



Contrasting Benthos Communities and Prey Selection by Red Knot *Calidris canutus* in Three Nearby Bays on the Channel Coast

Authors: Quaintenne, Gwenaël, Bocher, Pierrick, Ponsero, Alain, Caillot, Emmanuel, and Feunteun, Eric

Source: Ardea, 101(2) : 87-98

Published By: Netherlands Ornithologists' Union

URL: <https://doi.org/10.5253/078.101.0203>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Contrasting benthos communities and prey selection by Red Knot *Calidris canutus* in three nearby bays on the Channel coast

Gwenaël Quaintenne¹, Pierrick Bocher^{1,*}, Alain Ponsero²,
Emmanuel Caillot³ & Eric Feunteun⁴

Quaintenne G., Bocher P., Ponsero A., Caillot E. & Feunteun E. 2013. Contrasting benthos communities and prey selection by Red Knot *Calidris canutus* in three nearby bays on the Channel coast. *Ardea* 101: 87–98.

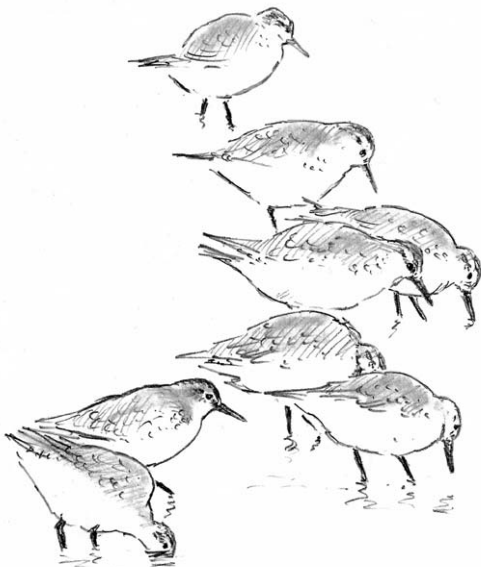
In this study, we describe food availability and diet selection of the Red Knot *Calidris canutus islandica* wintering in three estuarine bays on the French Channel coast. We examined whether the distribution of birds is related to the density and availability of high quality prey. Results indicate strong seasonal and inter-annual variation in the abundance of birds and considerable variation in prey-item abundance and diet selection depending upon site. At Mont Saint-Michel Bay, the prey community was dominated by Baltic Tellins, *Macoma balthica*. As expected from their high meat-to-shell ratio, *Macoma* contributed more than 90% of the diet. Most of the cockles, *Cerastoderma edule* were too large and their quality too low to be preyed upon. Less than 100 km away, in Saint-Brieuc Bay, Red Knots mainly selected the Thin Tellin *Tellina tenuis*. Although *Tellina* are a lower quality prey than *Macoma*, they occurred at a high density and in some winters might explain why the number of Red Knots exceeds those at Mont Saint-Michel Bay. At Bay des Veys, Normandy, Red Knots were restricted to a small intertidal area and fed on *Abra tenuis*, *Macoma balthica* and *Hydrobia ulvae*.

Key words: bivalves, shorebird distribution, feeding ecology, diet selection, prey quality, Mont Saint-Michel Bay, Saint-Brieuc Bay, Bay des Veys

¹Laboratory Littoral, Environnement et Sociétés, UMR7266 CNRS-ULR, University of La Rochelle 17000 La Rochelle, France; ²Reserve Naturelle of Baie de Saint-Brieuc, site de l'étoile, 22120 Hillion, France; ³Reserve Naturelle du Domaine de Beauguillot, 50480 Sainte Marie du Mont, France;

⁴MNHN, Centre de Recherches et d'Enseignement sur les Systèmes Côtiers, UMR MNHN-CNRS-IRD-UPMC, BOREA, 38 rue du Port Blanc, 35800 Dinard, France;

*corresponding author (pbocher@univ-lr.fr)



Understanding how animals select their habitat is a fundamental issue concerning species and habitat conservation (Jonzén 2008). Shorebirds are highly dependent on a limited number of key stop-over and wintering sites, and hence are particularly vulnerable to habitat loss and most populations are in serious decline worldwide (Bart *et al.* 2007, Nebel *et al.* 2008, Delany *et al.* 2009). Food is a primary requirement for survival and therefore, the most important determinant of habitat quality (Piersma 2006). Intertidal sand or mud flats are the main foraging areas of coastal shorebirds feeding on macrofauna and bird distributions

across coastal bays have often been positively correlated with those of their benthic prey species (Colwell & Landrum 1993, Yates *et al.* 1993, Kalejta & Hockey 1994, Ribeiro *et al.* 2004, Spruzen *et al.* 2008, Quaintenne *et al.* 2011). Nevertheless, prey availability often does not equal prey density, and the available food stocks only represent a small fraction of the total food stocks (Zwarts & Wanink 1993).

In this paper, we focus on the Red Knot *Calidris canutus*, a shorebird species with a circumpolar distribution in summer, breeding in tundra habitats between mid-June and late July (Davidson & Piersma 2009).

