

# Influence of environmental gradients on the distribution of benthic resources available for shorebirds on intertidal mudflats of Yves Bay, France



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## ABSTRACT

The case study of Yves Bay (Pertuis Charentais, France) highlighted links between environmental gradients (*i.e.* sediment characteristics and emersion time) and prey distribution and availability for the two most numerous shorebird species overwintering in Yves Bay: the red knot *Calidris canutus* and the dunlin *Calidris alpina*. Two hundred and fifty-two stations were sampled on a predetermined 250 m regular grid covering the intertidal mudflats of this major wintering site in France for east-Atlantic migratory shorebirds. The distribution of principal benthic species abundance and biomass was modelled along two environmental gradients: sediment structure (particularly pronounced north–south sand–mud gradient) and emersion time. The effect of emersion time combined with sedimentary structure strongly explained abundances and biomasses of the main prey for *C. canutus* and *C. alpina* in the bay (*Cerastoderma edule*, *Hydrobia ulvae*, *Macoma balthica*, *Scrobicularia plana*, and *Nephtys hombergii*). This study highlighted prey species-specific spatial segregation/overlapping as well as spatial interferences in the trophic niche of the two shorebirds.

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## 1. Introduction

The niche relationships between sympatric species have received early interest in ecology (Hutchinson, 1957, 1959) and have been developed through the study of community structure (M'Closkey, 1976), inter-species interactions (Trainor et al., 2014), and behavioural ecology (MacArthur, 1958; Schoener, 1965). Feeding resource partitioning (*i.e.* trophic niche) in sympatric predators is the result of specialisation and co-evolutionary change in response to competition and complex interspecific interactions (Schoener, 1974). The prey spatial distribution together with prey size and taxa, plays a crucial role in the resource partitioning of predators, since it proceeds also from interspecific interactions among predators (Wells, 1978).

Most shorebird species are dependent on intertidal flats as feeding areas during the non-breeding period. Several species forage regularly together in the same habitat (intertidal mudflats) and share the same potential benthic invertebrates as a trophic resource. They often experience trophic niches overlap, and their segregation is partly the result of morphology, feeding methods, and a highly specialised diet (Baker and Baker, 1973; Nebel and Thompson, 2011). The trophic segregation between shorebird species can be described qualitatively (*e.g.* different prey species, prey quality, or preference), quantitatively (*e.g.* different prey sizes), as well as temporally (*e.g.* night/day foraging, different season) or spatially (*e.g.* in relation with the vertical or horizontal distribution of their prey). In the present study we investigate the spatial trophic segregation in two sympatric shorebird species: *Calidris canutus* and *Calidris alpina*, through the distribution of their feeding resource.

The red knot *Calidris canutus* and the dunlin *Calidris alpina* are

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long-distance migratory shorebirds that overwinter in intertidal mudflats. These two species are common and dominant shorebirds in the European mudflats, including the Pertuis Charentais and Yves Bay in France (Delaney et al., 2009). Locally, their trophic resource is composed exclusively of macrobenthic species with overlapping distribution on mudflats (Compton et al., 2008); however, both species exploit contrasted trophic niches (Bocher et al., 2014). Their trophic niches differ chiefly because of distinct ecomorphological patterns (digestive capacity/flexibility), and dunlin are smaller individuals that are much more constrained by prey sizes and digestive quality. Dunlin can be described as generalists (*i.e.* eating molluscs and worms), and their regime shifts according to environmental conditions (Kuwae et al., 2010). Red knot are predominantly deposit-suspensivorous mollusc eaters, with *Hydrobia ulvae* as a principal prey in the Pertuis Charentais (Quaintenne, 2010; Bocher et al., 2014).

In the present study, prey habitat preference was modelled to better understand spatially the trophic niche of dunlin and red knot. Two environmental gradients were used to model prey distribution: median grain size (MGS) and emersion time (ET). The change in distribution between prey species depending on their availability for both predator species was analysed in the specific context of Yves Bay in October 2010, just before the peak of predation pressure.

In tidally structured ecosystems such as intertidal mudflats, benthic distribution is influenced by a large set of environmental variables with complex interactions (Ysebaert et al., 2002). However, benthic distribution is mainly driven by two of them: MGS and ET (Thrush et al., 2003; Kraan et al., 2010; Compton et al., 2013). Indeed, among physical gradients, ET and MGS play a particularly important role in the functioning of intertidal areas, their biotic composition, and processes (Gray, 1974): these two gradients affect mobility, adsorption capacity, and desiccation resistance and are themselves correlated with other environmental variables such as particularities of local hydrodynamics or salinity (especially in estuaries). Links between sediment characteristics and animal distribution are complex two-way relationships (Rhoads and Boyer, 1982).

Previous studies used MGS or both gradients to predict/describe benthic species distributions (Sanders, 1958; Wells, 1978; Dankers and Beukema, 1981; Creutzberg et al., 1984; Beukema, 1993; Yates et al., 1993). The recent development of ecological modelling has allowed ecologists to describe these non-linear and asymmetric animal–sediment relationships in soft-bodied ecosystems with often zero-inflated data (Anderson, 2008; Compton et al., 2009) and taking account spatial autocorrelation (Kraan et al., 2010). We propose to model the complex habitat preferences of main prey of shorebirds along two gradients, ET and MGS, in Yves Bay in order to study the trophic segregation of dunlin and red knot according to prey availability distribution.

