Several wader populations visiting the Wadden Sea during migration or in winter are in decline (Stroud et al. 2004, van Roomen et al. 2005, Delany et al. 2009). Most strikingly, especially the East-Atlantic Flyway species and populations that most depend on the Wadden Sea show the steepest declines (Davidson 2003, Stroud et al. 2004). This suggests that these populations face a bottleneck in the Wadden Sea (Davidson 2003, van Gils et al. 2009). Previous analyses have confirmed that the quality and extent of intertidal foraging areas in the Wadden Sea have declined, especially for molluscivore shorebirds (Verhulst et al. 2004, van Gils et al. 2006a, Kraan et al. 2009).

Based on a long-term benthic mapping programme and ongoing research on the distributional ecology of Red Knots Calidris canutus in the western Dutch Wadden Sea (Piersma et al. 1993, Kraan et al. 2009), the three-way relationships between abundance of islandica-Knots, declining benthic food stocks and survival has recently been demonstrated (Kraan et al. 2009). The carrying capacity for islandica-Knots (breeding in the Nearctic, wintering in Western Europe; Davidson & Piersma 2009) depends on the area of intertidal mudflats of sufficient quality: only areas offering a predicted ash-free dry mass (AFDM) intake rate (van Gils et al. 2005a) of at least 0.3 mg/s (Piersma et al. 1995) are acceptable. Wintering numbers of Knots were closely related with annual estimates of this area (Kraan et al. 2009). Canutus-Knots, the other subspecies making use of the Dutch Wadden Sea, pass through the area during southward migration to West Africa (Piersma et al. 1993, Nebel et al. 2000). From the early 1980s to the mid-1990s their population has decreased by 34% to
339,000 birds (Stroud et al. 2004). However, due to difficulties in separating canutus- and islandica-Knots staging in the Wadden Sea (Piersma et al. 1993, Nebel et al. 2000), information about presence and refuelling rates is scarce (but see Piersma et al. 1993, Nebel et al. 2000). Here we aim to fill that gap in knowledge by illustrating the decreasing refuelling opportunities for canutus-Knots between 1996 and 2005 based on our annual large-scale benthic mapping in the western Dutch Wadden Sea.

**METHODS**

The western part of the Dutch Wadden Sea (53°N, 4–5°E), surveyed by us each year from 1996 to 2005, is bordered by the barrier islands of Texel, Vlieland and Terschelling at the north and the mainland coast of Friesland in the south and spans about 225 km² (Fig. 1). This area covers most, if not all, of the intertidal mudflats used by Red Knots roosting on Griend and Richel (Piersma et al. 1993, van Gils et al. 2006b), which are

![Figure 1](https://bioone.org/journals/Ardea/fig1.png)

**Figure 1.** Distribution of plots for 1998 (upper map) and for 2005 (lower map), offering a predicted AFDM intake rate (mg/s) sufficient for fuelling canutus-Knots. Sampling stations that provide sufficient AFDM intake rate (≥ 0.6 mg/s) are black and grey otherwise. Light grey areas indicate mudflats exposed during low low-tide, dark grey areas indicate water and land is represented by white areas.
the two most frequently used high tide roosts in the western Dutch Wadden Sea (Piersma et al. 1993).

Intertidal macrozoobenthic prey was annually sampled between July and early September. Sampling stations were arranged in a fixed grid with 250 m intervals (Fig. 1) and were visited either on foot during low tide (40% of the stations yearly) or by rubberboat during high tide. A comparison between neighbouring sampling stations showed that both sampling methods gave similar results (Kraan et al. 2007). To distinguish accessible from inaccessible prey for samples collected on foot, the top 4 cm (maximum bill length of Red Knots) and the bottom 4–20 cm were sieved separately. The cores were sieved over a 1-mm mesh and identified prey items were counted. Mudsnails Hydrobia ulvae were sampled on foot only, using a smaller core (1/267 m²) to a depth of 4 cm and sieving the sediment with a 0.5-mm mesh. Crustaceans and molluscs were collected and stored at –20°C for later analyses in the laboratory (van Gils et al. 2006b, Kraan et al. 2009), where size classes (to the nearest mm) were noted, enabling the determination of the digestible fraction (Zwarts & Wanink 1993). To determine the AFDM and shell mass of prey, the fleshy parts were removed from the shell and both shell and flesh were dried to constant mass in a ventilated oven at 55–60°C. Dry mass of both shell and flesh were determined. Then, the dried flesh was incinerated at 550°C for 5 h, after which the remaining ash-mass was subtracted from dry mass to determine AFDM. We used a species- and length-specific proportion of prey present in the top-layer, based on samples collected on foot, to calculate the available prey fraction in stations sampled by boat.

