early and late phase of the low-water period did the main flock of thousands of birds make use of the study area for foraging. Nevertheless, during all phases of the low-water period, flocks of between a few hundred and sometimes up to a few thousand birds used the intertidal areas near Schiermonnikoog for foraging. During the course of the autumn the proportion of the low-water period spent foraging increased (Fig. 3).

Diet composition of Knots and size selection of small buried bivalves

The analysis of droppings revealed that a substantial part of the diet consisted of small cockles *Cerastoderma edule*. The reconstructed diet expressed as a percentage of ingested biomass consisted on average of 44.8% small cockles, 36.9% *Macoma* and 18.3% *Hydrobia* (Fig. 4). The modal size classes taken by Knots were 9 mm for *Cerastoderma edule* (range 4–13 4mm), 15 mm for *Macoma balthica* (range 7–19 mm) and 2.5 mm for *Hydrobia ulvae* (range 0.5–6.5 mm). Compared with the benthic fauna present, it is clear that Knots were rather size selective in their diets, except for *Hydrobia* (Fig. 5).

Food availability for Knots near Schiermonnikoog

The density of *Macoma* varied greatly between the different stations within the study area (540±430, median = 360, range = 80–1,270 n/m^2). This variation was mainly caused by the presence or absence of first-year *Macoma* (see Fig. 5 for the dominance of spatfall). Edible Cockles were less abundant than *Macoma* (95±75, median = 75, range = 20–400 n/m^2). The density of *Hydrobia* varied greatly and the overall distribution was rather uneven (5,500±6,500, median = 5,000, range = 0–20,000 n/m^2). Other shellfish species such as *Mya arenaria, Scrobicularia plana* and *Abra tenuis* were found in negligible quantities.

Cerastoderma and *Hydrobia* occur on the mudflat surface, so the small mudsnails and the ingestible size classes of *Cerastoderma* were always within the reach of the Knots' bills, while *Macoma* were buried deeper in the sediment, with, for most of the time, only a limited proportion occurring in the upper 3.5 cm of the sediment. Even at the start of the autumn season, only 10–30% of preferred sized *Macoma* were within reach of Knots' bills, with an apparently further increase in burying depth throughout the season (Fig. 6).

Based on length-dependent meat AFDM content, the burying depth pattern of individual *Macoma* (Fig. 6) was translated into harvestable biomass (Fig. 7). When calculating