Yves Bay is a wintering site of international importance in most years for dunlin and red knot and of national importance every year for no less than nine shorebird species (Delaney et al., 2009). Dunlin and red knot account for more than 2/3 of overwintering shorebirds in this bay. Shorebird densities of dunlin observed in winter during the peak of presence of shorebirds are among the highest recorded with approximately four birds per hectare (Santos et al., 2005), with highest densities between October and January (see Supplementary Materials Annex xx [add at proof]).

In the present work, we firstly describe the main macrobenthic prey distribution in the specific context of Yves Bay and analyse how this distribution changes between the prey species, and also depending on the available fraction for red knot vs. dunlin. Then, we aim to predict their respective niches spatially by means of the two main abiotic environmental gradients of mudflats determinant

for their prey distribution, MGS and ET. We will first model the prey distribution depending on these two environmental gradients. We hypothesise that (1) our results will confirm the conclusions of previous studies in comparable mudflats concerning prey site-specific and species-specific habitat preferences (Bocher et al., 2007; Compton et al., 2009). Based on our knowledge of diets for red knot and dunlin in the Pertuis Charentais, we will compare this first distribution (*i.e.* the distribution of the total resource) with the distribution of available resources for red knot on the one hand and dunlin on the other hand. Due to quantitative and qualitative differences in their trophic niches (Bocher et al., 2014), we hypothesise (2) spatial differences in the distribution of their respective available prey along the two explanatory gradients. The final objective is to compare benthic distributions along these two environmental gradients and describe how environmental gradients can help predict the available biomass for shorebirds in a spatially structured environment.

## 2. Materials and methods

### 2.1. Study area

Yves Bay (46°02'N, 01°03'W) is located in the Pertuis Charentais, a series of straits around the islands of Oléron and Ré in the central part of the French Atlantic Coast (Fig. 1). This intertidal bay covers an area of 1200 ha of mudflat with a strong north–south substratum granulometric gradient. The sandier area in the north is partly covered with a seagrass bed, while the muddy-soft substratum towards the south is purely bare mudflat (Bocher et al., 2007). The lower tidal area of the bay is dedicated to oyster and mussel cultures. At the north of the bay, the coastal marshes are included in a nature reserve (*RNN du Marais d'Yves*, 192 ha) and used as a roost by shorebirds at high tide during the spring tide.

### 2.2. Sediment characteristics

Within each 500 m, a sediment sample was collected (Fig. 1) to a maximum depth of 8 cm. MGS ( $\mu\text{m}$ ) and the percentage of silt (fraction < 63  $\mu\text{m}$ ) were determined using a Malvern Mastersizer 2000 diffraction laser (particle sizes analysed from 0.04 to 2000  $\mu\text{m}$ ). MGS was preferred to the silt fraction — both are highly correlated with each other in our study case ( $r = -0.90$ ,  $n = 62$ , *Pearson*) — to facilitate later comparison with the literature. For the stations where sediment samples were not taken, MGS was estimated by spatial interpolation using kriging with a “gstat” R package (Pebesma, 2004).

### 2.3. Emersion time (ET)

The time interval during which the mudflat stays emerged was estimated by using sea level predictions from a regional tidal model. This model resolves the shallow water equations on a high-resolution finite element grid by using the TELEMAC software (Hervouet, 2007). The spatial resolution of the grid varies from several km in deep water to about 30–50 m near the coast. More details about the method, open boundary forcing, and the calibration can be found in (Nicolle and Karpitchev, 2007; Nicolle et al., 2009), where the model was applied for predicting tides and storm surges.

The current model version uses a recently updated finite element grid based on the latest bathymetric surveys and Lidar data as described in (Guizien et al., 2014) and in (Fossette et al., 2015), where the model was applied for tracking passive tracers and jellyfish in the Pertuis Charentais.

