



Exploitation of intertidal feeding resources by the red knot *Calidris canutus* under megatidal conditions (Bay of Saint-Brieuc, France)



Anthony Sturbois^{a,b}, Alain Ponsero^a, Nicolas Desroy^{c,*}, Patrick Le Mao^c, Jérôme Fournier^{d,e}

^a Réserve Naturelle de la Baie de Saint-Brieuc, site de l'étoile, 22120 Hillion, France

^b VivArmor Nature, 10 boulevard Sévigné, 22000 Saint-Brieuc, France

^c IFREMER, Laboratoire Environnement et Ressources - Station de Dinard, 38 rue du Port Blanc, BP 80108, 35801 Dinard cedex, France

^d CNRS, UMR 7208 BOREA, 61 rue Buffon, CP 53, 75231 Paris cedex 05, France

^e MNHN, Station Marine, 38 rue du Port Blanc, 35801 Dinard cedex, France

ARTICLE INFO

Article history:

Received 3 March 2014

Received in revised form 11 September 2014

Accepted 2 November 2014

Available online 13 November 2014

Keywords:

Diet

Benthos

Intertidal flat

Megatidal environment

Bay of Saint-Brieuc

ABSTRACT

The feeding ecology of the red knot has been widely studied across its wintering range. Red knots mainly select bivalves and gastropods, with differences between sites due to variation in prey availability. The shorebird's diet is also influenced or controlled by the tidal regime. The aim of this paper is to demonstrate the adaptation of foraging red knots to the megatidal environment. The variation in their diet during tidal cycles was studied in the bay of Saint-Brieuc, a functional unit for this species. The method used combined macrofauna, distribution of foraging birds and diet data. Comparative spatial analyses of macrofauna and distribution of foraging red knots have shown that the bay's four benthic assemblages are exploited by birds. By analysing droppings, we highlighted that bivalve molluscs are the main component of their diet, as shown in most overwintering sites. Fifteen types of prey were identified and *Donax vittatus* was discovered to be a significant prey item. The relative proportion of each main prey item differs significantly depending on the benthic assemblage used to forage. All available benthic assemblages and all potential feeding resources can be used during a single tidal cycle, reflecting an adaptation to megatidal conditions. This approach develops accurate knowledge about the feeding ecology of birds which managers need in order to identify optimal areas for the conservation of waders based on the areas and resources actually used by the birds.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

The feeding ecology of red knots has received special attention, especially in terms of prey size distribution, digestibility, accessibility, profitability and intake rates. Several authors have studied the red knot's winter feeding ecology and its diet composition over a large spatial scale in New Zealand (Piersma, 1990) and in North-western Europe (Quaintenne et al., 2009, 2011) or in more localised areas, i.e.: in the Wadden Sea (Bijleveld et al., 2014; Dekinga and Piersma, 1993; Kraan et al., 2009; van Gils et al., 2005a; Zwarts et al., 1992), Wash estuary (UK) (Goss-Custard et al., 1977; Prater, 1972), Tagus estuary (Portugal) (Moreira, 1994) and on the Banc d'Arguin (Mauritania) (Onrust et al., 2013; van den Hout et al., 2014; van Gils et al., 2013; Zwarts et al., 1990).

Bivalves and gastropods are the main contributors to the red knot's diet (Boere and Smit, 1981; Dekinga and Piersma, 1993; Folmer et al., 2010; Zwarts and Blomert, 1992). Across Western Europe, Quaintenne et al. (2011) showed that only six prey species (the bivalves *Macoma balthica*, *Angulus tenuis*, *Cerastoderma edule*, *Scrobicularia plana* and

Abra tenuis and the gastropod *Peringia ulvae*) make up 98% of the red knot's diet. However, dominant prey species may vary dramatically between distant sites as well as neighbouring ones (Quaintenne et al., 2009, 2014). On a given site, the diet can vary from year to year and along the overwintering season as reported by van Gils et al. (2006), Dekinga and Piersma (1993) and Zwarts et al. (1992). Shorebirds' diet is also influenced, and indeed, controlled by the tidal regime (McLusky and Elliott, 2004; van Gils et al., 2006). In intertidal flats with semi-diurnal mesotidal regimes, as in the Dutch Wadden Sea, the habitats used by waders for foraging are relatively uniform (Beukema, 1976). Flocks of birds forage on a few dominant prey species. *A contrario*, under megatidal conditions, as in the bay of Saint-Brieuc, several distinct benthic assemblages are distributed along a continuum with regard to the bathymetric gradient (Augris and Hamon, 1996). Consequently, the diet composition in heterogeneous areas can be expected to be more diversified.

In this context, a large-scale study of the diet of red knots based on the analysis of prey items by sampling faecal droppings was conducted in the bay of Saint-Brieuc. The aim of this article is to demonstrate the adaptation of foraging activity of red knots in a megatidal environment and more particularly the variation in the diet during tidal cycles, on the scale of a presumed functional unit for the red knot.

* Corresponding author. Tel.: +33 2 23 18 58 62.
E-mail address: nicolas.desroy@ifremer.fr (N. Desroy).

2. Material and methods

2.1. Study area

The bay of Saint-Brieuc (48°32'N; 2°40'W) is located on the northern coast of Brittany and in the south-western part of the Normand-Breton gulf (Fig. 1). The bay encompasses 800 km² up to the 30 m isobath and is subjected to an extreme megatidal regime. The tidal range varies between 4 m at neap tides and nearly 13 m during spring tides. The study area is divided into two large coves (Morieux and Yffiniac coves) extending over 2900 ha of flats ranging from mud to sand. It includes the National Nature Reserve of the bay of Saint-Brieuc created in 1998 (1140 ha) and represents a functional entity for waders. This nature reserve has been designated as an area of international importance for waders and especially for red knots (3000 on the average, *i.e.* 6% of the national overwintering population) during the last decade (Ponsoero and Le Mao, 2011).

2.2. Field sampling

2.2.1. Cartography of benthic assemblages

The distribution of macrofauna was established from a survey conducted in October 2010. 131 sites covering 2900 ha of intertidal area were sampled over a regular sampling network (Bijleveld et al., 2012) (Fig. 1). At each site, three replicates of sediment samples for macrobenthos analysis were collected using a 9.6 cm² handcorer, to a depth of 25 cm. The contents of the cores were gently sieved on site through 1-mm square mesh. The retained material was preserved for analysis in 5% buffered formaldehyde with added rose Bengal. The macrofauna was identified to the lowest possible taxon and enumerated. Two samples of sediment (surface of 3.2 cm², depth of 5 cm) were collected from additional cores and subsequently analysed for grain size distribution and organic matter. All the sites were located by means of a GPS (Global Positioning System, Garmin Etrex Legend HCx).