As the diet of Red Knots consists of prey species of variable size (Piersma et al. 1993), we used an optimal diet model to predict intake rate (mg/s, AFDM) for every sampled position in each year. This particular model, the so-called digestive rate model (Hirakawa 1995, van Gils et al. 2005a) explains prey selection on the basis of digestive quality (energy content over ballast mass), such that the average long-term energy intake is maximized under a digestive constraint (Hirakawa 1997). Red Knots typically exploit prey in accordance with the digestive rate model (van Gils et al. 2005a, 2006b, Quaintenne et al. 2010). As processing capacity is determined by gizzard size, predicted intake rate not only depends on the density and the digestive quality of the prey, but also on the size of the gizzard. We used a 6-g gizzard to predict intake rates for net rate maximizing canutus-Knots passing through the Dutch Wadden Sea in autumn. This gizzard size is based on 52 Red Knots caught and colour-ringed in the Dutch Wadden Sea, of which the gizzards were non-invasively measured (Dietz et al. 1999) in the period 1998–2004; these particular birds were re-sighted on the Banc d’Arguin afterwards, which ensured that they belonged to the canutus subspecies.

To fuel up at maximum rates, canutus-Knots require an instantaneous AFDM intake rate of 0.6 mg/s, which is based on the maximum daily amount of energy of 544 kJ that Red Knots can assimilate (irrespective of gizzard size; Kvist & Lindström 2003, van Gils et al. 2003), the energetic density of their food of 22 kJ/g AFDM (Zwarts & Wanink 1993), and an average working day of 12 h (van Gils et al. 2005b). Wintering islandica Knots require a minimum AFDM intake rate of 0.3 mg/s to maintain a daily energy balance (Piersma et al. 1995, Kraan et al. 2009).

To estimate which proportion of the Knots in the Dutch Wadden Sea belong to the canutus subspecies, we used data on body mass, primary moult and bill length from Red Knots captured in mist nets in July–August in 1995–2005 (Table 1). These measures distinguish the two subspecies as canutus-Knots on average have a higher body mass because they fatten-up, do not moult their primaries until reaching the wintering grounds, and are longer-billed than islandica-Knots (Nebel et al. 2000).

**Table 1.** Number and biometrics of Red Knots captured during July–August in 1995–2005 in the western Dutch Wadden Sea.

<table>
<thead>
<tr>
<th>Year</th>
<th>Catching period</th>
<th>n</th>
<th>Mass (g)</th>
<th>Bill length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>1996</td>
<td>17 July – 21 Aug</td>
<td>28</td>
<td>144</td>
<td>100–197</td>
</tr>
<tr>
<td>1997</td>
<td>4–21 Aug</td>
<td>72</td>
<td>142</td>
<td>97–197</td>
</tr>
<tr>
<td>2002</td>
<td>No catching</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**RESULTS**

A visual comparison between the first year of full grid coverage (1998) and the last year (2005) of the study period revealed considerable changes in the extent of
intertidal mudflats that fulfilled the minimum intake requirements for *canutus*-Knots (Fig. 1). The suitable foraging area decreased by 86% from 3996 ha in 1996 to 576 ha in 2005 (Fig. 2; GLM log-transformed data: slope = −0.058, $F_{1,8} = 4.477, P = 0.02$).

The biometric data from mist-netted Red Knots shows that the proportion of Red Knots without primary moult has declined (Fig. 3A; GLM arcsine-transformed data: slope = −0.046, $F_{1,8} = 5.507, P = 0.047$), as has the proportion of Red Knots with body mass values higher than 150 g (Fig. 3B; GLM arcsine-transformed data: slope = −0.031, $F_{1,8} = 13.043, P = 0.007$). However, the proportion of long-billed Red Knots ($\geq 35.5$ mm) did not change (Fig. 3C; GLM arcsine-transformed data: slope = 0.001, $F_{1,8} = 0.031, P = 0.865$). There was no correlation between any of these biometric measures and the yearly extent of suitable foraging area.

**DISCUSSION**

The data on body mass and moult suggest that *canutus*-Knots have been in decline over the last decade, especially accounting for the fact that over this period *islandica*-Knots showed a numerical decline with 44% (Kraan et al. 2009). Because *canutus*-Knots are storing extra fuel during July–August, they require a higher AFDM intake rate ($\geq 0.6$ mg/s) than *islandica* Knots ($\geq 0.3$ mg/s). Therefore, they must find areas that offer more or better food, which have become increasingly sparse (Figs 1, 2). The area of sufficient quality for *canutus*-Knots declined with 86% (Fig. 2), whereas *islandica*-Knots’ feeding area ‘only’ declined with 55% from 5775 ha to 2581 ha between 1996 and 2005 (Kraan et al. 2009). Analyses of spatial patterns in benthic richness with respect to bottom disturbance by shellfish dredging has indicated that these declines in no small part may be due to these economic activities in an otherwise protected nature reserve (Piersma et al. 2001, van Gils et al. 2006a, Kraan et al. 2007).