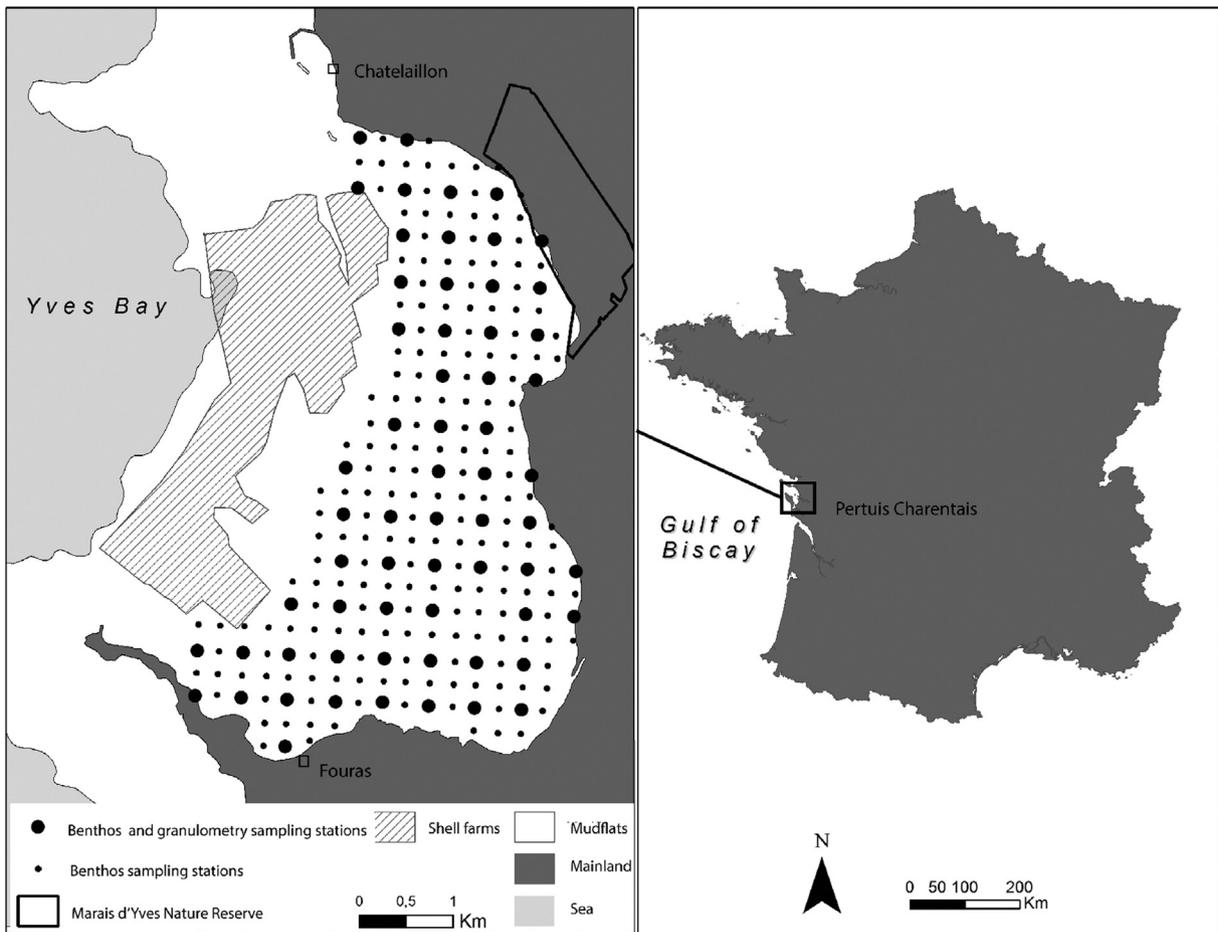


Fig. 1. Map of Yves Bay and the sampling grid, with location in France.

#### 2.4. Benthic macrofauna sampling

From 18 October to 2 November 2010, benthic macrofauna were collected over a predetermined 250 m grid covering estuarine intertidal mudflats of Yves Bay (Fig. 1) following a proven sampling protocol (Bocher et al., 2007; Kraan et al., 2009; Bijleveld et al., 2012). Each station was located using a handheld GPS device. Out of 252 stations sampled, 74 were sampled by foot (during low tide) using a sediment core covering an area of 0.018 m<sup>2</sup> down to a depth of 20–25 cm. The top fraction (first 4 cm in the sediment) was separated from the bottom fraction to be able to segregate the accessible benthos fraction for red knot and dunlin. We took an additional core (70 mm diameter) covering 0.0038 m<sup>2</sup> to a depth of 4 cm for sampling exclusively the very abundant mudsnail *Hydrobia ulvae* (Pennant) (Bocher et al., 2007). When the tide covered the mudflats with water (0.4–2.0 m) and for the very soft and inaccessible southern part of the bay, sampling was done from boats using inflatable zodiacs or other small vessels. From the boats, two mud cores (100 mm diameter) covering a total of 0.018 m<sup>2</sup> to a depth of 20–25 cm were taken. Only one core was taken into account for *Hydrobia ulvae*, and both were taken into account for any other macrobenthic species. Sampling from boats or by foot yielded identical estimates (Kraan et al., 2007). The top fraction in the cores sampled by boat was interpolated from the proportions observed in cores sampled by foot, based on size-species-specific proportions in the top fraction as in (Kraan et al., 2009).

The cores were sieved over a 1 mm mesh, except for the *H. ulvae*

cores, which were sieved over a 0.5 mm mesh. All living molluscs were collected in plastic bags and frozen until laboratory treatment. Polychaetes and crustaceans were preserved in 70% ethanol.

#### 2.5. Determination of benthic densities and biomasses

Later in the laboratory, molluscs were determined and counted, and their maximum length was measured to the nearest 0.1 mm with Vernier callipers. *H. ulvae* were size-categorized from 0 mm up to 6 mm (e.g. size class 2 consists of individuals with lengths ranging from 2 to 2.99 mm). The flesh of every mollusc specimen except *H. ulvae* was detached from the shell and placed individually in crucibles (pooled by size, class, flesh and shell together). Crucibles containing molluscs were dried in a ventilated oven at 55–60 °C to a constant mass and then weighed (DM ±0.01 mg). Dried specimens were then incinerated at 550 °C for 4 h to determine their ash mass and then a proxy of their energy content: the ash free dry mass (AFDM). *H. ulvae* flesh biomass (AFDM<sub>flesh</sub>) was estimated for each station from the total biomass (AFDM<sub>flesh+shell</sub>) with the following linear regression:  $AFDM_{flesh} = 0.6876 \times AFDM_{flesh+shell} + 7E-05$  ( $R^2 = 0.99$ ;  $N = 60$  ind.).