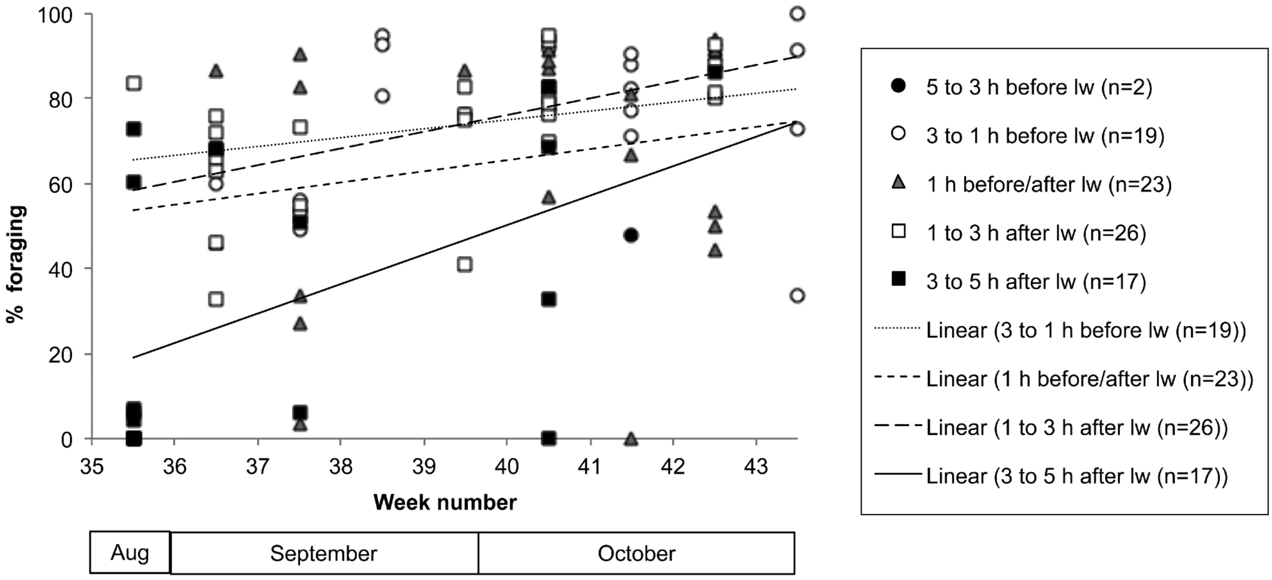

Fig. 3. Percentage of foraging birds in flocks of Knots in the course of autumn 1990 in the study area near Schiermonnikoog during five different phases of low water (lw) (periods of two hours). Activity scans (total n=86) were made of representative parts of flocks, with a maximum of 1,000 birds.

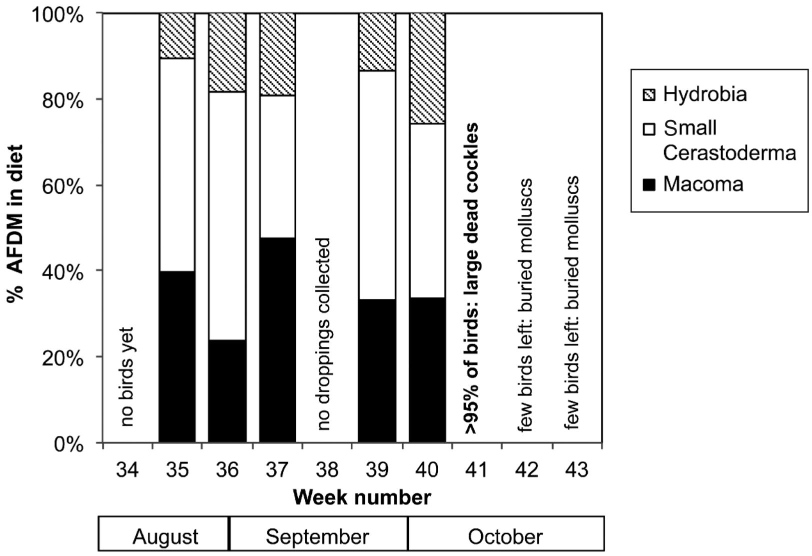

Fig. 4. The reconstructed diet as percentage of ingested biomass, based on droppings, according the protocol of Dekinga & Piersma (1993). In week 34 no birds were yet present. In weeks 38, 41, 42 and 43 no droppings were collected. In week 40 the first flocks of Knots were observed scavenging on dying large cockles (<5% of the total numbers present). Before that week the Knots were never observed scavenging. In week 41, >95% of all Knots present were scavenging on large dying and dead cockles. In weeks 42 and 43 most birds had left and the remaining birds were foraging on buried molluscs.

harvestable biomass in *Macoma,* we took into account the decrease in an individual *Macoma*'s meat AFDM content in the course of autumn, around 8% at most (Poot & Roelen 1993).

The average harvestable biomasses of the three species of molluscs taken by Knots in this study are presented in Table 1 (total 12 stations) and compared with the percentage of the biomass in the diet. The ranges of the three highest harvestable biomass figures for Knots determined at the 12 stations were, for *Cerastoderma, Macoma* and *Hydrobia* respectively, 3.5–4.0 g, 1.1–1.6 g and 0.7–1.2 g meat AFDM/m^2. In Table 1 the average figures of all 12 stations are presented and the proportions of the harvestable biomass of the three species are compared with the proportions found in the diet. Both bivalve species were selected by the Knots exactly according the proportional presence of harvestable biomass in the sediment, while fewer *Hydrobia* than expected were consumed.

