Why Afro-Siberian Red Knots Calidris Canutus Canutus have Stopped Staging in the Western Dutch Wadden Sea During Southward Migration

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Why Afro-Siberian Red Knots *Calidris canutus canutus* have stopped staging in the western Dutch Wadden Sea during southward migration

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Afro-Siberian Red Knots *Calidris canutus canutus* use the western Dutch Wadden Sea as a refuelling area during southward migration from Taimyr to West Africa. Here we document the decline of their food stocks in this area, based on a yearly large-scale benthic mapping effort, from 1996 to 2005. For each benthic sampling position, intake rate (mg/s, ash-free dry mass) was predicted by an optimal diet model based on digestive rate maximization. Over the ten years, when accounting for a threshold value to meet energetic fuelling demands, subspecies *canutus* lost 86% of its suitable foraging area. Over this period, the proportion of probable *canutus* in mist-net catches in July–August declined relative to overwintering *islandica* Knots. This suggests that *canutus* dropped even more in numbers than *islandica*, for which we showed earlier a food-explained decline in numbers. We discuss the possible causality between a decline in the quality of intertidal mudflats in the Dutch Wadden Sea and population declines of Knots in the West-African wintering quarters.

Key words: connectivity, East-Atlantic Flyway, foraging, habitat suitability, macrozoobenthos, migration, molluscivore shorebirds, predicted intake rate

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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 km^2 (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. 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 m^2) 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 ingestible 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-

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

Year	Catching period	*n*	Mass (g)		Bill length (mm)	
			Mean	Range	Mean	Range
1995	27 July – 29 Aug	49	144	112–194	34	30–38
1996	17 July – 21 Aug	28	144	100–197	34	29–38
1997	4–21 Aug	72	142	97–197	33	28–38
1998	28 July – 31 Aug	175	136	99–188	33	28–39
1999	10–13 Aug	256	138	99–211	34	27–39
2000	31 July – 31 Aug	136	143	109–207	34	28–39
2001	3 July – 20 Aug	260	134	102–194	34	27–38
2002	No catching	-	-	-	-	-
2003	29 July – 30 Aug	242	135	99–197	34	29–40
2004	20 July – 27 Aug	122	135	108–204	34	29–39
2005	7 Aug	29	135	116–157	34	30–37

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 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).

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
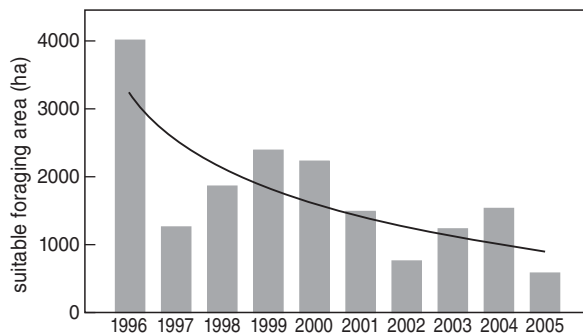
Figure 2. Sampling area (ha) offering sufficient AFDM intake rate (≥ 0.6 mg/s) for fuelling *canutus*-Knots for each of the study years. Note that the suitable foraging area was standardized to the total area covered during 2002, when the largest number of samples (2762) was taken.

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 (≥ 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 (≥ 0.6 mg/s) than *islandica* Knots (≥ 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
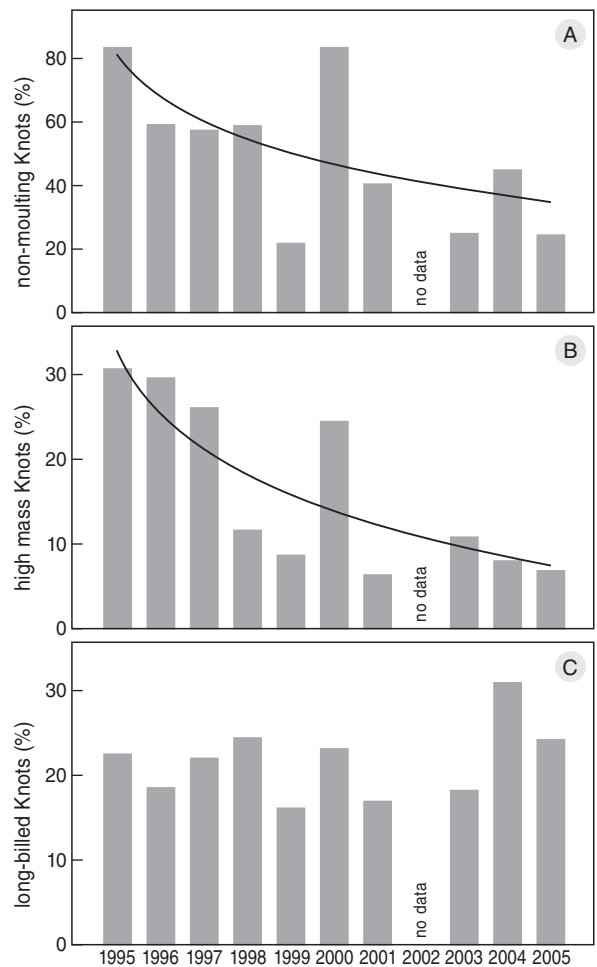

Figure 3. (A) Percentage of Red Knots without primary moult, (B) with a body mass equal to or above 150 g and (C) with a bill length ≥ 35.5 mm in mist-net catches in July–August 1995–2005 (see Table 1).

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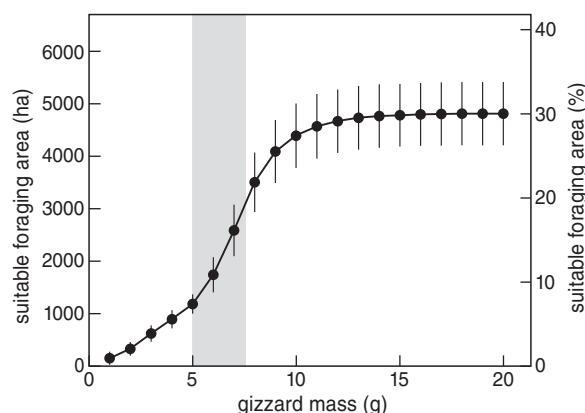
Figure 4. Model result of suitable foraging area (ha; mean ± SE) during 1996–2005 for a minimally required AFDM intake rate of 0.6 mg/s as a function of gizzard mass (left axis: area expressed in ha; right axis: area in % of total area). Grey bar indicates the mean ± SD gizzard mass observed during the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

clusions 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).

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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 Kanoeten 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 opvetten dekt, nam tussen 1996 en 2005 de oppervlakte geschikt foerageergebied met 86% af. Ook nam het percentage Kanoeten 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 Kanoeten van de ondersoort *canutus* in West-Afrika direct gekoppeld is aan de dalende voedselkwaliteit van wadplaten in de Nederlandse Waddenzee.