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Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds

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Summary

1. Whether intertidal areas are used to capacity by shorebirds can best be answered by large-scale manipulation of foraging areas. The recent overexploitation of benthic resources in the western Dutch Wadden Sea offers such an ‘experimental’ setting.
2. We review the effects of declining food abundances on red knot *Calidris canutus islandica* numbers, based on a yearly large-scale benthic mapping effort, long-term colour-ringing and regular bird-counts from 1996 to 2005. We focus on the three-way relationships between suitable foraging area, the spatial predictability of food and red knot survival.
3. For each benthic sampling position, red knot intake rate (mg AFDM s⁻¹) was predicted by a multiple prey species functional response model, based on digestive rate maximization (this model explained diet and intake rate in earlier studies on red knots). This enabled us to derive the spatial distribution of the suitable foraging area, which in each of the 10 years was analysed with a measure of autocorrelation, i.e. Moran’s *I*.
4. Over the 10 years, when accounting for a threshold value to meet energetic demands, red knots lost 55% of their suitable foraging area. This ran parallel to a decrease in red knot numbers by 42%. Although there was also a decrease in patchiness (i.e. less information about the location of the suitable feeding sites), this did not yet lead to additional loss of birds.
5. To cope with these landscape-scale declines in food stocks, an increase in the capacity for instantaneous food processing would be required. Although we show that red knots indeed enlarged their muscular gizzards, the increase in gizzard size was not enough to compensate for the decreased feeding area.
6. Survival of *islandica* knots in the western Dutch Wadden Sea, based on colour-ring resightings, declined from 89% in the first half of our study period to 82% in the second half of our study period and could account for almost half of the decline in red knot numbers; the rest must have moved elsewhere in winter.
7. Densities of red knots per unit suitable foraging area remained constant at 10 knots ha⁻¹ between 1996 and 2005, which suggests that red knots have been using the Dutch Wadden Sea to full capacity.

Key-words: carrying capacity, foraging information, intertidal macrozoobenthos, survival, Wadden Sea

Introduction

Whether habitats are used to capacity by their inhabitants, i.e. ‘carrying capacity’, is a question that has long occupied

research agendas of workers in intertidal areas. This focus was a response to societal concerns about the continuing loss of extent and quality of wetland areas, and concerns about the fates of shared international resources, i.e. the migrant shorebirds using these habitats in the non-breeding season (e.g. Goss-Custard 1977; Goss-Custard & Moser

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1988; Van de Kam *et al.* 2004; Verhulst *et al.* 2004; Burton *et al.* 2006). Often, an area's carrying capacity is expressed as the maximum number of bird-days, or the maximum numbers to survive winter, given the total food stocks available (Goss-Custard 1985; Sutherland & Anderson 1993; Goss-Custard *et al.* 2002, 2003; Van Gils *et al.* 2004).

Yet, besides the size of the stocks of suitable food, numbers of foragers also depend on the ways that food is distributed. Clear spatial patterning of prey enables foragers to distinguish among different prey densities more accurately and to optimize their movements by spending most time in rich areas (Benhamou 1992; Walsh 1996; Klaassen, Nolet & Bankert 2006; Van Gils *et al.* 2006b; Klaassen, Nolet & Van Leeuwen 2007; Van Gils 2009). For example, positive spatial autocorrelation implies that high-density areas are found close to other high-density areas (Legendre 1993; Fortin & Dale 2005). However, if the degree of recognizable patchiness correlates with overall food abundance, this may have additional consequences. Taking a decline in shellfish stocks in intertidal areas as an example: (i) the size of shellfish patches could be getting smaller, down to a point where they are no longer recognized by a forager, i.e. they are below the 'grain' (Kotliar & Wiens 1990; Schmidt & Brown 1996); (ii) the distribution of shellfish could become more random (i.e. spatially unpredictable), implying that the strength of the autocorrelation for a given distance declines, which makes shellfish more difficult for foragers to find (Iwasa, Higashi & Yamamura 1981; Mangel & Adler 1994; Olsson & Holmgren 2000; Van Gils 2009). Declining prey stocks might result in a decreasing abundance of foragers. In time, there might not be enough foragers to gather foraging information from and, consequently, the last suitable foraging areas become more difficult to discover (e.g. Templeton & Giraldeau 1996), leading to an Allee effect because of limited information sharing (Courchamp, Clutton-Brock & Grenfell 1999; Stephens & Sutherland 1999; Stephens, Sutherland & Freckleton 1999; Jackson, Ruxton & Houston 2008).

Field studies experimenting with landscape-scale declines of food stocks are impractical and unethical (Courchamp *et al.* 1999). However, in the Dutch Wadden Sea, as a result of intensive exploitation of natural resources in this protected nature reserve, such an 'experiment' has now been carried out (e.g. Piersma *et al.* 2001; Lotze *et al.* 2005; Van Gils *et al.* 2006a; Kraan *et al.* 2007; Swart & Van Andel 2008). The mechanical harvesting of cockles *Cerastoderma edule*, allowed in three-quarters of the intertidal flats, has decreased both the quality (flesh-to-shell ratio) and the abundance of available cockles for red knots *Calidris canutus* (Van Gils *et al.* 2006a). Note that fisheries impact shorebirds not only in the Wadden Sea, but also in coastal areas worldwide (e.g. Atkinson *et al.* 2003; Baker *et al.* 2004). Here we examine the three-way relationships between food, predictability of food and population changes of molluscivore shorebirds, capitalizing on the experimental habitat modifications carried out between the late 1980s and 2003 (Piersma *et al.* 2001; Van Gils *et al.* 2006a; Kraan *et al.* 2007).