2.2.2. Location of foraging areas

Considering the large scale of the study area (Fig. 1), observations were carried out during the winters of 2010/11 and 2011/12 in the coves of Yffiniac and Morieux, respectively. Birds were counted regularly during winter periods and in daytime with a telescope (Kite SP-ED 80). The number of feeding birds was recorded over 54 tidal cycles, under conditions which varied from neap to spring tides. For each group of birds, the species, total number of feeding and roosting individuals and the hour of the observations for information on tidal conditions were noted. The location of bird groups was calculated using a trigonometric formula based on the geographical position of the observer (determined with a Global Positioning System, Garmin Etrex Legend HCx) and measurements of the bird group's distance and angle from North:

$$X \text{ bird} = X \text{ observer} + \sin(\text{angle}) \times \text{distance}, \text{ with } X = \text{longitude}$$

$$Y \text{ bird} = Y \text{ observer} + \cos(\text{angle}) \times \text{distance}, \text{ with } Y = \text{latitude}.$$

The distance from observers and viewing angle from North were provided with laser range-finding binoculars (Newcon LRB 3000 pro, 7 × 40). The model of binoculars used could measure up to 700 m, limiting any disturbance to the birds.

2.2.3. Sampling of droppings

The assimilation rate of prey is quite short; less than 45 min after ingestion (Piersma, 1994). Droppings were thus collected after waiting at least 1 h, following the recommendations of Dekinga and Piersma (1993). Acknowledging this rapid rate of assimilation, picking up droppings on high-tide roosting site is insufficient, since they only reflect the diet of the last hour of rising tide. Droppings were sampled in all existing benthic assemblages, with a strategy taking account of the tidal conditions, red knot phenology, location (Yffiniac or Morieux cove) and digestion time (Piersma, 1994).

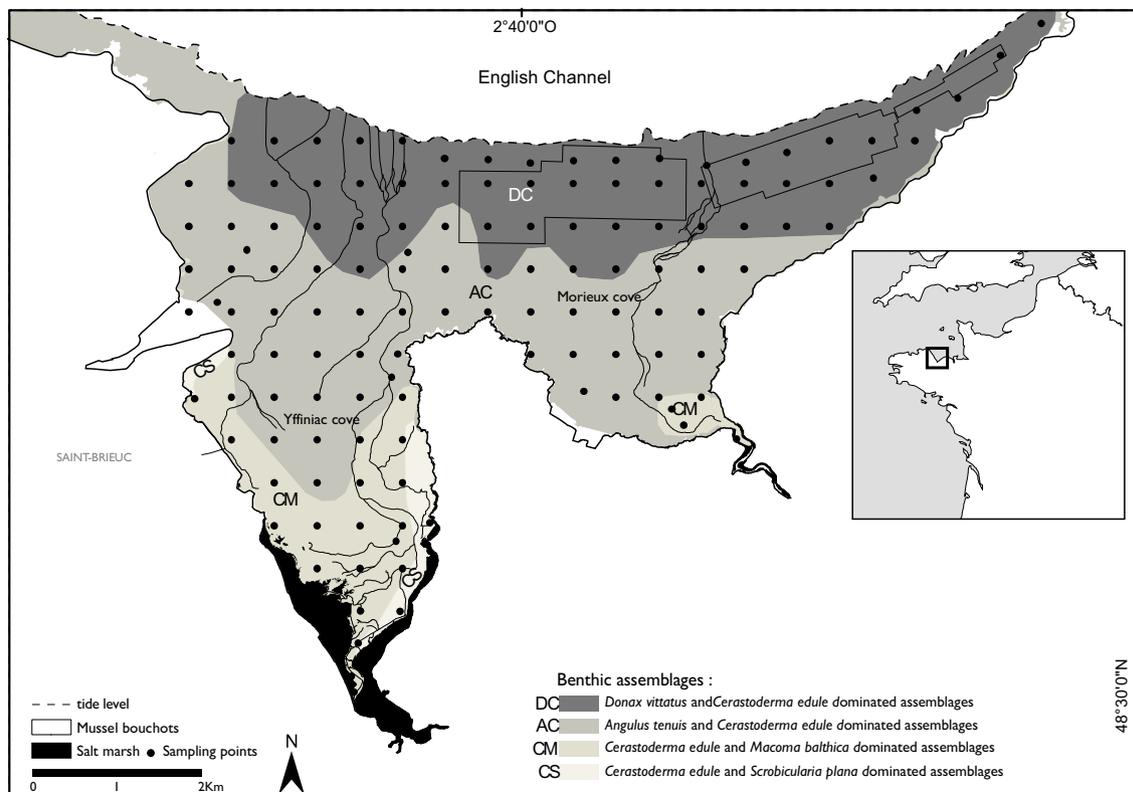


Fig. 1. Benthic intertidal assemblages identified in the bay of Saint-Brieuc. Points correspond to 131 stations of the regular sampling network.

Field sampling was performed in daytime and during ebb tide from November to March, twice a month (spring and neap tides) in each cove, avoiding disturbance to birds. A total of 30 droppings per benthic assemblage was collected each day and localised with a GPS. Each dropping was picked up carefully with a plastic tube from the surface of the sand flat to minimise the presence of sediment particles. Each sample was preserved in a 70% alcohol solution (De Smet et al., 2013). To prevent from sampling errors between benthic assemblages, particular attention was devoted to the movements of birds.

2.3. Laboratory analysis

2.3.1. Macrofauna and sediment facies

The macrofauna was identified to the lowest possible taxon and enumerated. The biomass of each taxon was determined as g of ASFD per 0.1 m² (loss of weight of dry organisms after 6 h at 520 °C). After separating the flesh from the shell of bivalves, each individual's flesh ash-free dry mass (AFDM_{flesh}) and shell dry mass (DM_{shell}) was determined in order to evaluate the quality of preys (Kraan et al., 2007; Piersma et al., 1993). Sediment samples were cleaned with water and following decanting was allowed during 24 h. Sediments were then dried at 70 °C for 24 h and sieved through AFNOR standard sieves, and weighed. The dried samples were combusted at 540 °C for 4 h in order to determine the organic content (Hedges and Stern, 1984).

2.3.2. Droppings

Bivalves and molluscs are entirely ingested and crushed in the muscular gizzard of the red knot. The composition of droppings can be defined by hard fragments, which frequently used to describe the red knot's diet (Dekinga and Piersma, 1993; Onrust et al., 2013).