To increase their digestive capacity, and thereby the range of sampling stations theoretically yielding suitable feeding conditions (Kraan et al. 2009), Red Knots could increase their gizzard size (Fig. 4). However, 52 gizzards of *canutus*-Knots caught in the Dutch Wadden Sea and resighted on Banc d’Arguin later showed that *canutus*-Knots in fact slightly decreased gizzard size between 1998 and 2004 (average ± SD = 6.2 ± 1.3 g; GLM log-transformed data: slope = −0.025, $F_{1,50} = 5.502, P = 0.023$). This is consistent with previous con-
conclusions that during refuelling Red Knots on migration maintain the smallest possible gizzards (van Gils et al. 2003, 2007). Enlarging their gizzards would increase a number of cost factors. For example, growing and maintaining such a large gizzard increases the average daily metabolic rate (Piersma et al. 2003, van Gils et al. 2003) and affects manoeuvrability during escapes from predators (Dietz et al. 2007).

We have not been able to determine the decline in numbers of *canutus*-Knots in the Dutch Wadden Sea, as we did for wintering *islandica*-Knots (Kraan et al. 2009). Yet, on the basis of the decline in suitable foraging habitat, coupled to the notion that the Wadden Sea is used by Knots up to carrying capacity, we would expect the decline in *canutus* to amount to over 86%. That numbers are decreasing is supported by observation elsewhere along the flyway of the Knots. On the Banc d’Arguin, Mauritania, where 75% of the population winters (Stroud et al. 2004), numbers have declined over the last two decades (van Gils et al. 2009). During this time food densities have increased (van Gils et al. 2009), suggesting that the declines in numbers are not due to local changes at the wintering sites. Major population declines also occurred further south: in Guinea-Bissau (Stroud et al. 2004), in Namibia and at Langebaan Lagoon, South Africa (Wearne & Underhill 2005). We suggest that the decline in suitability of the western Dutch Wadden Sea as a refuelling site during southward migration may have led to decreases in the relatively unspoiled wintering areas in West- and southern Africa (see also van Gils et al. 2009).

**Figure 4.** Model result of suitable foraging area (ha; mean ± SE) during 1996–2005 for a minimally required AFDM intake rate of 0.6 mg/s as a function of gizzard mass (left axis: area expressed in ha; right axis: area in % of total area). Grey bar indicates the mean ± SD gizzard mass observed during the years 1998–2004.

**ACKNOWLEDGEMENTS**

Kees van de Star, Tony van der Vis, Hein de Vries and Johan Tuntelder, the crew of Royal NIOZ-research vessel RV Navicula, are acknowledged for all their help. We thank Vereniging Natuurmonumenten for permission to work on and around the island of Griend. A large number of volunteers and students contributed to the collection of the field data on macrozoobenthos and birds and we hope they enjoy these dividends of their efforts.

**REFERENCES**


SAMENVATTING

De Nederlandse Waddenzee wordt tijdens de najaarstrek als opvetgebied gebruikt door de Afro-Siberische ondersoort van de Kanoet Calidris canutus canutus. Deze ondersoort broedt in Taimyr en overwintert in West-Afrika. In het onderhavige onderzoek documenteren we de achteruitgang van de oppervlakte aan geschikt voedselgebied in ons waddengebied op basis van bemonsteringen van de bodemfauna tussen 1996 en 2005. Met behulp van een voedselopnamemodel dat de energieopname van Kanoet kan voorspellen, hebben we de jaarlijks op elk monsterpunt te behalen opnamesnelheid (mg asvrij drooggewicht per sec) geschat. Uitgaande van een energetische behoefte die niet alleen de onderhoudsenergie, maar ook het opveten dekt, nam tussen 1996 en 2005 de oppervlakte geschikt voedselgebied met 86% af. Ook nam het percentage Kanoet van de doortrekkende ondersoort canutus af ten opzichte van de overwinterende ondersoort islandica. Voor de laatste konden we eerder al een door voedsel verklaarde achteruitgang laten zien. Wij concluderen dat de dalende populatie Kanoet van de onderzoeksgebieden in West-Afrika direct gekoppeld is aan de dalende voedselkwaliteit van wadplaten in de Nederlandse Waddenzee.

Corresponding editor: Julia Stahl
Received: 7 July 2009; accepted 22 July 2010