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

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

Gwenaël Quaintenne¹, Pierrick Bocher¹*, Alain Ponséro², Emmanuel Caillot³ & Eric Feunteun⁴


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

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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*, ashorebird species with a circumpolar distribution in summer, breeding in tundra habitats between mid-June and late July (Davidson & Piersma 2009).
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-Quénéch’du 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 Quénéch’du 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 (DMshell). The ash-free flesh dry mass (AFDMflesh) 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.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Subsites</th>
<th>Coordinates</th>
<th>Sampling dates</th>
<th>N samples</th>
<th>Sediment characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Latitude Longitude</td>
<td>Benthos Droppings</td>
<td>N</td>
<td>Median grain size (μm ± SD)</td>
</tr>
<tr>
<td>Saint-Brieuc Bay (SBB)</td>
<td></td>
<td>53°26’N 06°02’E</td>
<td>31 Jan, 3 Mar 2006</td>
<td>323 7</td>
<td>151 ± 37</td>
</tr>
<tr>
<td>Mont-Saint-Michel Bay (MSMB)</td>
<td>Cancale (CAN)</td>
<td>53°50’N 00°17’E</td>
<td>2 Feb 2006</td>
<td>95 5</td>
<td>47 ± 26</td>
</tr>
<tr>
<td></td>
<td>Cherrueix (CHE)</td>
<td>48°37’N 01°41’W</td>
<td>29 Jan 2006</td>
<td>100 6</td>
<td>111 ± 53</td>
</tr>
<tr>
<td></td>
<td>Roz (ROZ)</td>
<td>46°17’N 01°10’W</td>
<td>28 Jan 2006</td>
<td>100 6</td>
<td>158 ± 11</td>
</tr>
<tr>
<td>Bay des Veys (BDV)</td>
<td></td>
<td>53°50’N 00°17’E</td>
<td>30 Jan 2006</td>
<td>102 2</td>
<td>164 ± 56</td>
</tr>
</tbody>
</table>
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\_{flesh}\text{-to-}\text{DM}_{shell} ratios determined per study site, were used to calculate the relative AFDM\_{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 (± 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 ± 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 ± 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 ± SE 1.3% AFDM in the diet), on *Macoma* at Mont Saint-Michel (Mean ± SE Cancale: 99.5 ± 0.1%; Cherrueix: 99.3 ± 0.2%; Roz: 91.4 ± 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
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...
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-Quénéchdu 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 AFDM 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 AFDM_{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 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).
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 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.
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.

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SAMENVATTING


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**Appendix 1.** Frequency of occurrence (Occ., %), mean density (Dens., ind/m$^2$) and mean biomass (Biom., mg AFDM flesh/m$^2$) of mollusc species at each site (sampled in January–March 2006).

<table>
<thead>
<tr>
<th>Species</th>
<th>Saint-Brieuc Bay</th>
<th>Mont Saint-Michel Bay</th>
<th>Bay des Veys</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Bivalves</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cerastoderma edule</em></td>
<td>42</td>
<td>79</td>
<td>4386</td>
</tr>
<tr>
<td><em>Donax vittatus</em></td>
<td>6</td>
<td>7</td>
<td>15</td>
</tr>
<tr>
<td><em>Macoma balthica</em></td>
<td>5</td>
<td>4</td>
<td>30</td>
</tr>
<tr>
<td><em>Tellina tenuis</em></td>
<td>42</td>
<td>166</td>
<td>874</td>
</tr>
<tr>
<td><em>Ruditapes decussatus</em></td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>35</td>
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<tr>
<td><em>Mysella bidentata</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Scrobicularia plana</em></td>
<td>6</td>
<td>28</td>
<td>1175</td>
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<tr>
<td><em>Abra tenuis</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td><em>Mytilus edulis</em></td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>14</td>
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<tr>
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