After being rinsed, each dropping was sieved through a 20 µm mesh size (De Smet et al., 2013) and analysed under a binocular microscope. The relative abundance of each prey item was estimated according to a five abundance class system (1: <5%, 2: 5–25%, 3: 25–50%, 4: 50–75%, and 5: >75%).

2.4. Data analysis

2.4.1. Macrofauna

To define benthic assemblages, a hierarchical ascendant classification was performed using all data to distinguish between the groups of stations by applying the Bray–Curtis coefficient with a Euclidian sorting method. Multiple discriminant analysis (Legendre and Legendre, 1998) was carried out to evaluate the station groups derived from correspondence analysis and to correlate this separation with some selected variables. The first-rank species of molluscs (species of interest for red knot) were retained to characterise each identified assemblage.

2.4.2. Droppings

The frequency of occurrence for each prey item has been calculated globally (FOi%) and per habitat (FOhab%). FOi% was calculated as follows: (number of dropping samples where the prey item *i* is present/total number of dropping samples) × 100.

The frequency of occurrence of prey species in each habitat (FOhab%) was calculated, for the five class of abundance, according the formula: [(number of dropping samples where the prey species is present in the habitat and characterised by the class abundance *x*)/(total number of dropping samples in the habitat)] × 100

To determine differences between faecal samples on the scale of the bay, a χ^2 test was run.

To test spatial changes in the relative abundance of preys in droppings, a two-way ANOVA was performed after checking the homogeneity of variance. The factors tested were abundance of prey versus benthic assemblages. This ANOVA was followed by a Tukey multiple

comparisons test (Scherrer, 2007). All statistical analyses were performed with R software (R Development Core Team, 2013).

3. Results

3.1. Mapping of benthic assemblages

A total of 87 species was identified on the flats. Four distinct benthic assemblages were identified with respect to the first-rank species of molluscs (Fig. 1, Table 1): *C. edule* and *S. plana* dominate the assemblage of silty muds (CS, 70 ha), *C. edule* and *M. balthica* the assemblage of muddy sands (CM, 250 ha), *Angulus tenuis* and *C. edule* are predominant in the assemblage of sands (AC, 1200 ha), and *Donax vittatus*, *Angulus tenuis* and *C. edule* dominate the assemblage of low level sands (DC, 1380 ha). This last assemblage area is characterised by an area with mussel beds on wooden poles, called “bouchots” covering 320 ha (23.2% of the surface of the whole assemblage area). The main potential feeding resources for red knots (five first-rank bivalve species) are less abundant in this area (on the average 81.50 ind·m⁻² ± 77.60, max 242 ind·m⁻²) compared to the rest of DC without mussel bouchots (on the average 185.00 ind·m⁻² ± 231.00, max 1188 ind·m⁻²).

The emersion time of assemblages decreases from high to low water and influences the availability of prey for birds. Winter exposure time varies on the average from 84% for CS to 8% for DC, CM and AC being respectively available on the average 64% and 36% of the time (Table 2).

3.1.1. Distribution of foraging birds

The number of red knots during the two overwintering seasons of the study was on the average 3000 individuals and 2100 individuals respectively in the winters of 2010/11 and 2011/12. The distribution of foraging red knots was heterogeneous on the scale of the bay, with birds foraging mainly in Yffiniac cove and in the eastern part of Morieux cove. However, flocks foraged on all identified benthic assemblages, depending on the water level. The foraging areas of red knots represented 640 ha (22% of the intertidal area, Fig. 2). However, red knots avoided the entire mussel bouchot area and the central part of the bay.

3.1.2. Diversity of preys

A total of 15 prey items was identified in all 1001 collected droppings. Molluscs were clearly dominant as shown by FOi% (Table 3): *C. edule* (66.13%), *Angulus tenuis* (50.3%), *D. vittatus* (47.6%), *M. balthica* (43.1%), *S. plana* (14%), *P. ulvae* (19%) and *Mytilus edule* (7.4%) (Fig. 3). Other items were represented by *Pygospio elegans* (1.7%), Crustacean sp. (0.7%), *Rissoa parva* (0.4%), fishes (0.4%), *Spisula subtrouquata* (0.3%), Gastropod sp. (0.3%), *Urothoe poseidonis* (0.1%) and *Isopoda* sp. (0.1%).

3.1.3. Quality of preys

Since red knot ingests bivalves entirely, the crushing of shell fragments in the muscular gizzard induces additional energy consumption. Consequently, the quality of preys has been expressed regarding the ratio dry flesh/dry shell masses (Kraan et al., 2007; Piersma et al., 1993). Values of digestive quality are higher for *D. vittatus*, *M. balthica* and *Angulus tenuis* (respectively 0.06, 0.06, and 0.05 AFDM_{flesh}/DM_{shell}) than for *C. edule* (0.03 AFDM_{flesh}/DM_{shell}) and *S. plana* (0.04; Table 3).

3.1.4. Spatial changes in dropping composition

3.1.4.1. Change in prey occurrence. Changes in droppings composition observed between benthic assemblages were highly significant ($\chi^2 = 1071$, df = 18, $p < 0.01$) (Table 4).

In the silty mud assemblage (CS), *P. ulvae* (FOi% = 80%), *S. plana* (72%), and *M. balthica* (70%) were dominant in droppings. In the muddy sand assemblage (CM), the dominant species were *C. edule* (84.5%), *Angulus tenuis* (60.4%) and *M. balthica* (54.5%). Lower on the shore, on the sand flat (AC), *C. edule* (72.3%) and *Angulus tenuis* (65%)

Table 1
Abundance and biomass of first rank species of molluscs of interest for red knot in the different benthic assemblages and correspondent usable part (potential prey (p.p.)) with regard to the size of bivalves (*Angulus tenuis* 4–19 mm: Quaintenne et al., 2014; *Cerastoderma edule* 3–17 mm: Piersma et al., 1993; *Macoma balthica* 3–18 mm: Piersma et al., 1993; *Scrobicularia plana* 11–17 mm: Moreira, 1994; *Donax vittatus*: unknown). CS : *C. edule* - *S. plana* assemblage ; CM : *C. edule* - *M. balthica* assemblage ; AC : *A. tenuis* - *C. edule* assemblage and DC : *D. vittatus* - *C. edule* assemblage.