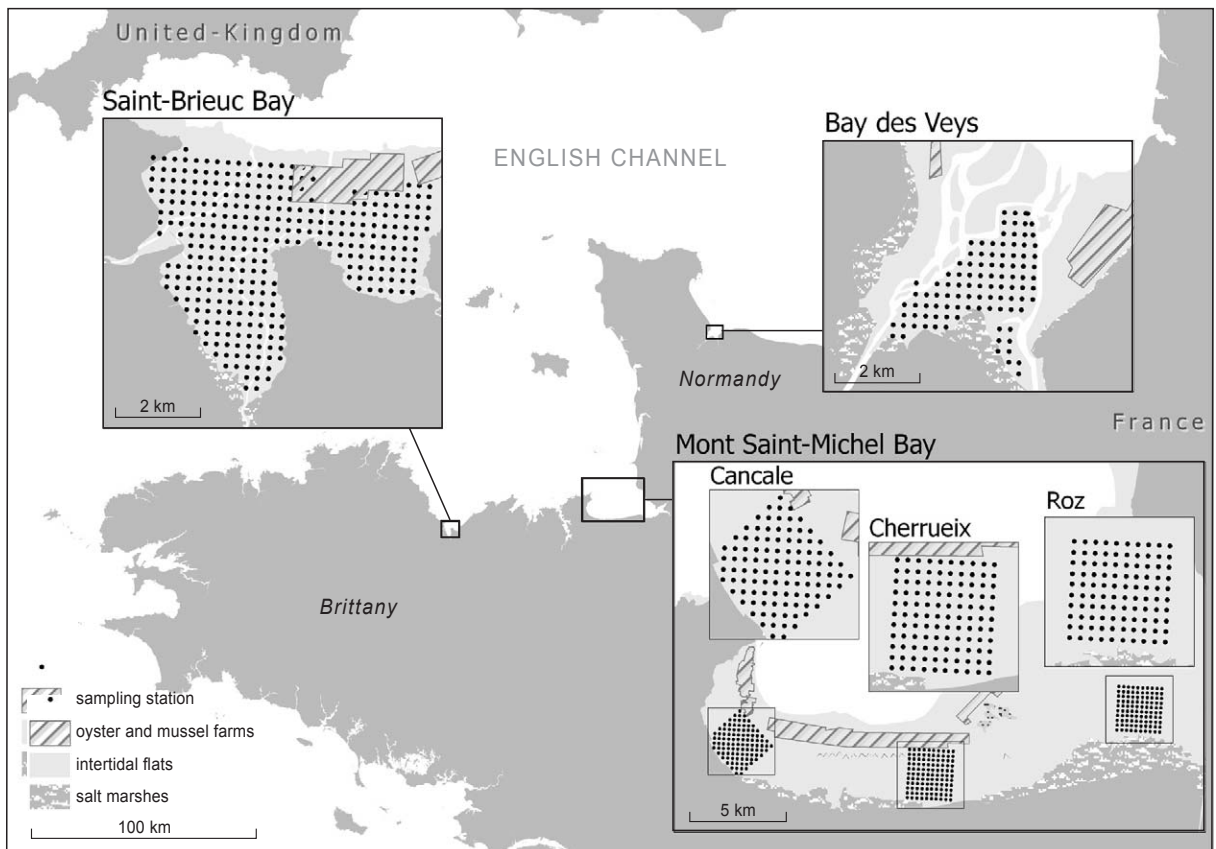


Figure 1. Location of the three study areas on the French Channel coast. Black spots mark sampling stations.

After breeding, the birds migrate south and are distributed on coastal wetlands and particularly on intertidal flats, where they winter. The species is divided into six subspecies, with *Calidris canutus islandica* breeding in north Greenland and Arctic Canada and wintering on the coasts of northwestern Europe (Buehler & Piersma 2008). The *islandica* population estimate is about 450,000 individuals, divided between the British Isles, the Wadden Sea and the coasts of France from August to March (Davidson & Piersma 2009, Bocher *et al.* 2012). Study of this species is particularly relevant as there has been a sudden serious decline in the population wintering in The Netherlands (from over 100,000 birds in 1999 to 20,000 birds in 2003). It is possible that the distribution has altered, but it is also possible that the population as a whole is in steep decline (Piersma *et al.* 2001, van Gils *et al.* 2006, Kraan *et al.* 2007). It is consequently relevant to collect information elsewhere in Europe concerning the relative quality of food resources of the secondary wintering sites used by this population of Red Knots. To this end, we sampled

the benthic macrofauna and reconstructed the diet of the Red Knot in three sectors of Mont Saint-Michel Bay, the second-most important wintering area for Red Knots in France (Bocher *et al.* 2012). We also sampled two more estuarine bays, the Bay of Saint-Brieuc in Brittany and the Bay des Veys in Normandy, which are less than 100 km away. These three Channel coast sites constitute a link between the traditional wintering sites on the coast of the British Isles and the Wadden Sea, where more than 80% of *islandica* Knots winter (Stroud *et al.* 2004), and their southern distribution limit on the French Central Atlantic and Portuguese coasts. The diet selection of Red Knots was studied, in relation to the accessibility, availability and the digestive quality of their main prey at each of the three sites. The Red Knot is presumed to select the Baltic Tellin *Macoma balthica* in northern Europe, due to its high energetic quality (Zwarts & Blomert 1992). We examined whether the distribution of Red Knots at favourable sites on the French Channel coast is related to the density and availability of high quality prey or to alternative prey.

METHODS

Study sites

The study at Mont Saint-Michel Bay was carried out at three subsites (Figure 1), selected on the basis of personal knowledge of the distribution of Red Knots and the previous study by Le Dréan-Quénec'hdu *et al.* (1995a). The Bay of Saint-Brieuc and Bay des Veys were chosen for their proximity to Mont Saint-Michel, which would facilitate exchange of birds during winter, and thereby their use as alternative sites (Figure 1). The three bays located in the central part of the southern edge of the Channel involve some of the largest intertidal soft-sediment systems in northwest Europe (Eisma 1998), whilst all except for the Bay des Veys (Bocher *et al.* 2012) harbour significant wintering populations of Red Knots.

Bird counting

The number of Red Knots counted at high tide, on roosting areas of the three sites from 1977/1978 to 2009/2010, was taken from the annual mid-winter (January) counts of the Wetlands International Programme (Mahéo 1977–2010). Trend analysis was performed with TrendSpotter software (Soldaat *et al.* 2007). Monthly counts were made in Saint-Brieuc Bay and Bay des Veys (2000–2008). Data for Mont Saint-Michel Bay (1980–1982) were extracted from Le Dréan Quénec'hdu *et al.* (1995a).

Resource sampling

Study sites were sampled between 28 January and 2 February 2006 (Table 1), except the eastern part of the Saint-Brieuc Bay, which was sampled in early March

2006. Macrofauna was sampled systematically at stations arranged in a grid of 250 m intervals using a handheld GPS (Garmin 45 and 12, WGS84 as a geographic coordinate system). Across the three study sites, a total of 720 sampling stations were visited (Figure 1). All stations were visited on foot during low tide and at each, a sediment core of 1/56 m² was taken to a depth of 20 cm, according to methods used by Bocher *et al.* (2007) and Kraan *et al.* (2009). Because Red Knots cannot access buried prey that is deeper than the 3.5 cm length of their bill (Zwarts & Blomert 1992), the upper 4 cm was separated from the rest of the core, to distinguish prey that was accessible. Sediment core fractions were sieved through a 1-mm mesh. The abundant mudsnail, *Hydrobia ulvae*, was sampled by taking one additional core of 1/270 m² to a depth of 5 cm sieved over a 0.5 mm mesh. All living molluscs were then stored at –20°C until they were processed. In the laboratory, the molluscs were identified to the species level, counted (to estimate density), and size (length) was measured to the nearest 1 mm (to determine ingestibility). For each bivalve (with a shell length larger than 5 mm), the flesh was separated from the shell and both parts were dried for 3 d at 55°C to determine the dry mass of the flesh and the shell (DM_{shell}). The ash-free flesh dry mass (AFDM_{flesh}) for each individual was determined after incineration at 550°C for 5 h. The harvestable prey for Red Knots was defined following Zwarts *et al.* (1992) and Zwarts & Blomert (1992), applying the concepts of accessibility (bivalves below the top 4 cm were excluded), ingestibility (large bivalves that could not be ingested were excluded) and profitability (bivalves that were too small and not profitable to predate were excluded). The available prey

Table 1. Study sites: their abbreviations, locations, sampling periods, number of samples (benthos and droppings) and sediment characteristics.

Sites	Coordinates		Sampling dates	N samples		Sediment characteristics		
	Latitude	Longitude		Benthos	Droppings	Median grain size (μm ± SD)	Sediment <63 μm (%)	(N)
Saint-Brieuc Bay (SBB)	53°26'N	06°02'E	31 Jan, 3 Mar 2006	323	7	151 ± 37	0.09	(26)
Mont-Saint-Michel Bay (MSMB)								
Cancale (CAN)	53°50'N	00°17'E	2 Feb 2006	95	5	47 ± 26	0.58	(9)
Cherrueix (CHE)			29 Jan 2006	100	6	111 ± 53	0.3	(9)
Roz (ROZ)	48°37'N	01°41'W	28 Jan 2006	100	6	158 ± 11	0.09	(9)
Bay des Veys (BDV)	46°17'N	01°10'W	30 Jan 2006	102	2	164 ± 56	0.14	(8)

was then defined as prey that was both accessible and ingestible. In the absence of worms and crustaceans in the diet of Red Knots, we limited the definition of prey harvestability to bivalves and gastropods.