Our study is based on a high-resolution benthic-mapping programme (Bocher *et al.* 2007; Van Gils *et al.* 2008; A.I. Bijlvel, J.A. Van Gils, J. Van der Meer, A. Dekinga, C. Kraan, H.W. Van der Veer & T. Piersma, unpublished data), long-term colour-ringing efforts (Piersma & Spaans 2004; Van Gils *et al.* 2006a) and comprehensive high-tide bird-counts (Van Roomen *et al.* 2006). The focal species, red knots of the *islandica* subspecies, are long-distance migrants that socialize in large flocks outside the breeding season in the Wadden Sea (Piersma *et al.* 1993; Nebel *et al.* 2000; Piersma 2007). An estimated one-third to half of the population visits the area at some stage during winter (Nebel *et al.* 2000; Van Gils *et al.* 2006a), whose total population number dropped by 25% between 1997 and 2003 to c. 250 000 (Van Gils *et al.* 2006a). As the diet of red knots consists of a number of prey species (e.g. Piersma *et al.* 1993; Van Gils *et al.* 2005a), we use a multiple prey species functional response model, the so-called 'digestive rate model' (DRM) (Verlinden & Wiley 1989; Hirakawa 1995; Farnsworth & Illius 1998; Van Gils *et al.* 2005a), to express food abundance in a single dimension, i.e. (predicted) intake rate (mg AFDM s^{-1}). This model exploits prey selection on the basis of digestive quality (energy content over ballast mass), while respecting a digestive constraint, to maximize the average long-term energy intake (Hirakawa 1997; Van Gils *et al.* 2003b). Red knots typically exploit prey in accordance with the DRM (Van Gils *et al.* 2005a, b; G. Quaintenne, J.A. van Gils, P. Bocher, A. Dekinga & T. Piersma, unpublished data), rather than adhering to the classical prey-selection model, the so-called 'contingency model' (Charnov 1976; Stephens & Krebs 1986).

Materials and methods

PREY DATA

Intertidal macrozoobenthic prey was sampled between July and early September each year from 1996 to 2005 in our study area, the western Dutch Wadden Sea. Sampling stations were arranged in a fixed grid with 250-m intervals, covering most, if not all, of the intertidal area used by red knots roosting on Griend and Richel (Piersma *et al.* 1993; Van Gils *et al.* 2006b), i.e. 225 km² (Fig. 1). From 1996 to 2005, we sampled between 1807 (minimum) and 2762 (maximum) stations annually, either on foot during low tide ($n = 10\ 252$) or by boat ($n = 14\ 980$). The first year of full coverage was 1998 (Fig. 1); in 1996 and 1997, the sampling scheme was still expanding.

Sampling locations were found with handheld GPS (Garmin 45 and 12, using WGS84 as map datum) and at each station 1/56 m² was sampled to a depth of 20–25 cm. To distinguish accessible from inaccessible prey, for samples collected on foot, the top 4 cm (maximum bill-length) was separately sieved. The cores were sieved over a 1-mm mesh, and individuals were counted and recorded per species. Mudsnailed *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. All crustaceans and molluscs were collected and stored at -20 °C for later analyses in the laboratory (see Piersma *et al.* 1993; Van Gils *et al.* 2006a, b, 2008; Kraan *et al.* 2007), where size classes (to the nearest mm) were noted, enabling the determination of the ingestible fraction (Zwarts & Wanink 1993). We used a species- and



Fig. 1. Distribution of predicted intake rate (mg AFDM s^{-1}) for 1998 (upper map) and for 2005 (lower map). Sampling stations that provide sufficient intake rate ($\geq 0.3 \text{ mg AFDM s}^{-1}$) 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 the white areas.

length-specific proportion of prey present in the top layer of walking points to calculate the available prey fraction in stations sampled by boat.

FROM PREY DENSITY TO INTAKE RATE

We predicted the intake rate (mg AFDM s^{-1}) for every sampled position in each year, using the DRM (Verlinden & Wiley 1989; Hirakawa 1995; Farnsworth & Illius 1998; Van Gils *et al.* 2005a). Prey types are included in the predicted diet depending on energy content, amount of ballast mass, handling time and the density of other high quality prey. Prey types are defined as any unique combination of energy content and ballast mass. Prey species, constituting a multitude of prey types, their characteristic, size-specific handling times and knot searching efficiencies, as well as other model details are presented in Piersma *et al.* (1995) and Van Gils *et al.* (2005a, b, 2006b).