Diet change from small buried bivalves to large dying cockles

From the last week of September (week 39) many dying and dead cockles were lying on the surface of the tidal mudflats. Herring Gulls *Larus argentatus,* Common Gulls *L. canus* and Eurasian Oystercatchers *Haematopus ostralegus* quickly discovered the food source and started to feed in large numbers upon the dead cockles. The area with large numbers of dying or dead cockles was about 0.5–1.0 km^2 in size (Fig. 1) and could be detected by smell at a distance of

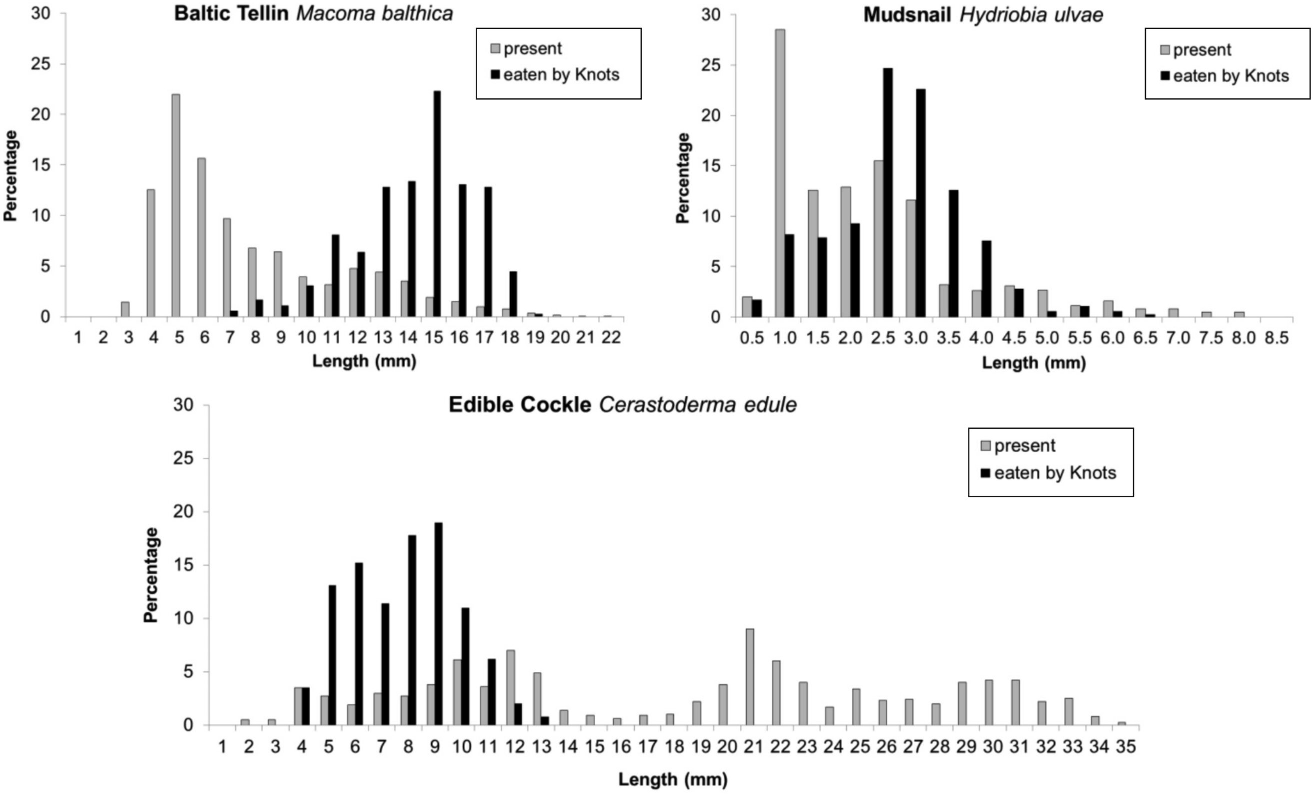

Fig. 5. Percent frequency distribution of length classes of *Macoma balthica*, *Hydriobia ulvae* and *Cerastoderma edule* present in the mud (light grey bars) and eaten by Knots (black bars).

a few hundred metres. The dying or dead cockles had opened shells so that the flesh content was easily available. The dead cockles were all 25–35 mm long, and normally too big to be swallowed by Knots. Opportunistic feeding on this prey by Knots occurred for the first time in the first week of October (week 40). At the same time, some Dunlins *Calidris alpina* also changed their feeding habits to forage on this readily available prey. In week 40, most of the Knots were still foraging in their typical probe-feeding manner in the same area. However, during week 41, almost all 15,000 Knots present changed their behaviour to feed on the dead cockles (Figs. 2 & 4) and no longer used the vast feeding areas in the middle of the Wadden Sea or near the Frisian coast. Instead, they were all concentrated in a relatively small area close to the island where the largest numbers of dead cockles were present (Fig. 1). After one week of foraging on the dying and dead cockles, almost all Knots left the area, the reason appearing to be that the food source had become depleted.