Because the maximum intake rate of Red Knots is limited by rates of digestion (van Gils *et al.* 2005, Quaintenne *et al.* 2010), prey items were ranked on the basis of digestive quality rather than by profitability. The digestive quality was expressed as the flesh-to-shell ratio.

Diet

Within areas where we sampled macrofauna, we also collected Red Knot droppings. Each dropping sample consisted of a set of 25 individual droppings that were pooled and were geo-referenced using a GPS. In total,

26 dropping samples were collected across all study sites (Table 1). In the laboratory, diet was reconstructed from these samples following the protocol of Dekinga & Piersma (1993). Shell fragments of bivalves and gastropods were retrieved from the dried droppings and the shell lengths of prey ingested were then reconstructed using allometric equations between shell length and hinge height (or width of the first whorl in the case of gastropods). The relative DM_{shell} contribution of each prey species in the diet resulted from the weighted shell fragments sorted by species. Subsequently, the size and species specific $AFDM_{\text{flesh}}$ -to- DM_{shell} ratios determined per study site, were used to calculate the relative $AFDM_{\text{flesh}}$ contribution for each prey species.

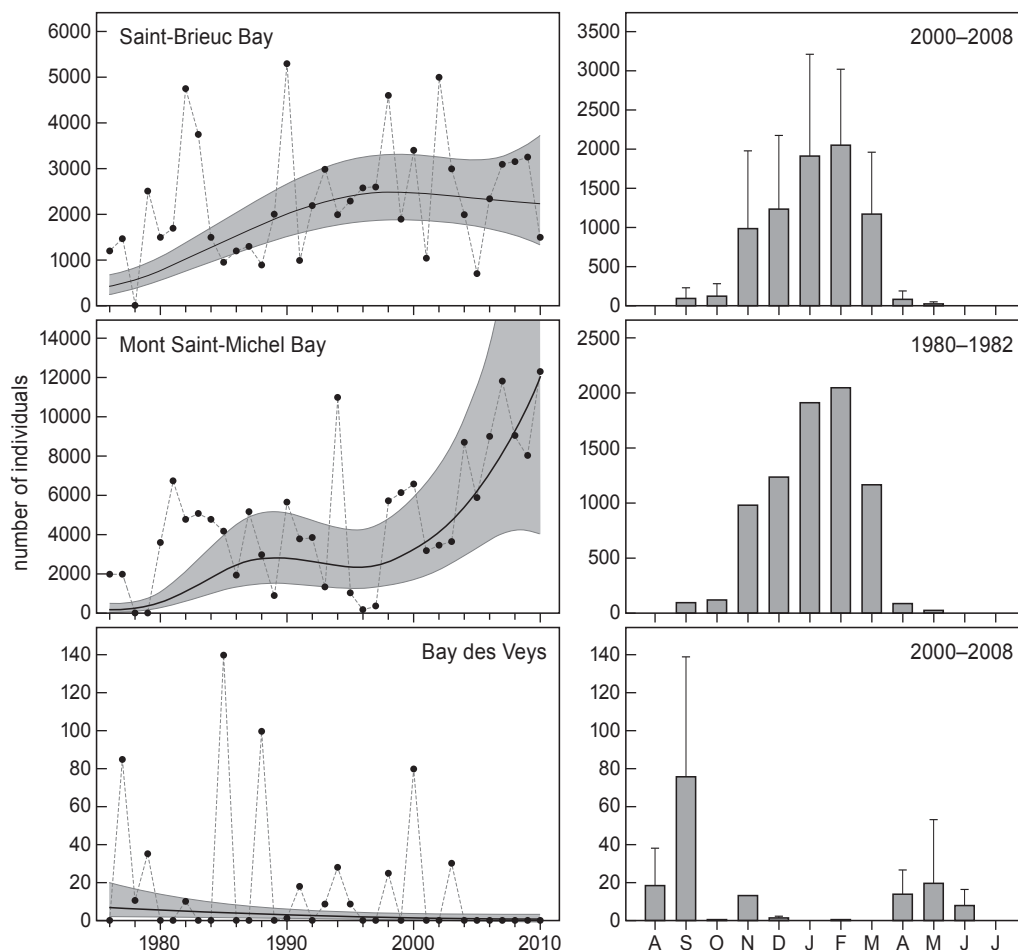


Figure 2. Annual abundance of Red Knots at the three study areas between 1976 and 2010 from IWC counts (mid-January). The grey shading indicates the 95% confidence intervals of the smoothed overall trend (solid lines) estimated by TrendSpotter (Soldaat *et al.* 2007). On the right, histograms represent the monthly abundance of Red Knots (\pm SD) between 2000 and 2008 in Saint-Brieuc Bay and Bay des Veys; and 1980–1982 in Mont Saint-Michel Bay.

RESULTS

Annual and seasonal occurrence of Red Knots

During the annual mid-winter counts, Red Knots numbered on average 5290 ± 3464 (SD) individuals in Mont Saint-Michel Bay and 2695 ± 1259 individuals in Saint-Brieuc Bay (Figure 2). In Bay des Veys the numbers rarely exceeded 50 birds. The occurrence of Red Knots at Mont-Saint-Michel and Saint Brieuc was strongly seasonal, with the arrival of birds in November, their peak numbers occurring in February and departure in late March to early April. The maximum occurrence of Red Knots in the Bay des Veys was recorded in September and May and coincided with the migratory patterns of *C. c. canutus*, the Afro-Siberian subspecies (Piersma 2007). At Mont Saint-Michel, the Red Knot population has increased over the last 35 years (Figure 2) with no significant trend over the last ten years. At Saint-Brieuc, the population has increased over the last 35 years, with no trend over the last ten years.

Available mollusc resources

On the three sectors of Mont Saint-Michel, the dominant bivalve species were *Cerastoderma edule* and *Macoma balthica* and these represented most of the available biomass for Red Knot in the three sectors (Figure 3, Appendix 1). The gastropod *Hydrobia ulvae* was only recorded at Cancale and Roz at a low density. At Saint-Brieuc, the mollusc community was dominated by *Cerastoderma* and *Tellina tenuis*; the latter was rare at Mont Saint-Michel. Both species constituted the bulk of the available mollusc biomass at Saint-Brieuc (Figure 3). *Macoma* and *Hydrobia* were only found in low densities on the muddiest part of Saint-Brieuc. In the Bay des Veys, *Cerastoderma* was the dominant species; *Macoma*, *Abra tenuis* and *Hydrobia* were present in high densities, but only in a very restricted area on the higher part of the bay close to the salt marshes. The contribution of prey species to total, accessible and available food stocks are presented in the three upper boxes of Figure 4. From the total to accessible biomass, the contribution of *Cerastoderma* increased because the species is restricted to the upper fraction of sediment and never found deeper than 4 cm. In contrast, from accessible to available stocks of prey, the contribution of *Cerastoderma* decreased because larger individuals were excluded. The contributions of *Macoma* and *Tellina* decreased from the total to accessible biomass, but increased from the accessible to available biomass.