Predicted intake rate does not only depend on the density and digestive quality of prey, but also on the size of the gizzard, as processing capacity is determined by gizzard size (Van Gils *et al.* 2003a). Based on ultrasonographic 'field' measurements of gizzards (see Dietz *et al.* 1999; Dekinga *et al.* 2001), we used a 6-g gizzard (fresh

mass) to predict intake rates for satiating *islandica* knots (Van Gils *et al.* 2003a, 2005c).

To meet their demands on daily intake, which is limited by the time available for foraging combined with the attainable intake rate (Van Gils *et al.* 2007), *islandica* knots require a minimum intake rate of $0.3 \text{ mg AFDM s}^{-1}$ to maintain a daily energy balance (Piersma *et al.* 1995).

A binary approach was chosen to deal with stations that did or did not meet the required minimum intake rate. Sampling stations with a predicted intake rate of at least $0.3 \text{ mg AFDM s}^{-1}$ were given a value of 1 and a 0 otherwise [see Piersma *et al.* (1995) and Van Gils *et al.* (2006a) for validations of this approach]. In the Results section, we present a sensitivity analysis of the effects of changing this threshold value.

SPATIAL ANALYSES OF BENTHOS

To describe changes in the spatial predictability of food abundance, we analysed the spatial distribution of intake rates with Moran's I (Cliff & Ord 1981; Legendre & Fortin 1989; Fortin & Dale 2005). For each year, we determined the spatial patterning of the predicted intake rates, with due consideration of a threshold value to meet the

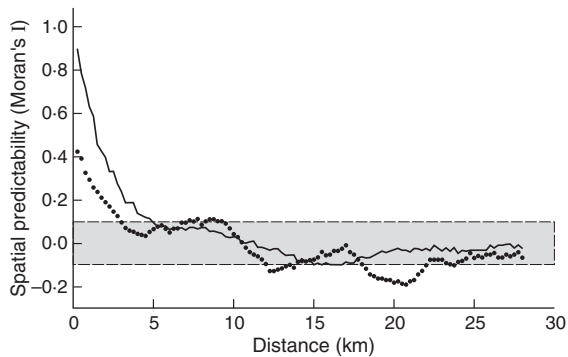


Fig. 2. Correlogram based on the presence/absence of sufficient intake rate for red knots in 1996. x-axis shows the distance-interval (m), whereas the y-axis shows the value for Moran's I . The background autocorrelation (solid line), shaped by the intrinsic contour of the intertidal habitat itself, differs from the spatial patterns of intake rate (squares). The grey band mark the significance threshold.

demands on daily intake, using the before mentioned binary approach. The spatial structure intrinsic to the physical shape of the intertidal mudflats, the so-called 'background autocorrelation', was analysed as well (Kraan *et al.* in press).

Significance was determined by bootstrapping with 1000 runs (Manly 1997), but due to the large number of pairs in each distance-class, nearly all values were significantly different from random. To be able to describe biologically meaningful spatial patterns, we put an arbitrary significance threshold at $I = \pm 0.1$ (Kraan *et al.* in press). This means, for example, that patch-sizes or range (e.g. Robertson 2000; Fortin & Dale 2005) are defined as the distance where the value of Moran's I crosses the ± 0.1 threshold. An example is presented in Fig. 2, where the correlogram (see Legendre & Fortin 1989) of the suitable sites for *islandica* knots in 1996 is shown. To review changes in spatial predictability, we used the amplitude of Moran's I at the first distance-class (250 m), i.e. the so-called 'structural variance' used in semi-variance analyses (Robertson 2000; Fortin & Dale 2005; Kraan *et al.* in press), as the information parameter. Spatial analyses were performed with SAM (Rangel, Diniz-Filho & Bini 2006).

BIRD-COUNTS

Since 1975/1976, regular bird-counts have been made during high-tide in the Dutch Wadden Sea. The count-data, consisting of two types, are analysed together and presented as a monthly average (Van Roomen *et al.* 2005). These two types are: (i) up to five simultaneous high-tide counts per season across the whole area; (ii) counts performed on a monthly basis in a subsection of sites (Van Roomen *et al.* 2005). Missing count-data are imputed with a model taking into account a site, month and year factors (see Underhill & Prys-Jones 1994; Bell 1995).

In the present analyses for the seasons 1996/1997–2005/2006, we used September–April counts only, as other months' counts include both the *islandica* and the *canutus* subspecies of red knot. *Canutus* knots use the Wadden Sea as their (re)fuelling-site in August before continuing to western Africa and some might summer in the Wadden Sea after their return from the wintering areas (Piersma *et al.* 1993; Nebel *et al.* 2000). Also, only counts from the western part of the Dutch Wadden Sea, i.e. the area between Texel, Terschelling and the Frisian mainland coast, were used. This area overlaps with the extent of our research area and has previously been shown to be used by red

knots as a single 'functional unit' (*sensu* Tamisier 1979; Tamisier & Tamisier 1981; see Piersma *et al.* 1993; Van Gils *et al.* 2006b).