	CS				CM				AC				DC			
	Density (m ²)		afdw (g·m ⁻²)		Density (m ²)		afdw (g·m ⁻²)		Density (m ²)		afdw (g·m ⁻²)		Density (m ²)		afdw (g·m ⁻²)	
	Total	p.p.	Total	p.p.	Total	p.p.	Total	p.p.	Total	p.p.	Total	p.p.	Total	p.p.	Total	p.p.
<i>Peringia ulvae</i>	187.30	187.30			12.16	12.16			0.44	0.44	–	–	–	–		
sd	315.22	315.22			25.86	25.86			2.14	2.14						
Max	551	551			117	117			11	11						
<i>Angulus tenuis</i>	28.60	28.60	0.22	0.22	24.50	23.50	0.12	0.12	102.37	93.84	0.44	0.44	59.4	38.20	1.39	0.13
sd	64.04	64.04	0.48	0.48	69.80	65.76	0.31	0.31	129.63	128.1	0.77	0.76	92.20	50.59	0.20	0.19
Max	143	143	1.08	1.08	297	275	1.28	1.28	605	605	3.66	3.66	440	231	0.94	0.89
<i>Cerastoderma edule</i>	195.80	149.6	3.48	1.91	28.50	9.00	0.97	0.14	47.14	14.14	4.62	0.33	11.00	2.40	1.64	0.07
sd	240.34	206.20	4.84	2.61	64.60	16.15	2.344	0.31	83.10	23.70	8.63	0.54	31.50	16.40	3.71	0.49
Max	473	440	10.93	4.94	286	55	7.27	1.10	363	110	35.66	2.21	198	121	12.64	3.66
<i>Macoma balthica</i>	24.20	24.20	0.31	0.31	10.00	9.00	0.17	0.12	–	–	–	–	–	–	–	–
sd	12.56	12.56	0.16	0.32	19.80	19.69	0.33	0.28								
Max	44	44	0.84	0.84	77	77	1.20	1.20								
<i>Donax vittatus</i>	–	–	–	–	–	–	–	–	6.73	6.73	0.16	0.16	82.40	82.40	0.21	0.21
sd									17.50	17.50	0.43	0.43	174.50	174.50	0.62	0.62
Max									99	99	2.38	2.38	1089	1089	3.85	3.85
<i>Scrobicularia plana</i>	162.84	22.22	7.54	0.18	7.50	1.50	0.33	0.02	–	–	–	–	–	–	–	–
sd	364.34	49.20	16.87	0.41	24.30	5.14	1.178	0.06								
Max	814	110	37.72	0.91	88	22	5.24	0.24								
Bivalves mean	411.44	224.62	11.55	2.62	70.50	43.00	1.59	0.40	156.24	114.71	5.22	0.93	152.8	123.00	3.24	0.41
sd	353.00	218.00	15.90	2.81	111	78.5	2.81	0.66	153.00	132.00	8.74	1.08	202.00	186.00	4.03	1.07
Max	858	462	38.60	5.97	374	308	8.17	2.16	627	627	36.60	4.59	1188	1188	16.1	7.64

were the most frequently observed species in droppings. Finally, in the lowest level of sand (DC), *D. vittatus* (90.9%) and *C. edule* (36.8%) had the highest occurrences.

3.1.4.2. Change in prey abundance. The frequency of occurrence of each prey item depending on classes of abundance (FOhab%) differed significantly (ANOVA: $F_{3,11} = 8.10$, $p < 0.001$) among the four benthic assemblages, depending on the tide (Fig. 4). During spring tides, *Donax vittatus* represents more than 75% of preys in the assemblage DC. There were highly significant differences in dropping compositions between assemblages, except between CM and AC (Tukey's HSD test: $p > 0.05$). This result is probably due to the lack of difference in *C. edule*'s relative abundance in droppings from these two assemblages (Tukey's HSD test: $p = 0.49$).

4. Discussion

Benthic assemblages are distributed in belts along an inshore–off-shore gradient of increasing grain-size distribution of sediments. Congruent to this gradient, the number of species increases from higher to lower belts (respectively 7 and 43 species in CS and DC). The specific composition varies over space depending on the emersion time. In the high flat, the benthic assemblage occupies a sheltered mudflat dominated by *S. plana* (162.80 ind·m⁻²) and *C. edule* (195.80 ind·m⁻²). In the low part of the flat, sediment and macrofauna are characteristic of a

Table 2
Availability of the different benthic assemblages identified in the bay of Saint-Brieuc according to exposure time: (CS) *Cerastoderma edule* and *Scrobicularia plana* dominated assemblage in silty muds, (CM) *Cerastoderma edule* and *Macoma balthica* dominated assemblage in muddy sands, (AC) *Angulus tenuis* and *Cerastoderma edule* dominated assemblage in sands, and (DC) *Donax vittatus* and *Cerastoderma edule* dominated assemblages in low level sands.

Benthic assemblage	Surface (ha)	Height of land emergence (m)	Duration of exposure will average per day (h)	sd	%
CS	70	9	20.2	2.26	84
CM	250	7.5	15.4	0.89	64
AC	1200	4.5	8.5	0.82	36
DC	1380	<4	3.5	1.43	8

more exposed area. Clean fine to medium sands make up the sediment and *Angulus tenuis* (102.37 ind·m⁻²) and *C. edule* (47.14 ind·m⁻²) are the dominant bivalves, with abundances reaching 605.00 ind·m⁻² and 363.00 ind·m⁻² respectively. At the lowest levels of the tidal flat, *D. vittatus* progressively occurs (82.40 ind·m⁻²) with abundance reaching 1000 ind·m⁻².

The biocenotic succession observed in the bay of Saint-Brieuc corresponds to a classical pattern already described in many intertidal flats such as in the Mont Saint-Michel bay (Meziane, 1997; Thorin et al., 2001) or along the Dutch Wadden Sea (Beukema, 1989). However, in the bay of Saint-Brieuc, the prevailing hydrodynamic conditions, associated with the grain-size of sediment in the lowest levels of the flat (mean value of 205.22 μm), are responsible for the presence of *D. vittatus*, which inhabits fine sand habitats (Degraer et al., 2006).

The foraging area represents 640 ha (22% of the whole intertidal area), which is over twice as large as the first estimation made by Quaintenne et al. (2011) on the same site. Our observations clearly show that all benthic assemblages are exploited. However, the mussel bouchot area is unattractive for red knots (Fig. 2). This can be explained by a deficit of trophic resources, the presence of three-dimensional structures (bouchots: wooden poles, 3 m high) and anthropogenic disturbance (Dias et al., 2008; Granadeiro et al., 2006; Yasué et al., 2008).

The resource harvestable by red knot depends on profitability, ingestibility, digestibility and accessibility of prey (van Gils et al., 2005b; Zwarts and Blomert, 1992). The size of bivalves ingestible and profitable for red knot (Moreira, 1994; Piersma et al., 1993; Quaintenne et al., 2014) and the correspondent biomass (Table 1), explain the exploitation of the five species of bivalves by red knot in the study area.