Prey size selection

The size distribution of ingested prey differed from the

size distribution data available for the habitat (as indicated by the Chi-squared statistics in Figure 5). There was a selection towards large size classes of *Macoma* at Mont Saint-Michel of about 14.0 mm (mean shell length ingested \pm SD at Cancale: 14.3 ± 2.0 mm; at Cherrueix: 14.6 ± 2.3 mm; at Roz: 9.3 ± 4.2 mm), especially at Roz, where larger individuals were relatively less abundant than small ones, but were selected (Figure 5). Red Knots at the Bay des Veys selected the bivalve *Abra tenuis* between 2.0 and 6.0 mm, with a mean length of 5.4 ± 0.6 mm. Only small-size classes of *Cerastoderma*, found in low densities, were eaten by Red Knots (mean shell length ingested 7.2 ± 1.5 mm). Larger size classes of *Cerastoderma* were abundant at most sites but were too large to be ingested.

Quality of prey

The flesh-to-shell ratio of each main accessible prey species averaged by size classes of 3 mm is compared in Figure 6. Ratios differed by species (GLM $F_{3,2113} = 667.7$, $P < 0.001$) and by size classes ($F_{5,2113} = 179.2$, $P < 0.001$). *Macoma* had on average a higher flesh-to-shell ratio ($0.16 \pm$ SD 0.50 , $n = 574$) than the other species. *Abra* was the next-highest quality prey with a ratio of 0.11 ± 0.50 ($n = 73$). *Tellina*, with a mean ratio of 0.07 ± 0.02 ($n = 482$), had a higher digestive quality value compared to *Cerastoderma*, with a mean ratio of only 0.04 ± 0.01 ($n = 997$).

Diet

Red Knots in the south Channel bays fed only on molluscs and no remains of worms or crustaceans were found in collected faeces. The four most abundant bivalves (*Tellina tenuis*, *Macoma balthica*, *Cerastoderma edule* and *Abra tenuis*) and the gastropod (*Hydrobia ulvae*) made up the bulk of the Red Knot's diet for the three study areas. The contribution of these prey species in terms of AFDM to the diet at each site is depicted in the bottom graph of Figure 4. The diet of Red Knots in the five sectors differed significantly (two-way ANOVA performed on arcsine-transformed percentages, $F = 126.9$, $P < 0.001$). To summarise, Red Knots specialised on *Tellina* at Saint-Brieuc ($95.3 \pm$ SE 1.3% AFDM in the diet), on *Macoma* at Mont Saint-Michel (Mean \pm SE Cancale: $99.5 \pm 0.1\%$; Cherrueix: $99.3 \pm 0.2\%$; Roz: $91.4 \pm 5.0\%$) and had a rather diverse diet at the Bay des Veys, with 63.6% of *Abra*, 12.9% of *Macoma* and 8.2% of *Cerastoderma* and less than 15.0% of *Hydrobia* (Figure 4). Focussing on the available prey fraction, only *Tellina* predominated at Saint-Brieuc (70%), *Macoma* at Cancale (60%), *Macoma* and *Cerastoderma* in similar proportions at

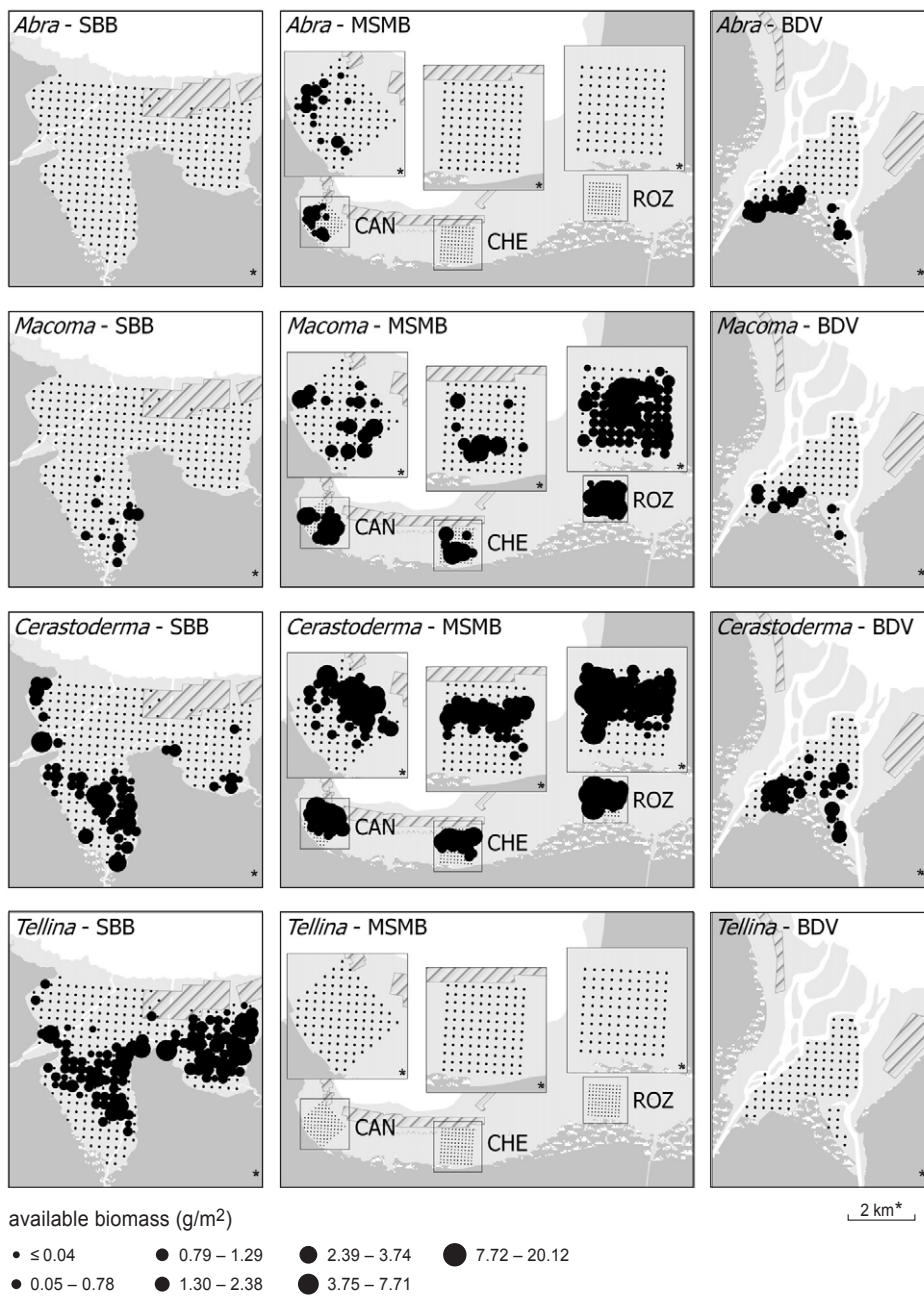


Figure 3. Distribution of available biomass (g/m²) of main bivalve prey species (*Tellina tenuis*, *Macoma balthica*, *Abra tenuis* and *Cerastoderma edule*) of Red Knots over the entire area and subsites. For the Mont Saint-Michel Bay the three squares are enlargements of the smaller squares on the map.