SURVIVAL OF RED KNOT

Islandica knots were caught in the Wadden Sea with mistnets from the 1998/1999 to the 2005/2006 season. All birds were individually colour-marked to enable survival analyses based on resightings of these individuals (Brochard *et al.* 2002; Piersma 2007). In this way, 3694 red knots were marked in total, varying between 175 and 686 per season. Nine seasons of colour-ring resightings (1998/1999–2006/2007), where a season lasts from one summer to the next, allowed survival to be estimated for eight successive seasons. We applied the standard Cormack–Jolly–Seber method in the MARK-programme (White & Burnham 1999) to estimate the annual survival (Φ) with a correction for the slight overdispersion of the data ($\hat{c} = 1.41$). This resulted in a division of survival in two time periods (see Results section): $\Phi_{(\text{period } 1)}$ for the period before the 2002/2003 season, and $\Phi_{(\text{period } 2)}$ from then on. Furthermore, the predicted suitable foraging area matched the same partitioning in periods (see Results section). Therefore, this division was also continued in the analyses of carrying capacity (see Results section). The relative support for each different model, i.e. model fit when varying the breakpoints and the comparison with a linear model excluding a breakpoint, was based on log-likelihood (e.g. Johnson & Omland 2004; Crawley 2007).

Results

A visual comparison between the first year of full grid coverage (1998) and the last year (2005) of the study period revealed the considerable changes in the extent of sampling stations that fulfilled the minimum intake requirements for *islandica* knots (Fig. 1). There was a significant decrease of 55% in the area suitable for foraging (Fig. 3a; GLM log-transformed data; $F_{1,8} = 45.68$; $P < 0.01$; log-likelihood = 12.61; from 5775 ha in 1996/1997 to 2581 ha in 2005/2006). However, a better-fitting model was obtained by introducing a breakpoint in the GLM, thereby dividing the study period into two periods, i.e. 1996/1997–2001/2002 and 2002/2003–2005/2006 (Fig. 3a; log-likelihood = 16.39).

Between 1996 and 2005, the spatial predictability of intake rate, i.e. the structural variance, based on the amount of autocorrelation in the first distance-class (250 m), declined (Fig. 3b; GLM log-transformed data; $F_{1,8} = 15.91$; $P < 0.01$; log-likelihood = 9.59). All spatial patterns differed from the background (habitat-based) autocorrelation (Fig. 2). The best-fitting model was obtained by treating 1996/1997–2003/2004 as a separate period from the years thereafter (Fig. 3b; log-likelihood = 13.00). The reduction of patch-size, i.e. the range, from 3000 (1996) to 1500 m (2005) was not significant at the 5% level, however (GLM log-transformed data; $F_{1,8} = 3.29$; $P = 0.11$).

The abundance of *islandica* knots decreased in the course of our study period (Fig. 3c; GLM log-transformed data; $F_{1,78} = 15.64$; $P < 0.01$; log-likelihood = 5.14). However, a model with a breakpoint indicated a break in trends after the winter of 2000/2001, and this was the superior model

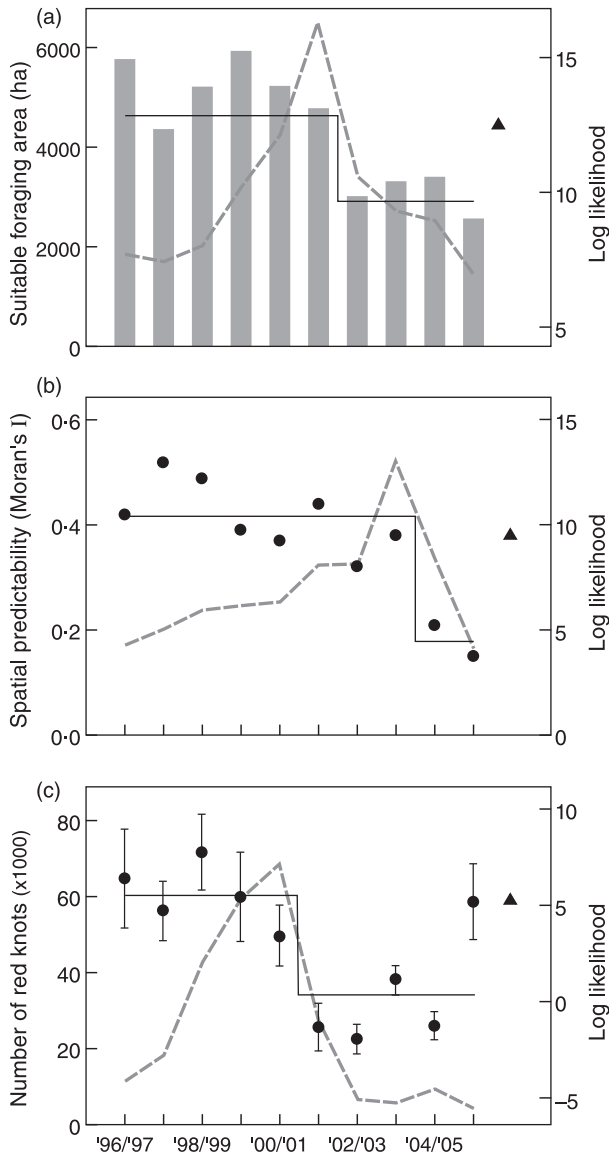


Fig. 3. (a) Part of the sampling area (ha) that offered sufficient intake rate (≥ 0.3 mg AFDM s^{-1}). (b) Predictability of intake rate, expressed as the amplitude of Moran's I in the first distance-class (250 m). (c) Abundance of red knots (mean \pm SE) in the western Dutch Wadden Sea during winter (September–April) from 1996/1997 to 2005/2006. Model fit (scaled on right axis) is shown for GLM with (dark grey line) or without (triangle) breakpoint that divides the data into two periods. Based on the best model, the mean (solid black line) for the two periods is shown.