We observed Knots that spent several minutes feeding on a dead cockle, constantly pecking at it and tearing pieces of flesh from it. It was difficult to estimate how much flesh the birds were able to get out of a dying cockle, as it was often not possible to distinguish whether a bird had only pecked at a dead cockle or actually eaten some of the flesh.

Interactions

During scans of Knots foraging on small buried shellfish, it was only occasionally observed that the focal Knot drove away another Knot or *vice versa*. The interactions never lasted long and consisted mostly of a small peck towards the other bird or a short chase. On a few occasions it was observed that a bird chased another bird away and took a

Table 1. Harvestable biomass of *Cerastoderma edule*, *Macoma balthica* and *Hydrobia ulvae* (g/m^2 AFDM) averaged for 12 different stations, also expressed as proportion of the total harvestable biomass available for Knots, compared with the proportion of biomass consumed by the Knots (diet reconstructed based on Dekinga & Piersma 1993). *Cerastoderma* and *Hydrobia* occur on the mudflat surface, so the small mudsnails (all sizes ingestible and taken by Knots in the range of 0.5–6.5 mm) and the ingestible size classes of *Cerastoderma* (range 4–13 mm) were always within the reach of bills of Knots. The harvestable biomass of *Macoma* for Knots is based on the selection of the size classes 7–19 mm eaten by Knots in autumn 1990 near Schiermonnikoog and present in the upper 3.5 cm of the sediment. Also presented is the selection ratio, % biomass in the diet of Knots divided by the % of the species present in the sediment as harvestable biomass. The three species are ordered according the importance in the diet.

Species	Avg. g/m^2 AFDM	St. Dev.	% harvestable biomass	% biomass in diet	Selection ratio
Cerastoderma	1.41	1.59	44.20%	44.80%	1
Macoma	0.63	0.49	36.10%	36.90%	1
Hydrobia	0.38	0.39	19.70%	18.30%	0.9
Total	2.42	1.53	100%	100%	

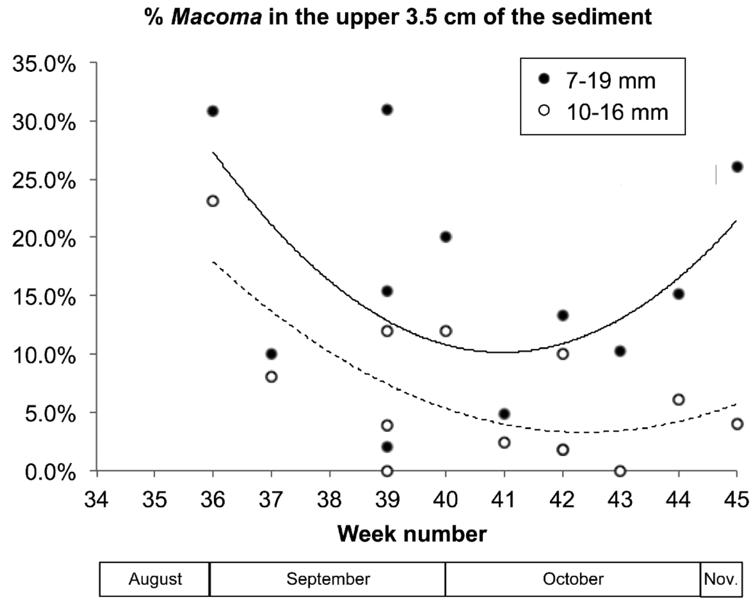

Fig. 6. Percentage of *Macoma balthica* shellfish of the size classes eaten by Knots (7–19 mm) in the upper 3.5 cm of the sediment in the course of autumn 1990 near Schiermonnikoog and of the size classes 10–16 mm, categorized as most profitable according Zwarts (1993). Fitted lines are second order polynomials.

buried *Macoma* that had apparently been discovered first by the bird that had been chased away. As the Knots foraged on dead cockles, the distribution of the birds reflected that of the cockles, which were rather spread out. Therefore the distance between individual Knots within flocks was greater than when they foraged on other prey.