Cherrueix (47 and 52%, respectively) and at Roz (52 and 47%, respectively). In the Bay des Veys, the available prey stock was more diverse and was composed of *Hydrobia* (35%), *Macoma* (29%), *Cerastoderma* (26%) and *Abra* (10%) (Figure 4).

DISCUSSION

By examining food availability and diet selection of overwintering Red Knots in three embayments on the French Channel coast, this study highlighted high heterogeneity in prey abundance and distribution

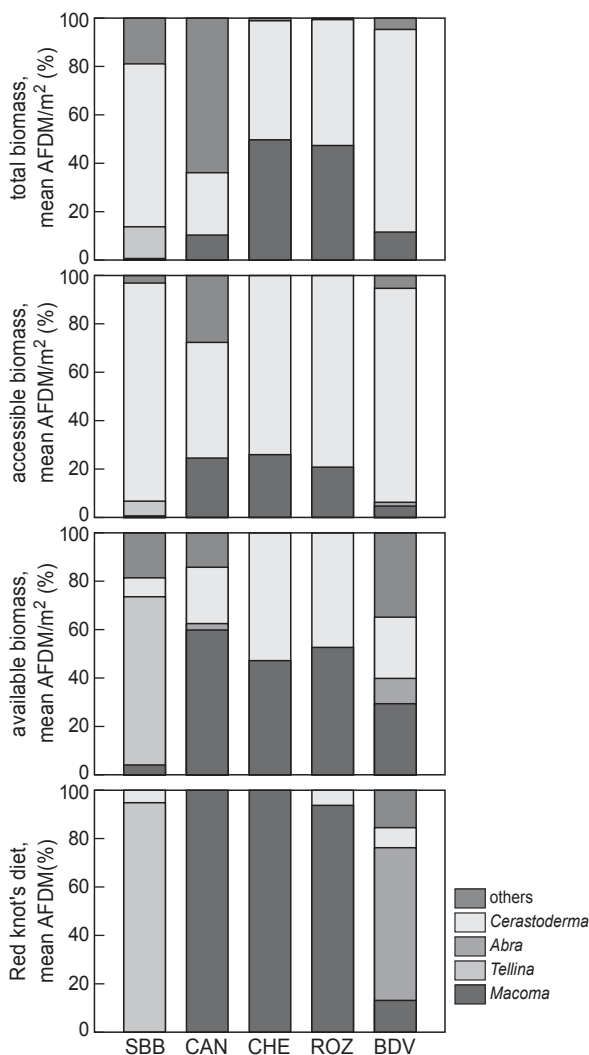


Figure 4. Comparison of the mean proportions of prey mollusc species (ash-free dry mass per square metre) from total, accessible and available biomasses against the Red Knot diet (mean percentage AFDM) at each site of the study: SBB (Saint-Brieuc Bay), Mont Saint-Michel Bay: CAN (Cancale), CHE (Cherrueix), ROZ (Roz) and BDV (Bay des Veys).

between sites. We also identified a strong seasonal and inter-annual variation in the abundance of birds.

The Red Knot *C. c. islandica* wintering along the French coast, with a mean of 35,000 individuals over the last ten years (maximum 45,000 in 2006), represents 9% of the flyway population. Nevertheless, despite the 6,000 km of coast length, 91% of this total number is concentrated at only six sites (Bocher *et al.* 2012). About one third of the bird total is located on sites bordering the North Sea and the Channel, while two thirds are distributed on the Atlantic coast. On the

Channel coast, only the bays of Saint-Brieuc and Mont Saint-Michel are of national or international importance (Bocher *et al.* 2012). Consequently, two of the study sites appear to be very important wintering sites for the whole distribution area of the population. The central position of the Channel coast between the traditional northern wintering areas (United Kingdom, Netherlands) and southern areas on the Atlantic coast (Delany *et al.* 2009), might represent the closest climatic refuge for Red Knots that leave more northerly areas during severe winters in search of better feeding areas and energetic conditions (Le Dréan-Quénec'hdu *et al.* 1995b).

In this study, we confirm that the Red Knot is a molluscivore species as at other sites in Europe and we show that it is highly selective for specific bivalves at two of the three studied sites. Considering that Red Knots are typical digestively constrained foragers (van Gils *et al.* 2005, Quaintenne *et al.* 2010), the observed diet can be explained by the available abundance and digestive quality of prey, which showed considerable variability, depending upon prey species and size. *Macoma* was presumed to be the preferred prey of Red Knots in Europe (Zwarts & Blomert 1992) because of its high flesh-to-shell ratio. At Mont Saint-Michel, consumed *Macoma* ranged from 5 to 19 mm in size, similar to at other sites in Europe (Prater 1974, Goss-Custard *et al.* 1977, Dekinga & Piersma 1993), but the largest *Macoma*, at about 14 mm, were preferred at the three Mont Saint-Michel subsites. Across Europe, most *Macoma* smaller than 9–10 mm are rejected because of their unprofitability in terms of $\text{AFDM}_{\text{flesh}}$ per handling time (Piersma *et al.* 1995). However, on the eastern-sampled subsites of Mont Saint-Michel bay, the density of small *Macoma* was higher (with 774 ind/m²) than at other sites in Europe as summarised in Bocher *et al.* 2007 (The Wash: 309 ind/m²; Dutch Wadden Sea: 126 ind/m²). Therefore, Red Knots accepted individuals <10 mm, even though they selected larger sizes. In the two others bays, *Macoma* were rare, causing Red Knots to feed on other prey. At Saint-Brieuc, we describe *Tellina tenuis* as an unusual prey species for Red Knots, compared to traditional wintering sites in Europe. *T. tenuis* was only described previously as a prey for Red Knots at Morecambe Bay, on the northwestern coast of England, by Prater (1972). Despite a thinner shell, *Tellina* remains a lower quality prey compared to *Macoma*, due to a poor $\text{AFDM}_{\text{flesh}}$ content. *Tellina* remains, however, a high quality prey compared to *Cerastoderma* and contributes to more than 90% of the Red Knot's diet in Saint-Brieuc. At the Bay des Veys, Red Knots mainly feed on *Abra tenuis*, a high quality