(Fig. 3c; log-likelihood = 7.23). From 1996/1997–2000/2001, on average 60 209 red knots were encountered in the western Dutch Wadden Sea between August and April, whereas thereafter this number was 34 007 (Fig. 3c). This means that the number of red knots decreased by 44% within a decade.

When the suitable foraging area and the number of *islandica* knots between both periods were compared, it was shown that both declined by about the same amount (Fig. 4a,b; comparison of averages \pm SE between both periods; log suitable area: $t = 5.80$; d.f. = 8; $P < 0.01$; log knot numbers: $t = 3.38$; d.f. = 8; $P = 0.02$). It follows that the aver-

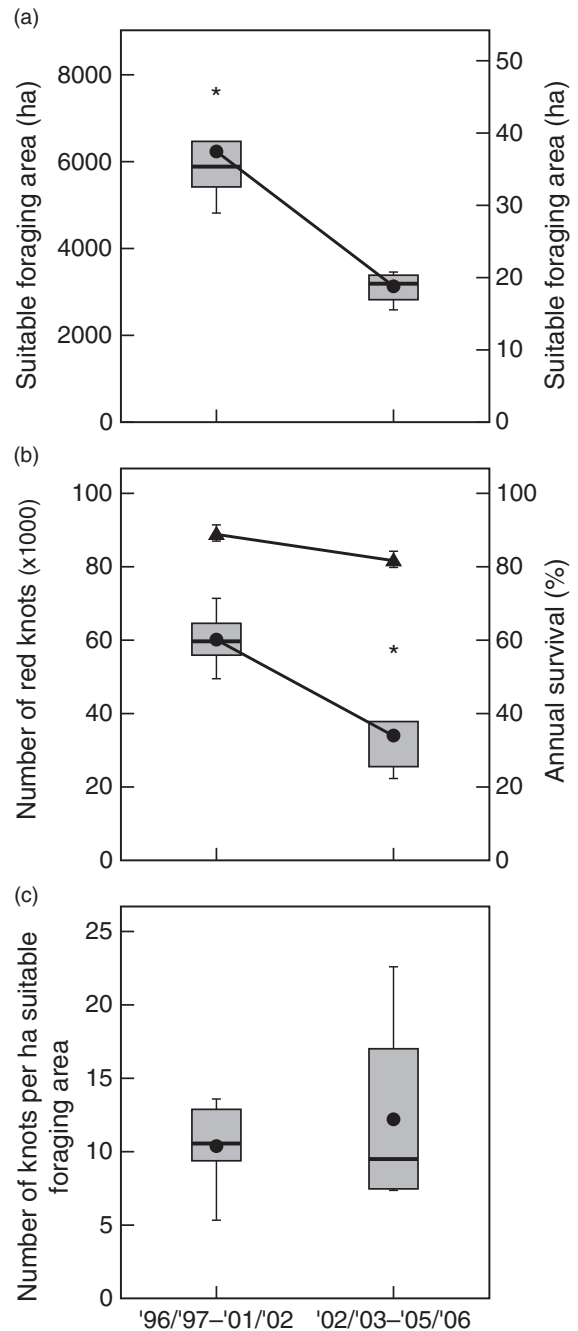


Fig. 4. (a) Decrease of suitable foraging area between 1996/1997–2001/2002 and 2002/2003–2005/2006 (left axis: suitable foraging area expressed in ha; right axis: suitable foraging area in % of total area). (b) Decline of red knot-numbers (box plots scaled on left axis) and annual survival [mean (triangle) \pm SE scaled on right axis] between both periods. (c) Because the 'slopes' in (a) and (b) are similar, the average number of red knots per ha suitable foraging area remained constant. Box-and-whisker plots give the mean (large dot), median (horizontal line inside the box), interquartile range (box), range (bars) and outliers (asterisk). [Correction added after online publication 17 Sept 2009: right y-axis scale of Fig. 4a now begins at 0, and first sentence of caption has been changed to 'Decrease of suitable foraging area between 1996/97–2001/2002 and 2002/2003–2005/2006']

age number of knots per ha suitable foraging area remained constant between both periods at *c.* 10 birds ha^{-1} (Fig. 4c;