In the bay of Saint-Brieuc, *C. edule*, *Angulus tenuis*, *M. balthica*, *S. plana*, and *P. ulvae* constitute important preys for red knots, as largely demonstrated in other sites in Europe (Folmer et al., 2010; Dekinga and Piersma, 1993; Nehls, 1992; Zwarts and Blomert, 1992; Boere and Smit, 1981).

Since red knots forage on dominant prey species, non-significant differences between dropping composition in CM and CA assemblages can be explained by the predominance of *C. edule* in these two units.

We confirmed the use of an unusual prey for the red knot, *Angulus tenuis*, as previously described by Quaintenne et al. (2011, 2014) in

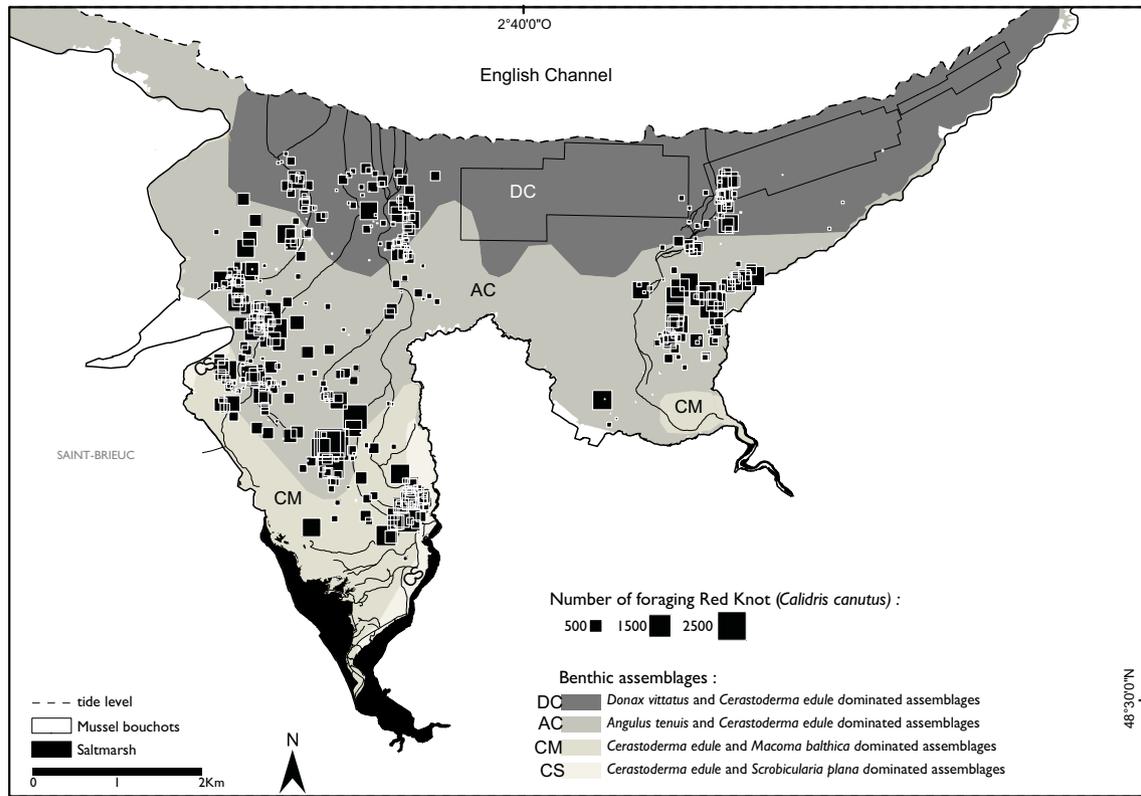


Fig. 2. Foraging area used by red knot and main benthic intertidal assemblages of the bay of Saint-Brieuc.

the bay of Saint-Brieuc and Prater (1972) in Morecambe bay. This species is easily digested (value of 5.39% AFDM_{flesh}/DM_{shell}) and reach in the study site (assemblage AC), approximately 600 ind·m⁻². Our results confirm that *Angulus tenuis* contributes significantly to the diet in the bay of Saint-Brieuc, especially in AC and DC but to a lesser extent than Quaintenne et al. (2014) who suggested that red knot is specialised on this species.

Inter-annual variations in bivalve densities can contribute to explain the variation of the contribution of each prey to the diet (van Gils et al., 2006).

The exploitation of *D. vittatus* by *Calidris canutus* has not yet been described, although *Donax variabilis* is a well-known prey for the subspecies *Calidris canutus rufa* on stopover sites of the Eastern shore of Virginia, US Atlantic coast (Cohen et al., 2010). Adopting the strategy of behaving as a swash rider, *D. variabilis* is present close to the water line and available as a prey for waders, whatever the tidal level considered (Levinton, 2001). Such a process has never been observed for *D. vittatus*. Therefore, in Western Europe predation on this species is only possible at lowest tide levels. The specialisation on *D. vittatus* by red knot, despite the presence of great abundance of *Angulus tenuis*, can be explained by both its high digestive quality (0.06 AFDM_{flesh}/DM_{shell}) and densities reached of approximately 1000 ind·m⁻². Cyclic spatial and temporal variability due to the tide also influences the exploitation of the flat by birds (Fleischer,

1983; Granadeiro et al., 2006; Rosa et al., 2007; van Gils et al., 2005a; van Gils et al., 2006) and contributes to explain the position of birds on the lowest parts of the flat during low tide.

In the bay of Saint-Brieuc, red knots are compelled to forage on highest levels of the flat during neap tide, especially on AC. However, we observed that red knots preferentially forage on DC assemblages as soon as the tide falls (Fig. 5) and form big flocks on areas with high

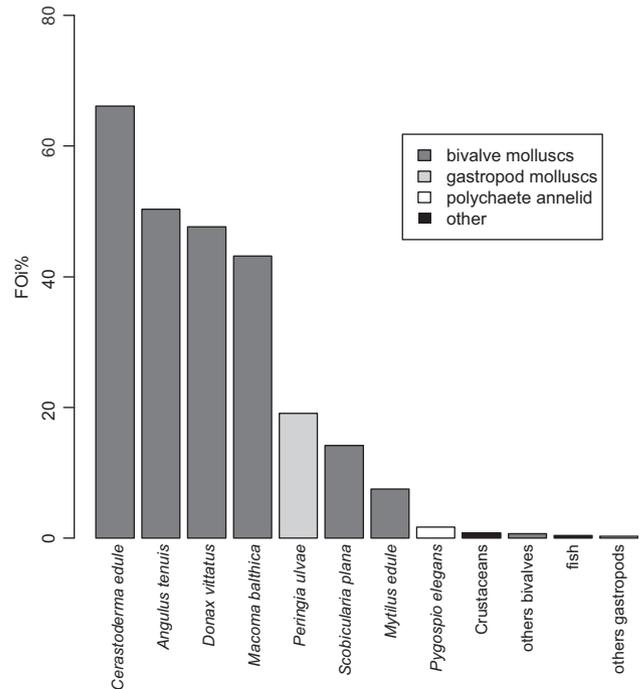


Fig. 3. Frequency of occurrence (FOi%) of different prey species identified in droppings.