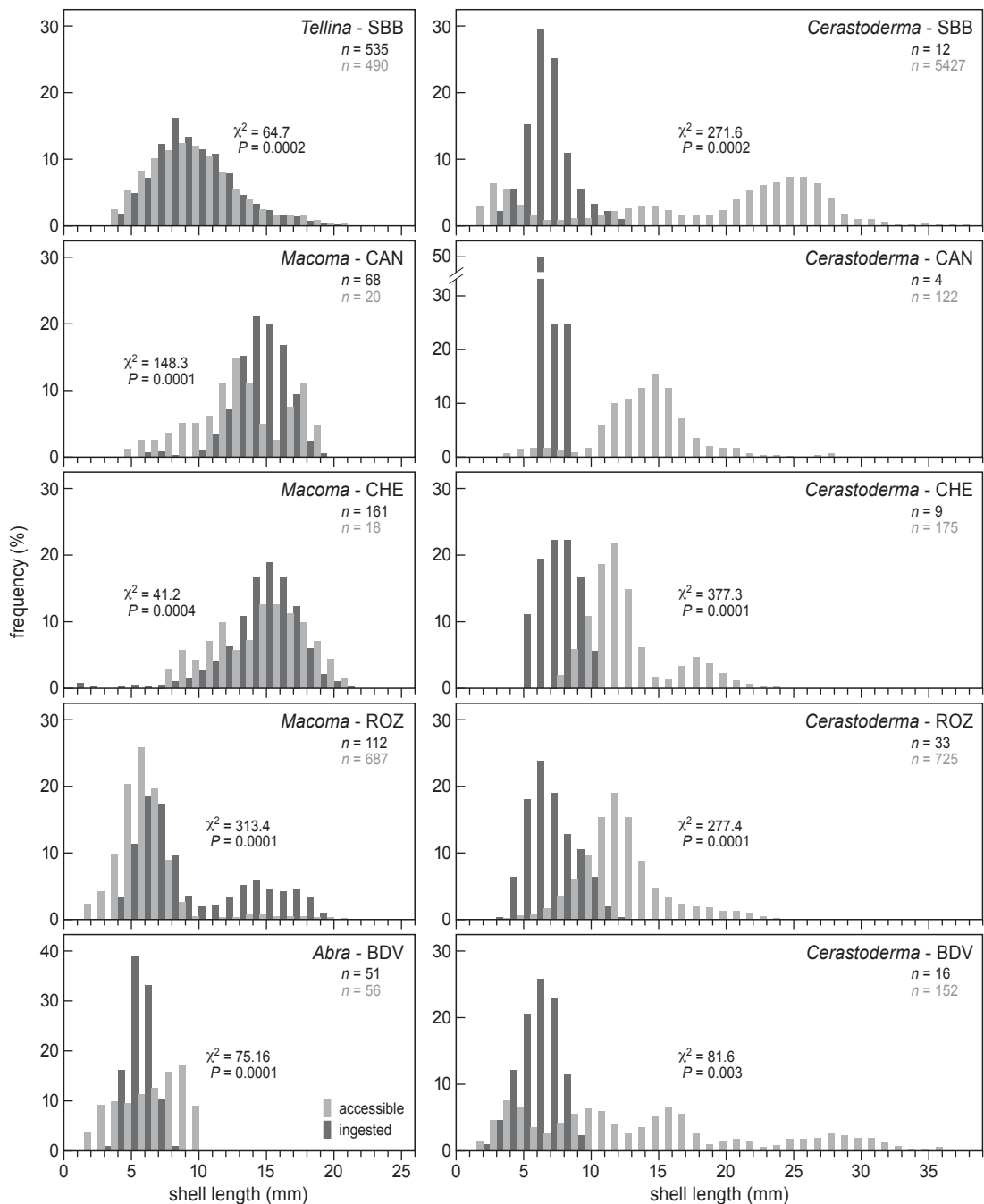


Figure 5. Comparison of the size distributions of four main bivalve prey species (*Tellina tenuis*, *Macoma balthica*, *Abra tenuis* and *Cerastoderma edule*) ingested by Red Knots (black bars) against the accessible size distributions (grey bars) at Saint-Brieuc Bay (SBB), Mont Saint-Michel Bay (CAN: Cancale, CHE: Cherrueix, ROZ: Roz) and Bay des Veys (BDV). The chi-squared statistics are given for all comparisons with P-values.

prey comparable to *Macoma*, but limited in size and also limited in abundance to a very narrow feeding area. In contrast, *Cerastoderma*, which was the dominant species of bivalve communities at all study sites,

was ignored by Red Knots. Indeed, this prey only contributed to less than 5–8% of its diet, probably because most *Cerastoderma* individuals were too large to be ingested. Individuals longer than 12 mm were not