Crustaceans and polychaetes were also identified, counted, and measured, but AFDM was not determined for these phyla. Crustaceans and polychaetes were not weighed due to insufficient numbers of entire individuals to build regression equations.

## 2.6. Available resources for shorebirds

Available prey biomasses for red knot *Calidris canutus* and dunlin *Calidris alpina* were determined from the original benthic dataset, first by isolating the accessible fraction (the top 4 cm of the core, corresponding to the maximal length of the bill for both species) and then considering suitable sizes of the prey (Piersma et al., 1993). Harvestable prey were discriminated by size based on previous studies of feeding ecology of both species in the French Pertuis Charentais (Quaintenne, 2010; Drouet, 2014). Red knot are considered exclusive molluscivore shorebirds, and thus only mollusc species were kept according to profitable and ingestible size (i.e. all *Abra* spp., *Cerastoderma edule* [3–10 mm], *Macoma balthica* [3–15 mm], *Scrobicularia plana* [4–12 mm], and all *H. ulvae*). For the dunlin, molluscs and annelids were kept (i.e. all *Abra* sp., *Cerastoderma edule* [2–8 mm], *Macoma balthica* [8–10 mm], *Scrobicularia plana* [2–12 mm], all *H. ulvae*, all *Retusa obtusa*, all *Nephtys hombergii*, and all *Hediste diversicolor*). However, part of their diet may consist of bivalve siphons, especially of large and deeply buried *S. plana*, which are highly localized in the mudflats of the Pertuis Charentais (Bocher et al., 2007). Siphon cropping was never quantified in our ecosystem, but represented a significant fraction of the diet in both shorebird species in previous studies (Zwarts, 1986; Moreira, 1997; Martins et al., 2013).

## 2.7. Modelling of benthic spatial distribution

Generalised linear models (GLMs) were used to model the benthic distribution of the principal benthic species in our system according to ET and MGS gradients (*C. edule*, *M. balthica*, *Nephtys hombergii*, *H. ulvae*, and *S. plana*), assuming the adequate family distribution depending on the prey species and dataset considered (e.g. Gaussian, Negative Binomial, Binomial). Variograms of model residuals were produced to confirm the absence of spatial autocorrelation, and models were validated by a visual inspection of the residuals. Explanatory variables included ET, MGS, their interaction, and their quadratic terms (Kraan et al., 2010). The response variables were the counts per core of the most occurring species (*C. edule*, *M. balthica*, *N. hombergii*, *S. plana*), presence/absence of macrobenthos, and biomass of *H. ulvae* and *M. balthica* for the total resource sampled, the available fraction for dunlin, as well as the available fraction for the red knot. Model selection was based on the Akaike information criterion considering best models with  $\Delta AIC > 2$  (Akaike, 1974; Burnham et al., 2011). In the case of models with equivalent AIC or when  $\Delta AIC < 2$ , the principle of parsimony was applied, keeping the model with the lower number of parameters. *H. ulvae* density and biomass showed some high residual values in the models, due to some local aggregations of individuals. Despite the difficulty to adjust the models with these values, we chose to keep them in the dataset because of their biological relevance for shorebirds, corresponding to a known fact and not to a sampling error (i.e. high densities of *H. ulvae* in ridges as a result of specific hydrodynamic conditions or floating ability of this mudsnail (Armonies and Hartke, 1995; Haubois et al., 2002)).

Statistical analyses of the data were performed using R version 3.2.1 (R Development Core Team, 2015) using packages *gstat* (Pebesma, 2004) and *MASS* (Venables and Ripley, 2002). ArcGIS® software version 10.1 by ESRI was used for mapping results.

## 3. Results

### 3.1. Sediment characteristics

The sediment size distribution in Yves Bay (Bay of Biscay, France) revealed a strong gradient of sandy to muddy sediment

(i.e. less than 8 km) with MGS ranging from 269 to 20  $\mu\text{m}$  and silt fractions ranging from 0 to 51% (from north to south) and could be the result of coarse sand coming from beach replenishment in the north (M-L. Cayatte and C. Goulevant, pers.com). This gradient is steeper than in previous studies analysing the effect of sediment size on benthic distribution (e.g. in Creutzberg et al., [1984] MGS ranged from 100  $\mu\text{m}$  to 300  $\mu\text{m}$  and silt fraction from 0 to 20%, in Kraan et al., [2010] MGS ranged from 100  $\mu\text{m}$  to 250  $\mu\text{m}$ ) and provides us with a quasi-experimental setting for testing the combined effects of physical substrate characteristics and ET on species distribution and densities, as well as the biomass distribution of macrobenthic prey in this mudflat ecosystem.