When the Knots were feeding on dead cockles, besides intraspecific interactions, Knots also experienced interspecific aggressive interactions with Eurasian Oystercatchers and Dunlins. The Knots were always chased away by the bigger oystercatchers and, although bigger, Knots occasionally lost encounters with Dunlins. During focal scans, only once was a Knot recorded as being aggressive towards another shorebird species, and in that case it was a smaller bird (a Dunlin). Interspecific interactions involving Knots in week 41 occurred more than twice as often (around 0.13 per minute) as interactions between Knots, the frequency of which remained similar during the whole study period (around 0.05 per minute). Before week 41, interspecific interactions were rare and did not exceed 0.015 per minute.

DISCUSSION

Dying large cockles as an easy food source for Knots and other birds

The cause of death of the cockles is unknown but was most likely due to oxygen shortage caused by the decomposition of a large bloom of the dinoflagellate Sea Sparkle *Noctiluca scintillans*, which occurred during the investigation period (own observations). As described by Cadée (1990), such incidences of local mortality of *Cerastoderma edule* caused by *Noctiluca* die-offs occur more often in the Wadden Sea. There is at least one other example of thousands of Knots foraging on gaping dying and dead cockles in the Wadden Sea, near Vlieland in autumn 2001 (A. Dekinga & A. Koolhaas unpub. obs.). It might be that this phenomenon of scavenging by Knots and other birds on dead shellfish occurs more often in intertidal areas, but perhaps on a less extensive scale than that described here. That Knots easily recognize gaping, dying cockles as food and can shift quickly to this source also became clear during foraging experiments on captive Knots on artificial mudflats at the Royal Netherlands Institute for Sea Research. Experimental birds were supposed to feed on live *Cerastoderma* of ingestible sizes between 6 and 15 mm, but due to sudden anoxic conditions in the sediment during one experiment, captive birds had an easy meal of flesh from open shells at the mud surface (Piersma *et al.* 2003). Large quantities of gaping, dying cockles at the surface of intertidal mud can also result from a temporary superabundance of freshwater (e.g. Bayer 1996).

Repercussions of the diet shift

Besides the potential increased risk of exposure to infection (e.g. Mendes *et al.* 2006), changing to an abundant, soft-bodied prey also has repercussions for the digestive capacity of Knots to process hard-shelled molluscs, as atrophy of the gizzard muscle can occur (Dekinga *et al.* 2001). Knots are, however, capable of recovering this muscle in a couple of days (van Gils *et al.* 2003) so, dependent on the food supply, the repercussions might be limited. In the event that abundant amounts of alternative soft food is available, it will certainly pay Knots to make the diet shift as this will allow them the possibility of building up large energy stores in a short time. In such a situation it is likely that the benefit of the body stores will outweigh the loss of digestive capacity due to gizzard atrophy. This speculation is consistent with the suggestion by Van Gils *et al.* (2006) that the time needed for Knots to recover atrophied gizzards to full strength is determined by the amount of fat stores.

On the other hand, it is possible that our Knots did not suffer from atrophied stomachs through feeding on *Cerastoderma* flesh, because it seems that under certain conditions Knots are capable of maintaining or increasing their digestive capacity for hard-shelled prey (Vézina *et al.* 2010). As it is likely that the *islandica* Knots we studied near Schiermonnikoog in the autumn of 1990 would remain in the Dutch Wadden Sea for the whole winter, they might have