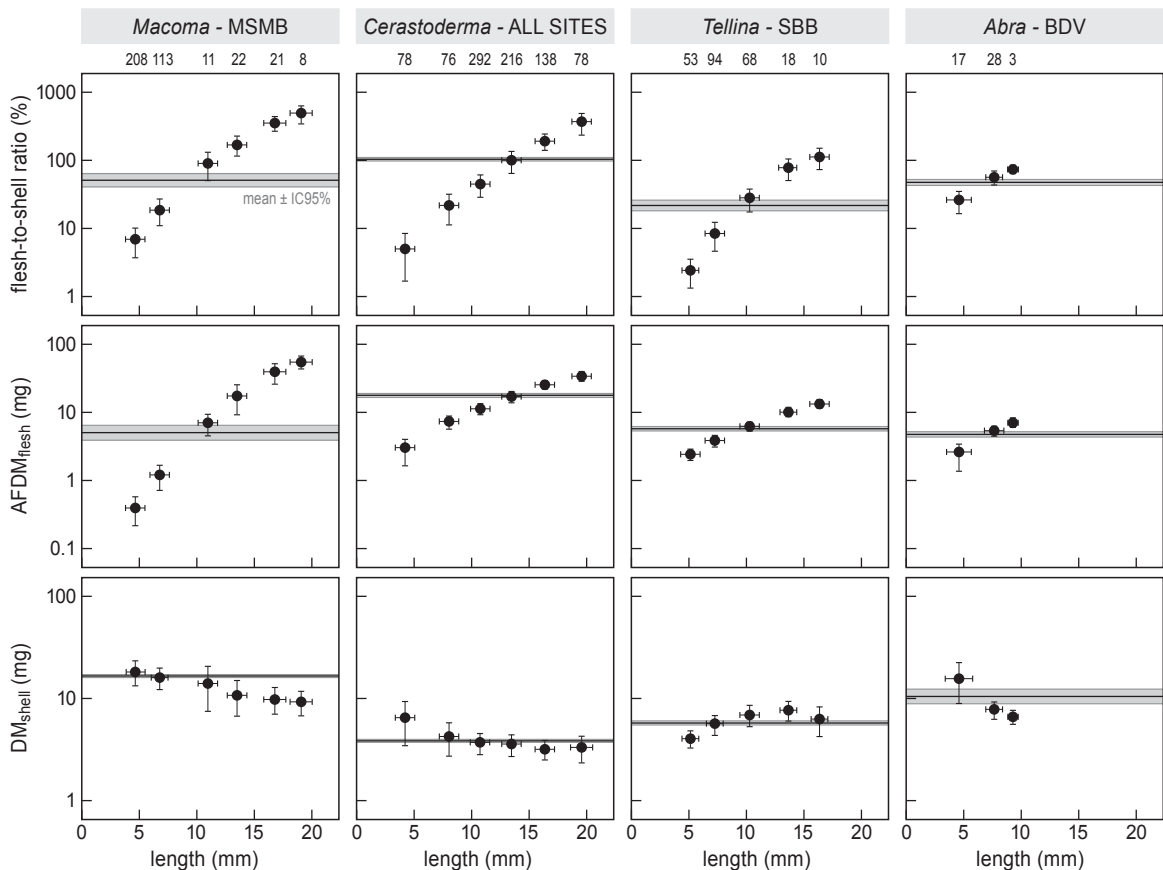


Figure 6. Comparison of ash-free dry mass of the prey flesh (AFDM_{flesh}; mg), shell dry mass (DM_{shell}; mg) and resulting flesh-to-shell ratio (i.e. an index of the prey's digestive quality) for each main available prey species of Red Knot (*Tellina tenuis* at Saint-Brieuc Bay, *Macoma balthica* at Mont Saint-Michel Bay, *Abra tenuis* at the Bay des Veys and *Cerastoderma edule*, an abundant prey across all sites but few selected by Red Knots). Values at each site are averaged by 3-mm size classes. Sample sizes are given for the different size-classes and species above the upper graphs.

ingested (Zwarts & Blomert 1992), whereas on the Channel coast, this prey was mainly represented by large individuals. *Cerastoderma* was furthermore a low quality prey in term of flesh-to-shell ratio, mainly because of its thick shell. Consequently, only small individuals (around 5 mm) are preyed upon during winter.

Although the inter-annual variation of the resource was not considered in this study, we observed that at all sites, the gastropod *Hydrobia ulvae* was rare or absent. This very abundant prey (Bocher et al. 2007) collected at others sites in Europe by Red Knots in winter (Quaintenne et al. 2010), cannot represent an alternative prey at sites of the south Channel Coast. However, *Hydrobia* might represent a safe, abundant and predictable stock of prey compared to stocks of buried bivalves, which can vary greatly in relation to recruitment success or burying depth from one winter to another (Reading & McGrorty 1978, Beukema 1982,

Zwarts & Wanink 1993). Further investigation into the variability of mollusc prey stocks needs to be conducted with regard to the strong inter-annual variation in the abundance of Red Knots when compared to other wintering areas along the French Atlantic coast.

ACKNOWLEDGEMENTS

We are very grateful for the help in the field of Frédéric Robin, Paola Mendez-Fernandez, Thierry Guyot, Gilles Radenac, Dominique Vilday, Jutta Leyer, Casper Kraan, Henrike Andresen, Ulrike Lash, Justine Vidal, Jérémy Allain, Julien Houron and Nicolas Toupoint. We also thank the managers of the Nature Reserves of Saint-Brieuc bay and the Domaine de Beauguillot for their collaboration, and two anonymous reviewers for helpful comments. Data-counts of the "Wetland International" Winter Census on waterbirds were provided by Roger Mahéo and Bernard Deceuninck. Financial support was received from Zone Atelier du Mont Saint-Michel (PEVS CNRS).

REFERENCES

- Bart J., Brown S., Harrington B.R.I. & Morrison R.I.G. 2007. Survey trends of North American shorebirds: population declines or shifting distributions? *J. Avian Biol.* 38: 73–82.
- Beukema J.J. 1982. Annual variation in reproductive success and biomass of the major macrozoobenthic species living in a tidal flat area of the Wadden Sea. *Neth. J. Sea Res.* 16: 37–45.
- Bocher P., Piersma T., Dekinga A., Kraan C., Yates M.G., Guyot T., Folmer E.O. & Radenac G. 2007. Site- and species-specific distribution patterns of molluscs at five intertidal soft-sediment areas in northwest Europe during a single winter. *Mar. Biol.* 151: 577–594.
- Bocher P., Quaintenne G., Delaporte P., Goulevant C., Deceuninck B. & Caillot E. 2012. Distribution, phenology and long term trend of Red knots *Calidris canutus* wintering or staging in France. *Wader Study Group Bull.* 119: 17–25.
- Buehler D.M. & Piersma T. 2008. Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci.* 363: 247–266.
- Colwell M.A. & Landrum S.L. 1993. Nonrandom shorebird distribution and fine-scale variation in prey abundance. *Condor* 95: 94–103.
- Davidson N.C. & Piersma T. 2009. Red knot, *Calidris canutus*. In: Delany S., Scott D., Dodman T. & Stroud D. (eds) *An atlas of wader populations in Africa and Western Eurasia*. Wetlands International & Wader Study Group, London, pp. 362–368.
- Dekinga A. & Piersma T. 1993. Reconstructing diet composition on the basis of faeces in a mollusk-eating wader, the Knot *Calidris-Canutus*. *Bird Study* 40: 144–156.
- Delany S., Scott D., Dodman T. & Stroud D. 2009. *An atlas of wader populations in Africa and Western Eurasia*. Wetlands International and Wader Study Group, Wageningen, Netherlands.
- Eisma D. 1998. *Intertidal deposits: River mouths, tidal flats, and coastal lagoons*. CRC Press, Boca Raton, Florida.
- Goss-Custard J.D., Jones R.E. & Newbery P.E. 1977. The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). *J. Appl. Ecol.* 14: 681–700.
- Jonzén N. 2008. Habitat selection: implications for monitoring, management, and conservation. *Isr. J. Ecol. Evol.* 54: 459–471.
- Kalejta B. & Hockey P.A.R. 1994. Distribution of shorebirds at the Berg River estuary, South Africa, in relation to foraging mode, food supply and environmental features. *Ibis* 136: 233–239.
- Kraan C., Piersma T., Dekinga A., Koolhaas A. & van der Meer J. 2007. Dredging for edible cockles (*Cerastoderma edule*) on intertidal flats: short-term consequences of fisher patch-choice decisions for target and non-target benthic fauna. *ICES J. Mar. Sci.* 64: 1735–1742.
- Kraan C., van Gils J.A., Spaans B., Dekinga A., Bijleveld A.I., van Roomen M., Kleefstra R. & Piersma T. 2009. Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *J. Anim. Ecol.* 78: 1259–1268.
- Le Dréan-Quénec'hdu S., Borer P. & Mahéo R. 1995a. Mont Saint Michel Bay: spatial distribution of major wader species. *Wader Study Group Bull.* 77: 55–61.
- Le Dréan-Quénec'hdu S., Mahéo R. & Boret P. 1995b. The Mont Saint Michel Bay: a site of international importance for wintering and migrating Palearctic waders. *Wader Study Group Bull.* 77: 50–54.
- Nebel S., Porter J.L. & Kingsford R.T. 2008. Long-term trends of shorebird populations in eastern Australia and impacts of freshwater extraction. *Biol. Conserv.* 141: 971–980.
- Mahéo R. 1977–2010. *Limicoles séjournant en France (littoral); contribution française aux dénombrements internationaux des oiseaux d'eau organisés par wetlands international*. Reports Office National de la Chasse et de la Faune Sauvage.
- Piersma T. 2006. Understanding the numbers and distribution of waders and other animals in a changing world: habitat choice as the lock and the key. *Stilt* 50: 3–14.
- Piersma T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *J. Ornithol.* 148: 45–59.
- Piersma T., van Gils J.A., de Goeij P. & van der Meer J. 1995. Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. *J. Anim. Ecol.* 64: 493–504.
- Piersma T., Koolhaas A., Dekinga A., Beukema J.J., Dekker R. & Essink K. 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *J. Appl. Ecol.* 38: 976–990.
- Prater A.J. 1972. The ecology of the Morecambe Bay. III. The food and feeding habits of knot (*Calidris canutus* L.) in Morecambe Bay. *J. Appl. Ecol.* 9: 179–194.
- Quaintenne G., van Gils J.A., Bocher P., Dekinga A. & Piersma T. 2010. Diet selection in a molluscivore shorebird across Western Europe: does it show short- or long-term intake rate-maximization? *J. Anim. Ecol.* 79: 53–62.
- Quaintenne G., van Gils J.A., Bocher P., Dekinga A. & Piersma T. 2011. Scaling up ideals to freedom: are densities of red knots across western Europe consistent with ideal free distribution? *Proc. R. Soc. B.* 278: 2728–2736.
- Reading C.J. & McGrorty S. 1978. Seasonal variations in burying depth of *Macoma balthica* (L.) and its accessibility to wading birds. *Estuar. Coast. Mar. Sci.* 6: 135–144.
- Ribeiro P.D., Iribarne O.O., Navarro D. & Jauregui L. 2004. Environmental heterogeneity, spatial segregation of prey, and the utilisation of southwest Atlantic mudflats by migratory shorebirds. *Ibis* 146: 672–683.
- Soldaat L., Visser H., van Roomen M. & van Strien A. 2007. Smoothing and trend detection in waterbird monitoring data using structural time-series analysis and the Kalman filter. *J. Ornithol.* 148: 351–357.
- Spruzen E.L., Richardson A.M.M. & Woehler E.J. 2008. Influence of environmental and prey variables on low tide shorebird habitat use within the Robbins Passage wetlands, Northwest Tasmania. *Estuar. Coast. Shelf Sci.* 78: 122–134.
- Stroud D.A., Davidson N.C., West R., Scott D.A., Haanstra L., Thorup P., Ganter B. & Delany S. 2004. Status of migratory wader populations in Africa and Western Eurasia in the 1990s. *International Wader Studies* 15: 1–259.
- van Gils J.A., de Rooij S.R., van Belle J., van der Meer J., Dekinga A., Piersma T. & Drent R. 2005. Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. I. Prey choice. *J. Anim. Ecol.* 74: 105–119.