Original values revealed a strong north–south granulometric gradient with a significant increase of MGS values with increasing latitude (linear regression;  $p$ -value  $< 0.0001$ ). MGS values predicted by the model were much lower in the south (minimum 20  $\mu\text{m}$ ) compared to the north (maximum 269  $\mu\text{m}$ ) for a given distance to the coast (Fig. 2).

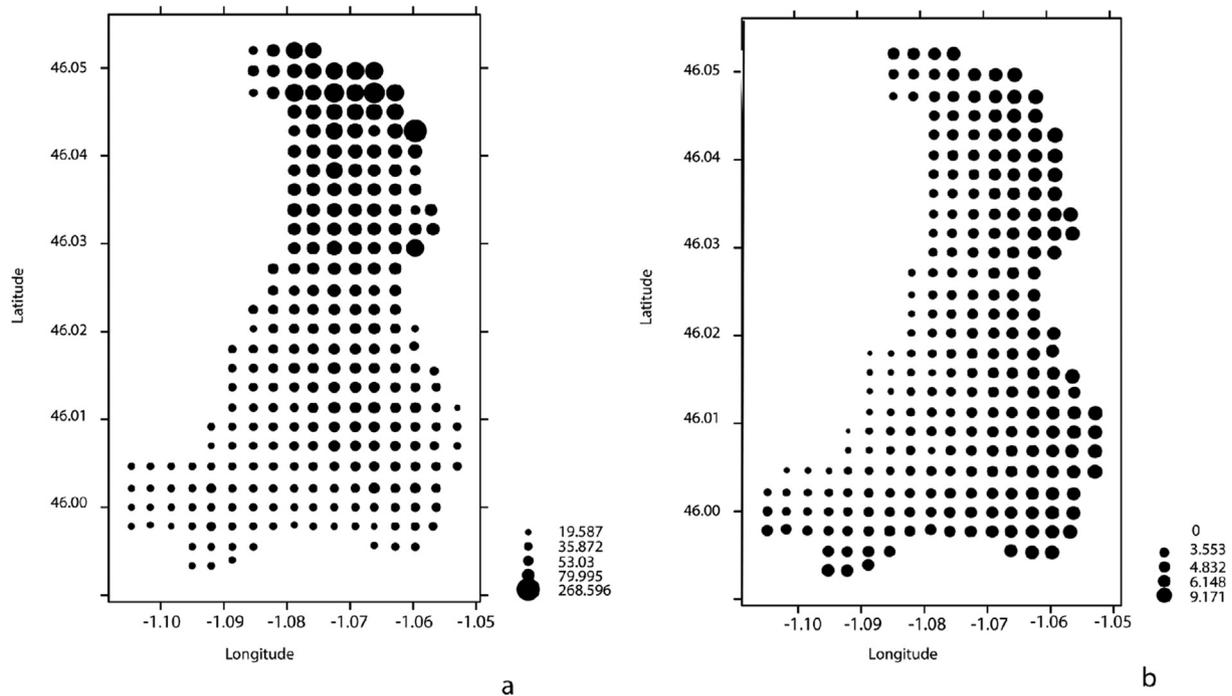
### 3.2. Emersion time (ET)

Across the stations, ET ranged from 0 to 9.2 h for a mean tidal cycle of 12.5 h, with three stations located in the limit subtidal/intertidal (ET = 0 h) (Fig. 2). The sampling stations did not cover all of the intertidal area, but the number of stations with low ET values was sufficient to apply our models. In our study system, the two variables (ET and MGS) were weakly correlated (Pearson coefficient = 0.39).

### 3.3. Benthic macrofauna

A total of 32 OTUs (operational taxonomic units) were identified for all macrobenthic organisms collected, with 26 identified to the species level. Among these 32 OTUs, 13 belong to the phylum Mollusca (8 bivalves and 5 gastropods), 7 to the subphylum Crustacea, and 12 to the phylum Annelida (Table 1). The mudsnail *Hydrobia ulvae* accounted for more than 91% of the total number of macrobenthos individuals, and four other taxa composed more than 70% of the remaining macrobenthos: the bivalves *Cerastoderma edule*, *Macoma balthica*, *Scrobicularia plana*, and the polychaete *Nephtys hombergii*. The most common and widespread main occurring species (i.e. present in more than 9% of the stations) were *Cerastoderma edule*, *Macoma balthica*, *Scrobicularia plana*, *Hydrobia ulvae*, and *Nephtys hombergii* (Table 1). The four common mollusc species represented more than 99% of the total molluscan biomass in the bay.

The spatial distribution of these four dominant mollusc species and the polychaete *Nephtys hombergii* in the bay were different (Fig. 3). *Scrobicularia plana* formed a belt along the coast with the highest densities in the upper intertidal zone, and mostly in the south. *Hydrobia ulvae* was the most occurring species (present in more than 70% of the sampling stations), with lower densities in the lowest part of the intertidal. *Cerastoderma edule* was patchily distributed and occurred in less than 10% of sampling stations, mostly concentrated in the north of the bay. *Macoma balthica* abundances were concentrated in the upper intertidal zone, but equally spread in latitude. The overall mollusc biomass was located mostly in the upper intertidal area, with no perceptible preference between the north and the south. *N. hombergii* was present in nearly 40% of the stations, with highest densities in the middle and lower intertidal area, mostly in the north of the bay.