Table 3

Digestive quality of the five main preys expressed by the flesh to shell dry mass ratio.

	AFDMFlesh/DMSHELL	sd
<i>Cerastoderma edule</i>	0.03	4.55
<i>Scrobicularia plana</i>	0.04	1.33
<i>Angulus tenuis</i>	0.05	1.93
<i>Macoma balthica</i>	0.06	2.18
<i>Donax vittatus</i>	0.06	1.28

Table 4
Frequency of occurrence (FOi%) of each prey item in dropping composition.

Benthic assemblage	Scro-pla	Per-ulv	Mac-bal	Ang-ten	Cer-edu	Don-vit	Myt-edu	Pygo-ele	Fish	Other-biv	Crus	Other-gast
CS	72.00	80.00	70.00	20.00	42.67	11.33	2.67	8.00	–	–	0.67	–
CM	13.75	21.25	54.58	60.42	84.58	30.42	0.42	2.08	–	–	1.67	–
AC	0.21	3.97	39.96	65.06	72.38	55.65	12.34	–	–	1.05	0.42	0.21
DC	–	0.75	3.76	13.53	36.84	90.98	8.27	–	3.01	1.5	0.75	1.5
Total	14.19	19.08	43.16	50.35	66.13	47.65	7.49	1.7	0.4	0.7	0.8	0.3

densities of *D. vittatus* (>400 ind·m⁻², 7.2% of DC assemblage and 3.4% of the flat). These results indicate that the limited surface areas could be very attractive for foraging birds despite their short exposure time (Table 2) as reported by De Smet et al. (2013) on the *Lanice conchilega* reef in the bay of the Mont Saint-Michel (1% of the total tidal flat).

5. Conclusion

The diet may vary dramatically between sites (Quaintenne et al., 2009, 2014) and on the same site from year to year and along the overwintering season (Dekinga and Piersma, 1993; Zwarts et al., 1992). This study has demonstrated that diet can vary spatially with respect to benthic assemblages and temporally with respect to tidal cycles, as well as during a single tide cycle (Fig. 5). During both spring and neap tides, red knots foraged on differentiated benthic assemblages and the corresponding prey species as the tide was ebbing, revealing a differential exploitation of benthic resources during tidal cycles.

With the perspective of conservation, it is necessary to preserve the succession of foraging habitats, since the red knot can adapt its diet by using alternative prey, thus coping with variations in bivalve densities.

This work is the first stage of a long-term study. The next step will be to determine the contribution of each habitat to the energy budget of wintering red knots. The final purpose is to model the use of the bay of Saint-Brieuc, as a complete functional entity, by red knot and others wading birds as carried out in the Wadden Sea (Piersma et al., 1995)

In megatidal environments, the diversity of assemblages and therefore of feeding resources help guarantee a sustainable carrying capacity for species. They should be taken into account by marine protected area managers to identify the optimal areas for the conservation of waders.

Acknowledgements

We sincerely thank everyone who helped us in the field or in the laboratory. Special thanks go to Leslie Verron, Emilie Bouchée, Severine Kwiecien, Clara Morey-Rubio, Alicia Simonin and Jean-Luc Simon (ONCFS, SD 22). We are very grateful to the anonymous referee (no. 3) for the helpful comments which have improve the quality of this paper and for the perspectives suggested.