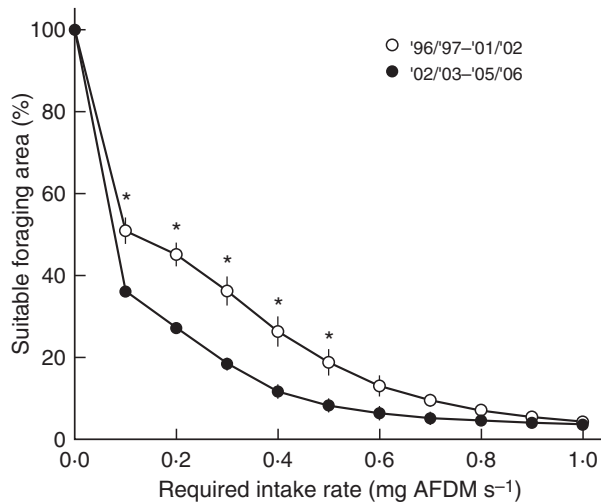


Fig. 5. Decrease of suitable foraging area (mean \pm SE) with increasing required predicted intake rates (mg AFDM s^{-1}) to maintain a daily energy balance. Open dots indicate the period 1996/1997–2001/2002, whereas the closed dots indicate 2002/2003–2005/2006. Asterisks mark significant differences.

$t = -0.424$; d.f. = 8; $P = 0.683$). Shifting the breakpoint in knot numbers one season ahead, thus matching the partitioning in periods of suitable foraging area, did not change this conclusion (c. 10 birds ha^{-1} ; $t = -1.131$; d.f. = 8; $P = 0.291$).

Whether a location is suitable for foraging is based on a binary division of predicted intake rates, where an intake rate of 0.3 mg AFDM s^{-1} acts as a barrier. To estimate the sensitivity of this barrier, we varied the threshold values to assess

the suitable foraging area in both periods, i.e. 1996/1997–2001/2002 and thereafter (Fig. 5). With increased required intake rates, the suitable foraging area decreases (Fig. 5), as fewer locations can provide the necessary amount of food. However, the differences between both periods were maintained until the outlying (and unlikely) values of required intake rates were reached (Fig. 5).

The model in which we distinguished between the annual survival of *islandica* knots in two periods (see Methods section) fitted better than a model with a year-dependent survival and was significantly better than the reduced model [$\Phi(p(\text{year}))$] without a difference in annual survival between the periods or years (likelihood ratio test; $\chi^2 = 4.22$; $P = 0.04$) (Table 1a). The annual resighting probability was 28% on average (SE = 3%) and varied between 11% (SE = 2%) in the 1999/2000 season to 35% (SE = 5%) in the 1998/1999 season (Table 1b). During 1996/1997–2001/2002, the annual survival \pm SE was estimated at $89 \pm 2\%$, whereas in 2002/2003–2004/2005 it was $82 \pm 2\%$.

Discussion

Capitalizing on an 'experiment' resulting from government-facilitated shellfish overexploitation in formally fully protected intertidal flats in the western Dutch Wadden Sea (Piersma *et al.* 2001; Lotze *et al.* 2005; Van Gils *et al.* 2006a; Kraan *et al.* 2007; Swart & Van Andel 2008), we examined changes in the three-way relationships between suitable foraging area, spatial predictability of food and red knot survival. *Islandica* knots, visiting the area in winter after their arctic breeding season in the period 1996–2005 (Piersma *et al.*

Table 1. (a) Model selection and (b) real function parameters, for the best-fitting model of the red knot survival analysis. AICc denotes AIC corrected for small-sample bias.

| | AICc | Delta AICc | AICc weight | Model likelihood | No. parameters | Deviance |
|---------------------------------------|----------|----------------|-------------|------------------|----------------|----------|
| (a) Model selection | | | | | | |
| $\phi(2\text{periods})p(\text{year})$ | 5766.10 | 0.00 | 0.58221 | 1.0000 | 10 | 336.757 |
| $\phi(\text{year})p(\text{year})$ | 5768.01 | 1.91 | 0.22438 | 0.3854 | 15 | 328.586 |
| $\phi(p)(\text{year})$ | 5768.31 | 2.20 | 0.19341 | 0.3322 | 9 | 340.973 |
| $\phi(\text{year})p()$ | 5823.69 | 57.59 | 0.00000 | 0.0000 | 9 | 396.359 |
| $\phi(p)()$ | 5845.40 | 79.30 | 0.00000 | 0.0000 | 2 | 432.115 |
| | Estimate | Standard error | 95% CI | | | |
| (b) Parameters | | | | | | |
| $\Phi_{(\text{period 1})}$ | 0.890 | 0.016 | 0.854–0.918 | | | |
| $\Phi_{(\text{period 2})}$ | 0.820 | 0.023 | 0.770–0.861 | | | |
| $P_{(1998/1999)}$ | 0.346 | 0.049 | 0.257–0.446 | | | |
| $P_{(1999/2000)}$ | 0.108 | 0.017 | 0.079–0.146 | | | |
| $P_{(2000/2001)}$ | 0.344 | 0.024 | 0.299–0.392 | | | |
| $P_{(2001/2002)}$ | 0.213 | 0.018 | 0.180–0.250 | | | |
| $P_{(2002/2003)}$ | 0.270 | 0.020 | 0.232–0.311 | | | |
| $P_{(2003/2004)}$ | 0.330 | 0.023 | 0.286–0.376 | | | |
| $P_{(2004/2005)}$ | 0.348 | 0.028 | 0.296–0.404 | | | |
| $P_{(2005/2006)}$ | 0.277 | 0.026 | 0.229–0.330 | | | |

Period 1 refers to 1998/1999–2001/2002; period 2 to 2002/2003–2005/2006.