**Fig. 2.** (A) Median sediment grain size distribution in Yves Bay, empirical values + interpolated values using kriging (on the right, in  $\mu\text{m}$ ); (b) ET per sampled station using sea level predictions from a regional tidal model (on the left, in h).

### 3.4. Modelling of benthos densities and biomass along the two environmental gradients

GLMs were applied to total resource and available resources for dunlin and red knot, respectively (Table 2).

Predictions were represented in two dimensions when only one gradient was used in the model (Fig. 4). When the interaction between the two gradients better predicted benthos densities or biomass, we represented the predictions in three dimensions: X and Y axes horizontally projected representing MGS and ET, respectively, and Z axis vertically projected representing the prediction of response variable (Fig. 5). Depending on the species, the data constrained us to only model densities or biomass.

*Macoma balthica* numbers were predicted to reach 3 individuals per core in areas with the highest ET, and the available fraction predicted for the shorebirds followed the same perceived habitat preference, reaching 2–2.5 individuals per core for the dunlin and the red knot (Fig. 4a).

Macrobenthos was predicted to be absent from the samples (oligotrophic areas) with the lowest ET, with a maximal probability of 60% when the total macrobenthic resource is considered. The predicted distribution for the available fraction for dunlin and red knot was comparable, with highest probabilities (90% for both shorebird species when the ET was null) (Fig. 4b).

Cockles were predicted to be found in higher numbers in areas with a large MGS (150  $\mu\text{m}$ –250  $\mu\text{m}$ ), with a maximum total resource predicted of  $\approx 3$  ind/core,  $\approx 2$  ind/core for dunlin and  $\approx 2.5$  ind/core for red knot (Fig. 4c).

*Scrobicularia plana* was predicted in higher densities in areas with the longest ET and the lowest MGS for the total resource as for the available fraction for dunlin (Fig. 5a and b). Available *S. plana* numbers for red knot were predicted to be found in areas with the highest ET (Fig. 5c). The number of individuals per core was predicted to reach 40.00  $\text{g m}^{-2}$  for the total resource, and the predictions for dunlin and red knot dropped down to 3.00  $\text{g m}^{-2}$  and

0.60  $\text{g m}^{-2}$ , respectively.

The highest biomasses of *Macoma balthica* (0.70  $\text{g}_{(\text{AFDM})}\text{m}^{-2}$ ) were predicted in areas with the longest ET for the total resource. Individuals available for dunlin were situated in areas combining large grain sizes and also long ET (up to 0.15  $\text{g}_{(\text{AFDM})}\text{m}^{-2}$ ), and for red knot in areas with higher ET (up to 0.40  $\text{g}_{(\text{AFDM})}\text{m}^{-2}$ ) (Fig. 5d–f).

*Nephtys hombergii* numbers were predicted to reach no less than 120 individuals per core in areas with the highest MGS and a minimal ET of 4 h. The available fraction for dunlin followed the same predicted distribution but with lower numbers (only the accessible fraction is available) (Fig. 5g, h).

*Hydrobia ulvae* biomass was predicted in higher density (up to 6.00  $\text{g}_{(\text{AFDM})}\text{m}^{-2}$ ) in habitats combining long ET and an MGS of about 150  $\mu\text{m}$  (Fig. 5i).

## 4. Discussion

This study presents the macrobenthic fauna distribution on an intertidal mudflat, with a strong granulometric gradient. This small bay appears as a rare opportunity for testing independently the influence of ET gradient and sediment structure on the distribution of macrobenthic species as these two variables are uncorrelated in this study case. The independence of these usually highly correlated variables may be explained by anthropogenic causes. Such a steep granulometric gradient is probably caused by the conjunction of natural hydrodynamic conditions and anthropogenic input of sand from beaches on immediate northern coasts of the entrance of the Bay, (Prof. Eric Chaumillon, LIENSs laboratory, pers. comm.), resulting in extremely coarse sediment in the north of the Bay. This study highlighted species-specific distributions for benthic species along the two gradients considered, with sometimes overlapping perceived habitat preferences. The existence of animal–sediment relationships in mudflat ecosystems is undisputed (Anderson, 2008), but many other factors can influence prey spatial distribution. In this study, we only used two environmental gradients to

**Table 1**  
Frequency of occurrence (Occ), mean densities with min. and max. values, total biomass, total number, and mean sizes with min. and max. values of benthic macrofauna, Yves Bay (2010).