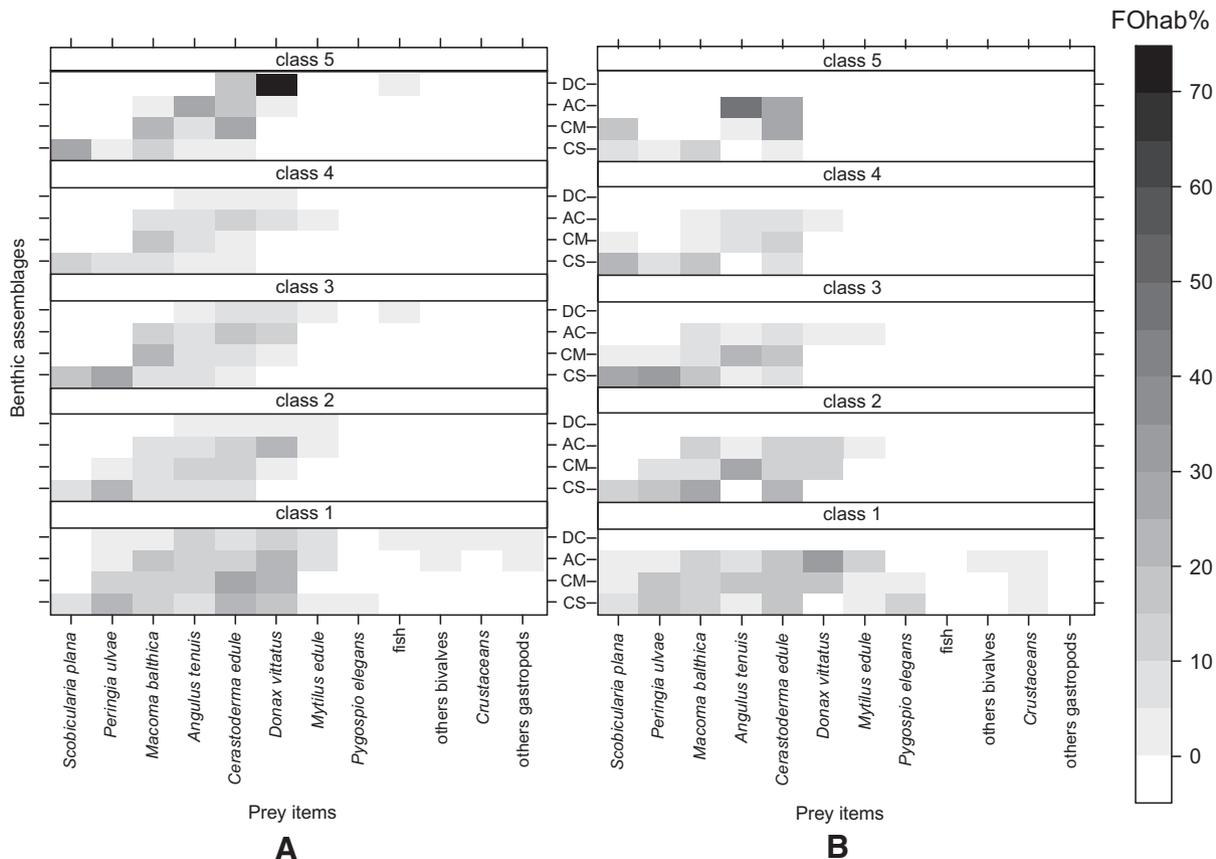


Fig. 4. Frequency of occurrence of prey species identified in droppings for each class of relative abundance (1 < 5%, 2 < 25%, 3 < 50%, 4 < 75%, 5 > 75%) in each habitat (FOhab%). Spring tide (A), neap tide (B).

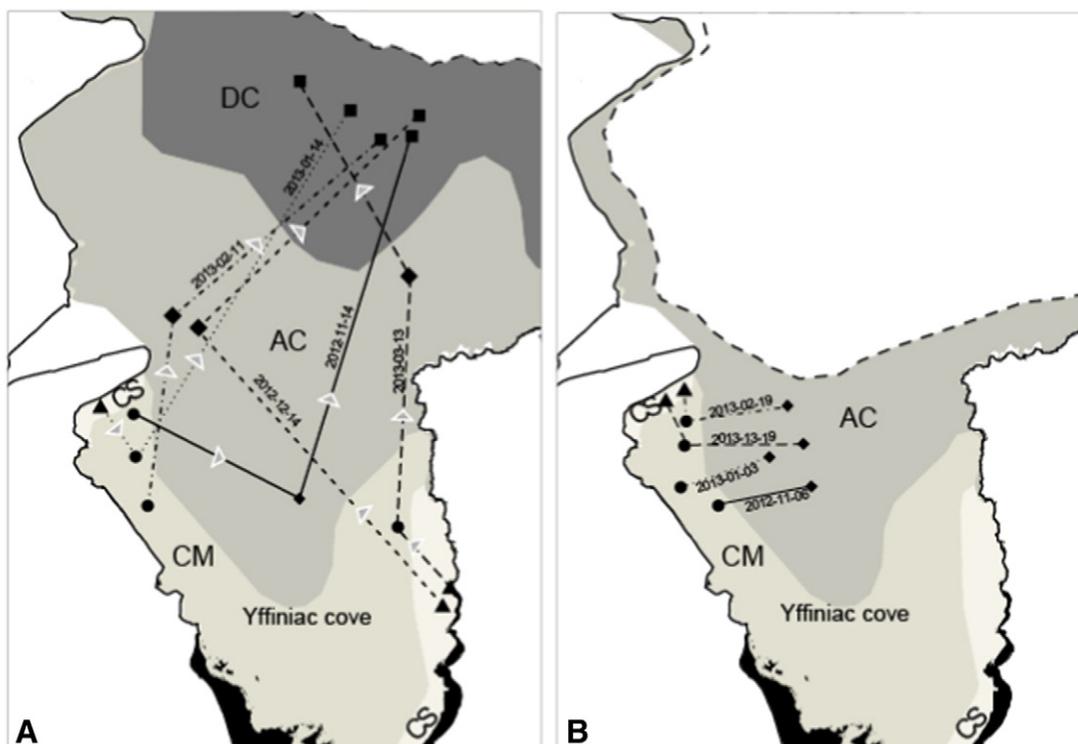


Fig. 5. Foraging trajectories of red knot on each sampled date: spring tide (A), neap tide (B).