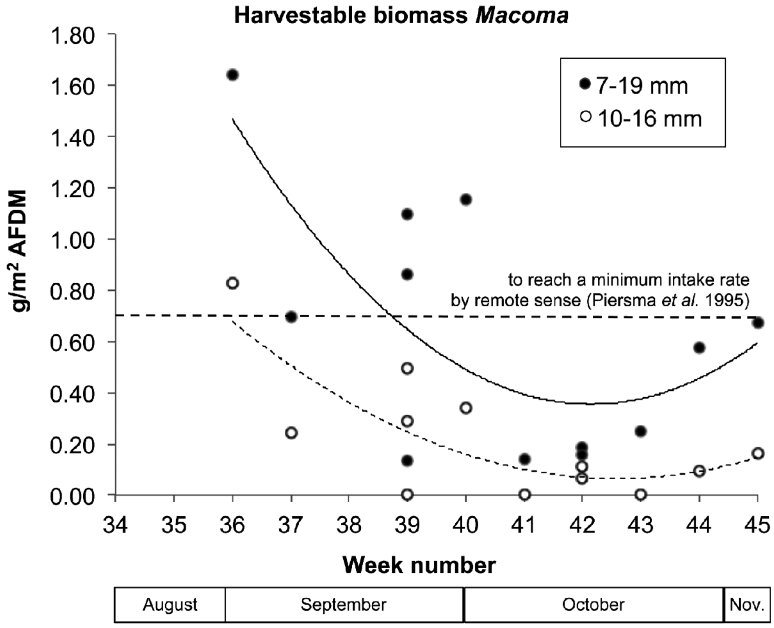

Fig. 7. Harvestable biomass of *Macoma balthica* shellfish in the upper 3.5 cm of the sediment of the size classes 7–19 mm eaten by Knots in the course of autumn 1990 near Schiermonnikoog and of the size classes 10–16 mm, categorized as most profitable according to Zwarts (1993). Fitted lines are second order polynomials. The horizontal dotted line indicates the threshold for the harvestable biomass of *Macoma* in order for Knots to reach the minimum intake rate to keep a constant body weight in thermo-neutral conditions by the remote sense foraging technique (Piersma *et al.* 1995).

had knowledge that they would have to rely on hard-shelled molluscs for the rest of the winter. Therefore, it is possible that our Knots maintained large gizzards.

Food availability of buried hard-shelled molluscs in the study area

Taking into account the depth distribution of each size class, the harvestable AFDM in g/m^2 of *Macoma* after the beginning of October was always <0.7 g/m^2 (Fig 7), the level necessary to enable Knots to maintain a constant weight in thermoneutral conditions (Kersten & Piersma 1989, Piersma *et al.* 1995). Because climate conditions in the Dutch Wadden Sea in autumn and later in winter are harsher than thermoneutral, the harvestable biomass of *Macoma* near Schiermonnikoog was not high enough for Knots to maintain their energy balance. That the life of the Knots in the course of autumn became more difficult is also illustrated by the increase in foraging activity during all phases of the low-tide period (Fig. 3).

The low proportion of *Macoma* in the diet in this study is consistent with the findings of Piersma *et al.* (1993b) who showed that the proportion of *Macoma* contributing to the diet of *islandica* Knots staging in autumn near Griend in the western Wadden Sea is <30% when the harvestable biomass of *Macoma* is <0.7 g/m^2 AFDM. Similar figures were found by Piersma *et al.* (1994) during spring migration in the Wadden Sea, with the proportion of *Macoma* contributing to the diet being minor when the harvestable biomass of *Macoma* was below 0.5–1.0 g/m^2 AFDM (*islandica* studied in one area of the Netherlands and *canutus* in an area of Germany). In making these comparisons we should bear in mind that the mean bill length of *islandica* Knots (33 mm) is slightly shorter than that of *canutus* (35 mm; Dick *et al.* 1976), which suggests that calculated harvestable biomass based on 3.5 cm in this study (Fig. 5) might be a little optimistic for *islandica*. Also, it should be mentioned that the proportion of *Macoma* in the diet is not directly proportional to the available biomass of the different prey species, as suggested by Table 1, but is also determined by differences in digestive constraints between the different species (van Gils *et al.* 2005a).