Species	Abr.	Occ. (%)	Density (ind/m <sup>2</sup> )	AFDM (mg/m <sup>2</sup> )	Nb	Size (mm)
<b>Bivalves</b>						
<i>Nucula nitidosa</i>		3.2	2.8 ± 17.3 (0–191.0)	–	11	4.5 ± 2.8 (2.1–10.6)
<i>Mytilus edulis</i>		0.4	0.3 ± 4.0 (0–63.7)	<0.1	1	–
<i>Cerastoderma edule</i>	CER	9.1	8.8 ± 32.3 (0–282.9)	307.6	37	10.7 ± 4.8 (2.1–23.9)
<i>Ruditapes sp.</i>		1.6	1.0 ± 7.8 (0–63.7)	<0.1	4	–
<i>Macoma balthica</i>	MAC	24.6	27.5 ± 64.7 (0–573.0)	1159.0	114	10.3 ± 4.0 (2.4–21.6)
<i>Scrobicularia plana</i>	SCR	9.1	13.6 ± 55.2 (0–445.6)	2152.4	55	18.4 ± 10.1 (3.5–35.5)
<i>Abra tenuis</i>		0.8	0.5 ± 5.7 (0–63.7)	<0.1	2	–
<i>Corbula gibba</i>		2.0	1.3 ± 8.9 (0–63.7)	<0.1	5	6.9 ± 2.3 (5.0–10.1)
<b>Gastropods</b>						
<i>Gastropoda sp.</i>		0.4	0.3 ± 4.1 (0–63.7)	–	1	–
<i>Hydrobia ulvae</i>	HYD	73.4	6148.4 ± 11,687.3 (0–78,213.3)	830.6	8267	2.4 ± 1.4 (0–6)*
<i>Retusa obtusa</i>		2.0	2.5 ± 20 (0–254.6)	–	10	2.7 ± 0.7 (0–3.4)
<i>Bittium reticulatum</i>		0.4	1.8 ± 28.5 (0–452.7)	–	8	–
<i>Cyclope neritea</i>		0.4	0.3 ± 4.0 (0–63.7)	–	1	–
<b>Crustaceans</b>						
<i>Cyathura carinata</i>		0.4	0.2 ± 3.6 (0–56.6)	<0.1	1	–
<i>Idotea chelipes</i>		0.4	0.2 ± 3.6 (0–56.6)	–	1	–
<i>Gammarus locusta</i>		1.6	2.3 ± 25.0 (0–382.0)	<0.1	9	6.7 ± 2.0 (5.7–10.9)
<i>Urothoe marina</i>		0.4	0.7 ± 10.7 (0–169.8)	–	3	–
<i>Corophium volutator</i>		2.0	68.1 ± 1015.1 (0–16,110.4)	–	66	–
<i>Pagurus sp.</i>		0.4	0.3 ± 4.0 (0–63.7)	–	1	–
<i>Carcinus maenas</i>		0.8	0.5 ± 5.4 (56.6–63.7)	–	2	–
<b>Polychaetes</b>						
<i>Arenicola marina</i>		1.2	0.7 ± 6.1 (0–56.6)	–	3	–
<i>Notomastus latericeus</i>		1.6	1.0 ± 8.0 (0–63.7)	–	4	–
<i>Diopatra spp</i>		2.0	1.8 ± 13.2 (0–127.3)	–	7	–
<i>Glycera convoluta</i>		0.4	0.2 ± 3.6 (0–56.6)	<0.1	1	–
<i>Nephtys spp</i>		2.4	1.5 ± 9.7 (0–63.7)	–	6	–
<i>Nephtys hombergii</i>	NHO	36.9	40.5 ± 66.0 (0–339.5)	230.4	169	22.2 ± 5.7 (10.5–42.2)
<i>Nereis spp</i>		0.8	0.4 ± 5.0 (0–56.6)	–	2	–
<i>Hediste diversicolor</i>		4.0	3.1 ± 17.6 (0–191.0)	–	13	60.8 ± 12.6 (31.0–77.4)
<i>Allithea succinea</i>		2.8	2.4 ± 16.6 (0–191.0)	–	10	53.1 ± 21.6 (21.1–93.1)
<i>Neanthes irrorata</i>		0.4	0.2 ± 3.6 (0–56.6)	–	1	–
<i>Pectinaria koreni</i>		0.4	0.3 ± 4.0 (0–63.7)	–	1	–
<i>Owenia fusiformis</i>		2.0	1.2 ± 8.1 (0–63.7)	–	5	–

\**Hydrobia ulvae* individuals were categorized by 1 mm size classes.

model macrobenthic distribution. However, in the context of the present study, given the spatial scale covered by the sampling grid (<12 km<sup>2</sup>), environment variables like pollution or factors affecting colonisation could be considered constant across the study site.