1993; Nebel *et al.* 2000), were faced with a decline in the extent of suitable foraging area, especially from 2002 onwards (Fig. 3a), and a decline in the spatial predictability of their food (Fig. 3b). For such a benthivorous predator, which also has to deal with tidal cycles (Van Gils *et al.* 2005b, 2006b, 2007), interference competition (Van Gils & Piersma 2004; Vahl *et al.* 2005) and predation by raptors (Piersma *et al.* 1993; Van den Hout, Spaans & Piersma 2008), these landscape-scale changes have population-level impacts.

DECLINE OF SUITABLE FORAGING AREA

The decline of suitable foraging area and the decline of *islandica* knots ran parallel (Fig. 4a,b), and the mean density of birds remained stable at *c.* 10 individuals per ha suitable foraging area before and after 2002 (Fig. 4c). This not only strongly indicates that the available suitable foraging area regulates red knot numbers in the western Dutch Wadden Sea, but also that the intertidal areas are used to full capacity by red knots (Goss-Custard 1977, 1985).

In addition to the absolute decrease of sites that are above the threshold predicted intake rate, also the spatial arrangement of the remaining area that still provided sufficient food is of importance. Red knots follow strategic itineraries across the intertidal landscape, utilizing a west–east gradient in exposure time, to be able to fulfil their energetic demands (Van Gils *et al.* 2005b, 2006b). For example, satiating *islandica* knots extend their working day routinely beyond 12 hours, up to 17 hours, to sustain their energy requirements (Van Gils *et al.* 2005b, 2007). However, the intertidal areas that would allow such an extension of the feeding day, when taking the energetic requirements into account, now no longer provide sufficient foraging opportunity simply because suitable sites are not lined-up in a west–east gradient anymore (compare Fig. 1, lower panel, with Fig. 6 in Van Gils *et al.* 2005b). Tidal flats that would enable an extension of the working day beyond 14 hours (3 hours shorter than what was sometimes necessary in 1997–2000) were nearly devoid of suitable foraging sites in the second period (Fig. 1, lower panel, compared with Fig. 6 in Van Gils *et al.* 2005b), which raises the question if it would still have been profitable to go that far east in the second period.

Although red knots may recently have been unable to extend their feeding day by moving along a west–east axis, they would have been able to boost their digestive capacity. For example, increasing gizzard size from 6 to 8 g, which increases the digestively constrained intake rate, would lead to an increase in the suitable foraging area for red knots with undersized gizzards (Fig. 6a). For the period 2002/2003–2005/2006, this would amount to *c.* 1000 ha. Indeed, average gizzard size of *islandica* knots increased in the second period (Fig. 6b). However, even though the increase in gizzard size between the two periods was small (0.4 g), it was significant [GLM using 125 measured gizzards between September and April and year nested within period (in 1996 and 2005 no gizzards were measured); $F_{3,121} = 5.76$; $P = 0.001$]. Yet, it

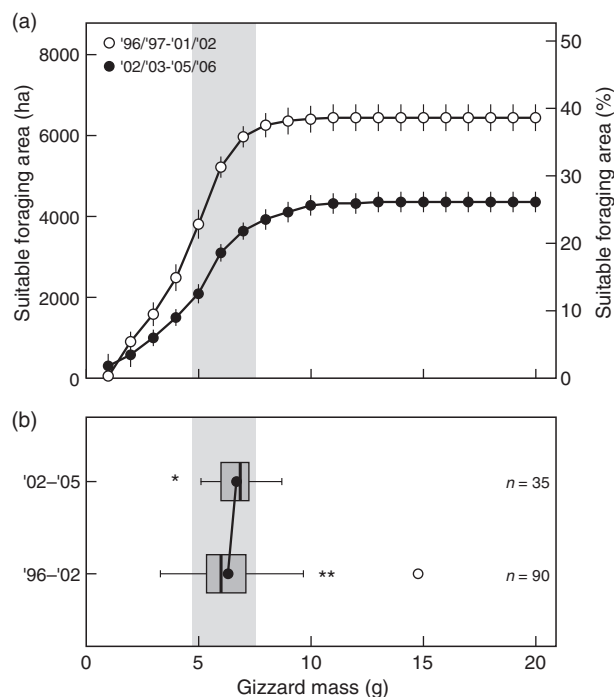


Fig. 6. (a) Suitable foraging area (ha; mean \pm SE) during 1996/1997–2001/2002 (upper line) and 2002/2003–2005/2006 (lower line) for a minimally required intake rate of $0.3 \text{ mg AFDM s}^{-1}$ as a function of gizzard mass (left axis: suitable foraging area expressed in ha; right axis: suitable foraging area in % of total area). (b) Distribution of gizzard masses (g) in 1996/1997–2001/2002 and 2002/2003–2005/2006. Grey bar indicates the mean \pm SD gizzard mass from 1996 to 2005. Box-and-whisker plots as described for Fig. 4. The open circle marks an outlier.