- van Gils J.A., Piersma T., Dekinga A., Spaans B. & Kraan C. 2006. Shellfish dredging pushes a flexible avian top predator out of a marine protected area. *PLoS Biol.* 4: 2399–2404.
- Yates M.G., Goss-Custard J.D., McGrorty S., Lakhani K.H., Durell S.E.A., Clarke R.T., Rispin W.E., Moy I., Yates T., Plant R.A. & Frost A.J. 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *J. Appl. Ecol.* 30: 599–614.
- Zwarts L. & Blomert A.M. 1992. Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. *Mar. Ecol. Prog. Ser.* 83: 113–128.
- Zwarts L., Blomert A.M. & Wanink J.H. 1992. Annual and seasonal variation in the food-supply harvestable by knot *Calidris canutus* in the Wadden sea in late summer. *Mar. Ecol. Prog. Ser.* 83: 129–139.
- Zwarts L. & Wanink J.H. 1993. How the food-supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body-weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Neth. J. Sea Res.* 31: 441–476.

SAMENVATTING

In dit artikel wordt de voedselkeuze van de Kanoet *Calidris canutus islandica* in drie estuaria langs de Franse Kanaalkust beschreven. Onderzocht werd in hoeverre de verspreiding van de vogels te maken had met de dichtheid en beschikbaarheid van kwalitatief waardevolle prooidieren. In de drie onderzoeksgebieden bestonden tussen de jaren grote verschillen in aantallen aanwezige vogels. De gebieden verschilden onderling ook sterk in het voorkomen van prooidieren, en daarmee ook in de voedselkeuze van de Kanoeten. De bodemfauna bij Mont Saint-Michel werd gedomineerd door het Nonnetje *Macoma balthica*, wat weerspiegeld werd in het voedsel van de Kanoet (meer dan 90% bestond uit Nonnetjes). Kokkels *Cerastoderma edule* kwamen er ook voor, maar deze waren voor de Kanoeten te groot om tot zich te nemen. Bij Saint-Brieuc, 100 km westelijker, aten de Kanoeten vooral Tere Platschelpen *Tellina tenuis*. Hoewel deze platschelp door zijn lagere vlees/schelp verhouding voor Kanoeten een minder aantrekkelijke prooi is dan het Nonnetje, kwam de schelp in zeer hoge dichtheden voor. In sommige jaren trokken de platschelpen meer Kanoeten aan dan de Nonnetjes van Mont Saint-Michel. Bij Les Veys, in Normandië, kwamen slechts weinig Kanoeten voor. Hun voedsel bestond uit een combinatie van de Tere Dunschaal *Abra tenuis*, het Nonnetje en het Wadslakje *Hydrobia ulvae*. (JP)

Corresponding editor: Jouke Prop

Received 7 March 2013; accepted 16 December 2013

Appendix 1. Frequency of occurrence (Occ., %), mean density (Dens., ind/m²) and mean biomass (Biom., mg AFDM_{fest}/m²) of mollusc species at each site (sampled in January–March 2006).

Species	Saint-Brieuc Bay			Mont Saint-Michel Bay						Bay des Veys		
				Cancale		Cherruëix		Roz				
	Occ.	Dens.	Biom.	Occ.	Dens.	Biom.	Occ.	Dens.	Biom.	Occ.	Dens.	Biom.
Bivalves												
<i>Cerastoderma edule</i>	42	79	4386	43	82	1308	42	96	803	54	443	3457
<i>Donax vittatus</i>	6	7	15	-	-	-	-	-	-	-	-	-
<i>Macoma balthica</i>	5	4	30	18	14	523	25	28	794	74	774	3118
<i>Tellina tenuis</i>	42	166	874	-	-	-	2	1	23	1	1	12
<i>Ruditapes decussatus</i>	<1	<1	35	12	9	576	1	1	14	-	-	-
<i>Mysella bidentata</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Scrobicularia plana</i>	6	28	1175	28	56	2681	-	-	-	1	1	25
<i>Abra tenuis</i>	-	-	-	15	46	9	-	-	-	-	-	-
<i>Mytilus edulis</i>	<1	<1	14	-	-	-	-	-	-	18	31	48
										-	-	-
Gastropods												
<i>Hydrobia ulvae</i>	14	121	56	15	26	19	-	-	-	5	6	3
<i>Nassarius reticulatus</i>	1	<1	26	-	-	-	-	-	-	-	-	-
<i>Grepidula fornicata</i>	-	-	-	-	-	-	1	1	72	-	-	-