References

- Augris, C., Hamon, D., 1996. Atlas thématique de l'environnement marin en baie de Saint-Brieuc (Côtes d'Armor). IFREMER.
- Beukema, J.J., 1976. Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea. *Neth. J. Sea Res.* 10 (2), 236–261.
- Beukema, J.J., 1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. *Helgoländer Meeresuntersuchungen* 43, 405–415.
- Bijleveld, A.I., van Gils, J.A., van Der Meer, J., Dekinga, A., Kraan, C., van der Veer, H.W., Piersma, T., 2012. Designing a benthic monitoring programme with multiple conflicting objectives. *Methods Ecol. Evol.* 3, 526–536.
- Bijleveld, A.I., Massourakis, G., van der Marel, A., Dekinga, A., Spaans, B., van Gils, J.A., Piersma, T., 2014. Personality drives physiological adjustments and is not related to survival. *Proc. R. Soc. B Biol. Sci.* 281, 20133135.
- Boere, G.C., Smit, C.J., 1981. Knot (*Calidris canutus* L.). In: Smit, C.J., Wolff, W.J. (Eds.), *Birds of the Wadden Sea*, Rotterdam, pp. 136–145.
- Cohen, J.B., Karpany, S.M., Fraser, J.D., Truitt, B.R., 2010. The effect of benthic prey abundance and size on red knot (*Calidris canutus*) distribution at an alternative migratory stopover site on the US Atlantic Coast. *J. Ornithol.* 151, 355–364.
- De Smet, B., Godet, L., Fournier, J., Desroy, N., Jaffré, M., Vincx, M., Rabaut, M., 2013. Feeding grounds for waders in the Bay of the Mont Saint-Michel (France): the *Limacina conchilega* reef serves as an oasis in the tidal flats. *Mar. Biol.* 160 (4), 751–761.
- Degraer, S., Wittoeck, J., Appeltans, W., Cooreman, K., Deprez, T., Hillewaert, H., Hostens, K., Mees, J., Vanden Berghe, E., Vincx, M., 2006. *The Macrobenthos Atlas of the Belgian Part of the North Sea*. Belgian Science Policy.
- Dekinga, A., Piersma, T., 1993. Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the Knot *Calidris canutus*. *Bird Study* 40, 144–156.
- R Development Core Team, 2013. *R language and environment for statistical computing*. Available at <http://www.R-project.org/>.
- Dias, M.P., Peste, F., Granadeiro, J.P., Palmeirim, J.M., 2008. Does traditional shellfishing affect foraging by waders? The case of the Tagus estuary (Portugal). *Acta Oecol.* 33, 188–196.
- Fleischer, R.C., 1983. Relationships between tidal oscillations and Ruddy Turnstone flocking, foraging, and vigilance behavior. *Condor* 85, 22–29.
- Folmer, E.O., Olff, H., Piersma, T., 2010. How well do food distributions predict spatial distributions of shorebirds with different degrees of self-organization? *J. Anim. Ecol.* 79, 747–756.
- Goss-Custard, J.D., Jenyon, R.A., Jones, R.E., Newberry, P.E., Williams, R.I.B., 1977. The ecology of the Wash II. Seasonal variation in the feeding conditions of wading birds (Charadrii). *J. Appl. Ecol.* 14, 707–719.
- Granadeiro, J.P., Dias, M.P., Martins, R.C., Palmeirim, J.M., 2006. Variation in numbers and behaviour of waders during the tidal cycle: implications for the use of estuarine sediment flats. *Acta Oecol.* 29, 293–300.
- Hedges, J.L., Stern, J.H., 1984. Carbon and nitrogen determinations of carbonate containing solids. *Limnol. Oceanogr.* 29 (3), 657–663.
- 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. *J. Mar. Sci.* 64, 1735.
- Kraan, C., van der Meer, J., Dekinga, A., Piersma, T., 2009. Patchiness of macrobenthic invertebrates in homogenized intertidal habitats: hidden spatial structure at a landscape scale. *Mar. Ecol. Prog. Ser.* 383, 211–224.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Elsevier Science, Amsterdam.
- Levinton, J.S., 2001. *Marine Biology: Function, Biodiversity, Ecology*. Oxford University Press, Oxford.
- McLusky, D.S., Elliott, M., 2004. *The Estuarine Ecosystem: Ecology, Threats, and Management*. Oxford University Press, Oxford (UK).
- Meziane, T., 1997. Le réseau trophique benthique en baie du Mont Saint Michel: intégration de la matière organique d'origine halophile à la communauté à *Macoma balthica*. University of Rennes I, France.
- Moreira, F., 1994. Diet and feeding rates of knots *Calidris canutus* in the Tagus estuary (Portugal). *Ardea* 82, 133–136.
- Nehls, G., 1992. Food Selection of Knots *Calidris canutus* in the Wadden Sea: The Importance of Seasonal and Annual Variation of Food Availability. *Wader Study Group Bull.*
- Onrust, J., de Fouw, J., Oudman, T., van der Geest, M., Piersma, T., van Gils, J.A., 2013. Red knot diet reconstruction revisited: context dependence revealed by experiments at Banc d'Arguin, Mauritania. *Bird Study* 60, 287–307.
- Piersma, T., 1990. Red knots in New Zealand eat molluscs too: preliminary diet observations at Miranda, Firth of Thames, and Farewell Spit in November 1990. *Stilt* 19, 30–35.
- Piersma, T., 1994. *Close to the Edge: Energetic Bottlenecks and the Evolution of Migratory Path Ways in Knots*. University of Groningen, Groningen, The Netherlands.
- Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P., Wiersma, P., 1993. Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the Western Wadden Sea in relation to food, friends and foes. *Neth. J. Sea Res.* 31, 331–357.
- Piersma, T., van Gils, J., 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.
- Ponsero, A., Le Mao, P., 2011. Consommation de la macro-faune invertébrée benthique par les oiseaux d'eau en baie de Saint-Brieuc. *Rev. d'Ecologie* 66, 383–397.
- Prater, A., 1972. The ecology of Morecambe Bay. III. The food and feeding habits of knot (*Calidris canutus* L.) in Morecambe Bay. *J. Appl. Ecol.* 179–194.
- Quaintenne, G., van Gils, J.A., Bocher, P., Dekinga, A., Piersma, T., 2009. 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 Biol. Sci.* 278, 2728–2736.
- Quaintenne, G., Bocher, P., Ponséro, A., Caillot, E., Feunteun, E., 2014. Contrasting benthos communities and prey selection by red knot *Calidris canutus* in three nearby bays on the Channel coast. *Ardea* 101, 87–98.

- Rosa, S., Granadeiro, J.P., Cruz, M., Palmeirim, J.M., 2007. Invertebrate prey activity varies along the tidal cycle and depends on sediment drainage: consequences for the foraging behaviour of waders. *J. Exp. Mar. Biol. Ecol.* 353, 35–44.
- Scherrer, B., 2007. Biostatistique. Gaëtan Morin éditeur, Montréal.
- Thorin, S., Radureau, A., Feunteun, E., Lefeuvre, J.C., 2001. Preliminary results on a high east–west gradient in the macrozoobenthic community structure of the macrotidal Mont Saint-Michel bay. *Cont. Shelf Res.* 21, 2167–2183.
- van den Hout, P.J., van Gils, J.A., Robin, F., van der Geest, M., Dekinga, A., Piersma, T., 2014. Interference from adults forces young red knots to forage for longer and in dangerous places. *Anim. Behav.* 88, 137–146.
- van Gils, J.A., Dekinga, A., Spaans, B., Vahl, W.K., Piersma, T., 2005a. Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. II. Patch choice and length of working day. *J. Anim. Ecol.* 74, 120–130.
- van Gils, J.A., Rooij, S.R., van Belle, J., van Der Meer, J., Dekinga, A., Piersma, T., Drent, R., 2005b. Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. I. Prey choice. *J. Anim. Ecol.* 74, 105–119.
- van Gils, J.A., Spaans, B., Dekinga, A., Piersma, T., 2006. Foraging in a tidally structured environment by red knots (*Calidris canutus*): ideal, but not free. *Ecology* 87, 1189–1202.
- van Gils, J.A., van der Geest, M., Leyrer, J., Oudman, T., Lok, T., Onrust, J., de Fouw, J., van der Heide, T., van den Hout, P.J., Spaans, B., 2013. Toxin constraint explains diet choice, survival and population dynamics in a molluscivore shorebird. *Proc. R. Soc. B Biol. Sci.* 20130861.
- Yasué, M., Dearden, P., Moore, A., 2008. An approach to assess the potential impacts of human disturbance on wintering tropical shorebirds. *Oryx* 42, 415.
- Zwarts, L., Blomert, A.M., 1992. Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. *Mar. Ecol. Progr. Ser. Oldendorf* 83, 113–128.
- Zwarts, L., Blomert, A.M., Ens, B.J., Hupkes, R., van Spanje, T.M., 1990. Why do waders reach high feeding densities on the intertidal flats of the Banc d'Arguin, Mauritania? *Ardea* 78, 39–50.
- Zwarts, L., Blomert, A.M., Wanink, J., 1992. Annual and seasonal variation in the food supply harvestable by knot *Calidris canutus* staging in the Wadden Sea in late summer. *Mar. Ecol. Progr. Ser. Oldendorf* 83, 129–139.