Part of the diet consisted of the alternative prey, small *Cerastoderma*. We found that six of 12 stations offered a harvestable biomass of *Cerastoderma* of the preferred length classes that was 1.5–6.5 times the level at which Knots can achieve an intake rate sufficient to maintain constant weight in thermoneutral conditions (0.6 g/m^2 AFDM; Piersma *et al.* 1995). *Cerastoderma* spatfall mostly occurs in spatially restricted patches, resulting in so-called ‘banks’, which explains the variation in harvestable biomass between the stations. Because oxygen shortage was likely to have been the cause of death of the large cockles, we assume that the small ingestible cockles also died and, in the course of October 1990, did not occur as (shallow) buried bivalve prey; but potentially they could have been available for the Knots as alternative prey like the large cockles.

For Knots on the intertidal mudflats near Schiermonnikoog in autumn 1990, *Cerastoderma* and *Macoma* were virtually the only available food, as other bivalve species were present in very low density (*Abra tenuis, Spisula subtruncata*) and/or were too big (*Mytilus edulis*) and/or buried too deeply to be harvestable by Knots (*Scrobicularia plana, Mya arenaria*). Also the harvestable biomass of *Hydrobia* in autumn 1990 near Schiermonnikoog was small and could not be a major prey substitute of *Macoma.* Compared to the best areas around Griend, the harvestable biomass of *Hydrobia* was always less in the study area near Schiermonnikoog in autumn 1990 (5%–29 % of the Griend stocks in five autumns during 1988–1992). Long-term studies near Griend have shown that *Hydrobia* is only a relevant alternative food source in the event that neither *Macoma* nor *Cerastoderma* (nor another bivalve species) are available in profitable and harvestable densities (Piersma *et al.* 1993b).

We also need to consider the – to us unknown – diet of the large numbers of Knots that flew from Schiermonnikoog to foraging areas closer to the Frisian mainland coast. There the burying depth of shellfish is shallower (Zwarts & Wanink 1993) than near Schiermonnikoog (this study compared with others in de Goeij 2001) or near Griend (Piersma *et al.* 1993b), so it is possible that prey available there is dominated by *Macoma*. However, just as near Schiermonnikoog, in the areas near the Frisian coast the harvestable biomass of *Macoma* for Knots would have decreased in the course of autumn due to a deeper burying depth (Zwarts & Wanink 1993) and a lower flesh content (Zwarts & Wanink 1991).

The diet shift explained

In the introduction we formulated two hypotheses for why the Knots shifted from their normal prey to the dying and dead cockles: (1) because the normal prey was not harvestable in large enough or decreasing quantities (the harvestable food hypothesis), or (2) because the dying cockles were a better prey type (the profitable food hypothesis).

There are several reasons that support the first hypothesis. We showed that in our study the availability of *Macoma balthica* was low because the most profitable size classes of *Macoma* tended to be buried too deeply for Knots. In fact, *Macoma* was buried deeper than in other areas in the Dutch Wadden Sea and The Wash in the UK (de Goeij 2001). Only *Macoma* smaller than 5 mm were on average within the reach of the bills of Knots, but as shown these were not taken since this size class is not generally profitable for Knots. Hence, with all other bivalve species and also *Hydrobia* being available in limited quantities, the diet of Knots foraging near Schiermonnikoog was dominated by small *Cerastoderma*.

In the past, Knots visiting the Dutch Wadden Sea normally specialized in feeding on *Macoma balthica* (Zwarts & Blomert 1992, Zwarts *et al.* 1992, Zwarts & Wanink 1993). However, more recently small cockles have dominated their diet (van Gils *et al.* 2003, 2006) due to a near absence of *Macoma*, attributed at least in part to the indirect effects of mechanical cockle dredging (van Gils *et al.* 2009). Also, in autumn 1990 the study area near Schiermonnikoog was subject to intense cockle-dredging activities (illustrated by a photo in Piersma & Koolhaas 1997, Fig. 3). The effects on food availability were not studied, but we estimated that in some areas up to 20% of the mud surface was affected.

It is clear that our findings relating to food availability strongly support the harvestable food hypothesis, but at the same time there are also arguments for the hypothesis that the dying cockles were a better prey type than the normal prey (the profitable food hypothesis). Because occasionally substantial pieces of flesh were seen being swallowed and this prey type was easy to find, profitability was probably high. However, we have no data on the intake rates of Knots foraging on dead cockles. On the other hand, the handling time seemed to be relatively long compared to ingesting buried shelled molluscs, and furthermore, an increasing amount of the feeding time was lost due to both intra- and interspecific interactions (*cf.* Gochfeld & Burger 1980).