would only have led to an increase in the suitable foraging area of *c.* 225 ha (Fig. 6a). That red knots only partially increased gizzard size may indicate that they minimize the overall rate of energy expenditure by carrying the smallest possible gizzard for the energy budget to be in balance (Van Gils *et al.* 2003a, 2007). Enlarging gizzard size increases a number of cost factors that we did not account for, as, for example, growing and maintaining such a large gizzard increases the average daily metabolic rate (Van Gils *et al.* 2003a) and affects manoeuvrability when escaping from predators (Dietz *et al.* 2007).

DECLINE OF FORAGING INFORMATION

When food abundance decreases (Figs. 1 and 3a), spatial patterns of food distributions change as well (Fig. 3b). The observed decline in structural variance, implying a more random distribution of food, reduces the amount of available foraging information. This is particularly unfavourable for predators foraging on prey that are hidden, e.g. covered in snow or beneath a layer of mud. Such animals, including bison *Bos bison* (Fortin 2003), tundra swans *Cygnus columbianus bewickii* (Klaassen *et al.* 2006), mallard *Anas platyrhynchos* (Klaassen *et al.* 2007) and red knots (Van Gils *et al.* 2003b), adjust their foraging behaviour to spatial structuring of their cryptic prey. To maximize their long-term intake

rate, they stay longer in rich areas and reside shorter in poor foraging sites by using foraging success as an indicator of prey density (Olsson & Holmgren 1998). Loss of spatial predictability of food and therefore adhering to a more random distribution, as encountered by red knots in the western Dutch Wadden Sea (Fig. 3b), means that food might be more difficult to find (Mangel & Adler 1994) and that patch sample information is less reliable, which increases the assessment error and time needed to detect that the area is poor (Iwasa *et al.* 1981; Olsson & Brown 2006). An increasing amount of time has to be devoted to the actual searching of cryptic prey, reducing the daily energy intake further. In addition, longer foraging periods lead to higher risks (e.g. predation risk), as described elsewhere (Van Gils *et al.* 2006b, 2007).

The decline of red knots should have been more rapid than the loss of suitable foraging area to be indicative of an Allee effect. In the latter case, the population size would have been below a critical threshold, upon which the inverse density dependence would become visible (Courchamp *et al.* 1999). Note, however, that if the decline of red knots would be more rapid than the decline of suitable foraging area, an alternative explanation might also hold: at low prey densities, interference competition would increase, which would lead to lower forager-to-prey ratios as predicted by some of the models considered by Van der Meer & Ens (1997). Predictability of good foraging sites over time, i.e. high temporal autocorrelation, may play a yet undetermined role as well. Untying these possible effects remains a challenge for the future.

POPULATION-LEVEL CHANGES

Following the joint decline of suitable foraging area and loss of information about their prey, survival of *islandica* knots decreased from 89% to 82%. As the mean life span (MLS) is a function $(-1/\ln[\phi])$ of annual survival (ϕ), we can express the difference in survival as a difference in MLS. MLS of birds with an annual survival of 89% is 8.6 years, whereas it is 5.0 years for birds with a survival rate of 82%. Therefore, the average MLS of *islandica* knots wintering in the western Dutch Wadden Sea shortened by 42% in the period 1996–2005.

Under the assumption that survival was at equilibrium with reproduction between 1996/1997 and 2001/2002 but not thereafter, we expect an annual decrease in population size of the locally wintering red knots during the second period $(89-82\%)/89\% = 8\%$. In terms of numbers, we would then expect an average number of 49 093 (SD = 5278) red knots during 2002/2003–2005/2006 [derived from the 1996/1997–2001/2002 counts with 60 209 as the average number of red knots, $(\sum_{t=1}^4 60\,209(1-0.08)^t)/4$, over the 4 years from 2002/2003 to 2005/2006]. The actual average number in the area was 34 007 (SD = 14 877), which means that reduced survival (with constant recruitment) only explained $100\% \times (60\,209 - 49\,093)/(60\,209 - 34\,007) = 42\%$ of the loss in numbers: more red knots 'disappeared' from the Dutch Wadden Sea than could be explained by the increased mortality (e.g. Van Gils *et al.* 2006a). Apparently,

many surviving red knots emigrated permanently out of this marine protected area [note that the Wadden Sea harbours one-third to half of the total *islandica* wintering population (Van Gils *et al.* 2006a)], and reduced food abundance may have indirectly lead to reduced breeding success (Ebbinge & Spaans 1995; Baker *et al.* 2004; Morrison, Davidson & Wilson 2007). In any case, the reduced annual survival clearly supports the suggestion that the Wadden Sea was filled to capacity in the decade during which this study took place (cf. Goss-Custard 1985; Goss-Custard *et al.* 2002).

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