At the time of our observations, we hardly realized that we were witnessing a remarkable phenomenon; we now would have chosen to measure total time spent on one cockle, and would have tried to estimate consumed meat per cockle by sampling freshly dead cockles and eaten cockles to compare meat contents. We assume that the Knots were able to ensure a sufficient or, more probably, a higher intake rate in terms of biomass than when foraging on buried molluscs (because the dead cockles were visible on the surface and readily available, and because cockle meat alone can presumably be digested more efficiently than a mixture of meat and hard shells). However, in the absence of data on intake rates, the question remains whether the extraction of meat from gaping shells is indeed profitable.

Soft-bodied prey in the diet of Knots

Worldwide, during the non-breeding period, the different subspecies of Knots feed mainly on hard-shelled molluscs swallowed whole (Piersma *et al.* 1993c). Only a few cases of Knots taking alternative prey have been reported, and generally these relate to limited numbers of birds (Masero 2002, Ntiamoa-Baidu *et al.* 1998). Foraging on soft-bodied prey on a large scale, as described here, is a relatively rare phenomenon. The best known example of large-scale and regular foraging by Knots on soft food during the non-breeding period is the that of the *C. c. rufa* subspecies feeding on the eggs of Horseshoe Crabs *Limulus polyphemus* during spring migration in Delaware Bay, USA (Morrison & Harrington 1992). Note that these eggs have rubbery shells that require grinding with the help of grit (T. Piersma, A. Dekinga & A. Koolhaas unpubl. obs.). Another example recently reported is feeding by the *C. c. roselaari* subspecies on the eggs of a fish, Gulf Grunion *Leuresthes sardina*, in the Gulf of California, Mexico (Hernández-Alvarez *et al.* 2013).

It was not previously known that the *islandica* subspecies is sufficiently flexible to make a major shift in diet to easily-available soft food during the non-breeding season, but this might be more common than has been realized. It would appear to be similar to Wadden Sea Knots switching to feed on small crustaceans just before departing on long-distance migrations. At the same time the birds decrease their stomachs as ultimate preparation for efficient travelling, a phenomenon also more common than previously thought (van Gils *et al.* 2005b).

Nowadays after cold spells, large quantities of dead, non-native American Jack Knife Clams *Ensis directus* wash ashore on the North Sea beaches of NW Europe and become available as food for shorebirds, mainly Sanderlings *Calidris alba* and Eurasian Oystercatchers (Reneerkens *et al.* 2009, Tulp *et al.* 2010). As this bivalve has also invaded the intertidal mudflats of the Wadden Sea, dying and dead *Ensis* could also be a potential food resource for substantial numbers of *islandica* Knots wintering in the Wadden Sea.

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Besides modestly contributing to shorebird science, the first two authors thought it would be a good practical joke to surprise their ‘old’ supervisor of more than 20 years ago with an unexpected late co-authorship and to make this paper an acknowledgement and remembrance of a great time. The joke succeeded with the first draft, but the final paper presented here is the work of all three authors. We managed to start up an old Apple Macintosh Classic computer stored in an attic to be able to recover the most critical files of this piece of student work. After such a long time, it was a great pleasure to rewrite the Schiermonnikoog story, now in the luxury of all the current knowledge on Knot’s bills, gizzards and confirmed minimal intake rates, and in contact again with 'old' colleagues. Anita Koolhaas is thanked for making 'old' data available on *Hydrobia* from Griend. Many thanks also to Peter van Horssen who was very helpful by creating the map based on an old satellite image from April 1990 (as the island and gullies have changed substantially in 20 years). Sincere thanks go to Jan van Gils for thoroughly reviewing two drafts of this paper, and to José A. Masero, two anonymous referees and the editors of the *Wader Study Group Bulletin* for all constructive suggestions to improve the final paper. After being presented as an official NIOZ report in 1993, we now with pleasure make it an official Royal NIOZ/'Groningen' publication as well.

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