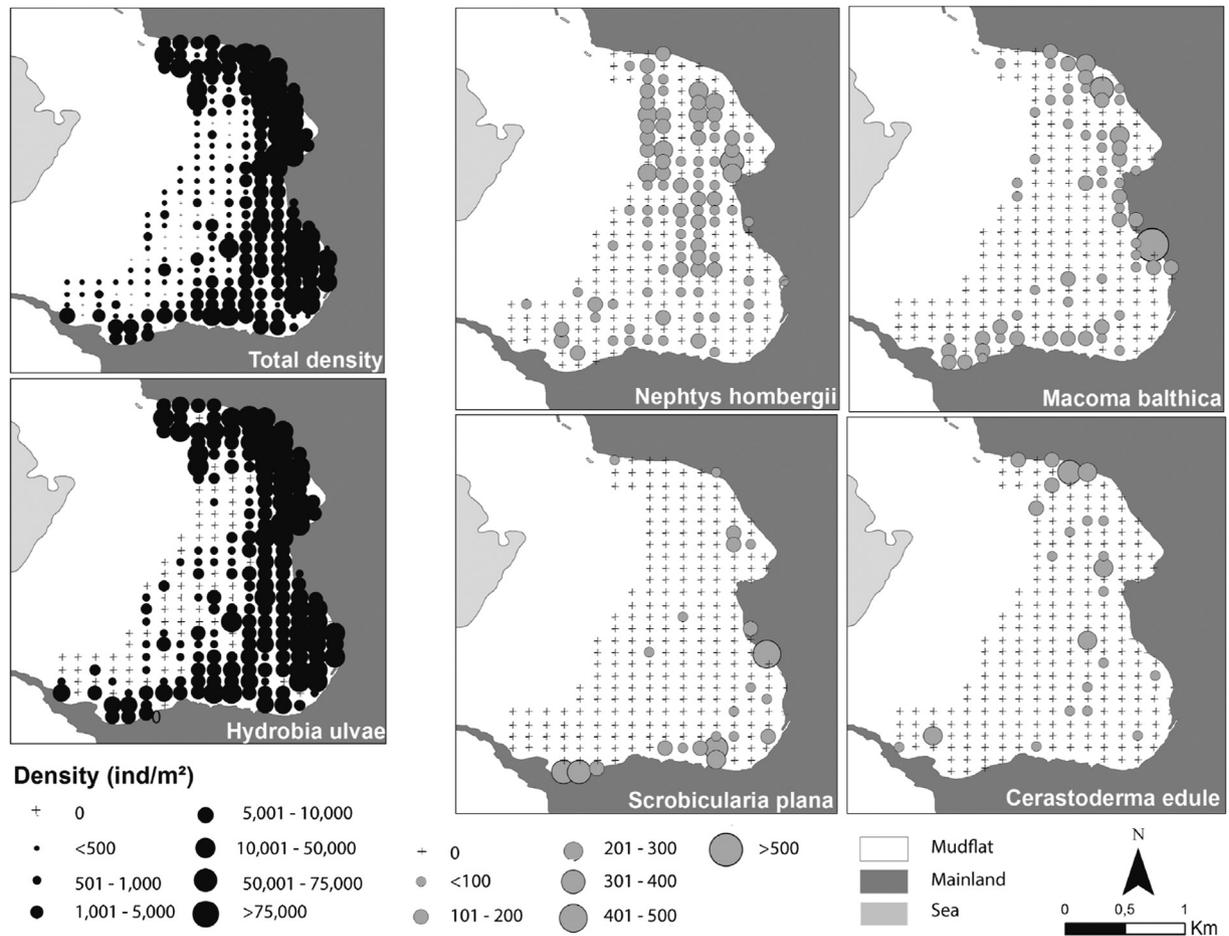
Among prey species, the principal occurring prey (species found in more than 20 stations out of 252, *i.e.* *Cerastoderma edule*, *Hydrobia ulvae*, *Nephtys hombergii*, *Macoma balthica*, and *Scrobicularia plana*) showed different distribution. Macrobenthos was concentrated in areas with the highest ET (*i.e.* near the coast) — a result that is consistent with all previous studies in intertidal mudflats, to the best of our knowledge — and explained mainly by the highest productivity of the upper intertidal areas, usually richer in nutrients thanks to a combination of reduced solute transport and increased microbial processes (Kuwae et al., 2003) and a higher exposition to light. When compared to previous studies, the distribution of the main species showed distributional trends consistent with those previously described for the Pertuis Charentais (Bocher et al., 2007; Compton et al., 2009).

Our predictions were applied on grids covering the entire range of ET values and MGS values interpolated. However, the combination of a high MGS (<200 μm) and low ET (<5 h) was not realistic for Yves Bay, and did not represent any observable combination in the field. We therefore predicted prey distributions on their potential niche (including unrealistic combinations between ET values and MGS values) instead of their 'realised' niche (taking into account

only the realistic combinations between the two variables) (Kraan et al., 2013). This bias forced us to constrain the grid representing *Nephtys hombergii* numbers, for instance (Fig. 5), and yielded light over-predictions for *Scrobicularia plana* in the grid cells corresponding with low MGS and high ET values as well as for *Macoma balthica* for high ET values.

The comparative analysis of the trophic niches of two dominant shorebird species in Yves Bay (*Calidris canutus* and *Calidris alpina*), based on the fraction of benthos that is potentially available to them (in terms of depth, size and taxa), highlighted trophic habitat overlap as well as segregation between the shorebird species via their prey habitat perceived preferences. Available resources for red knot and dunlin encompassed the main macrobenthic species in the system in terms of abundance and biomass. We showed contrasting distribution between prey species, but also depending on the harvestable sizes considered for a given species: habitat distribution was different between the available fraction for dunlin and red knot (*i.e.* for *M. balthica* and *S. plana* abundances).

All *Hydrobia ulvae* were available for dunlin and red knot; however, only a small portion of *S. plana* was available to them (1/3 for dunlin and 1/4 for red knot). As *Hydrobia* were dominant and widely spread over the bay, we could consider them as *ad libitum* for shorebirds. Segregation in space between the two shorebird species should therefore concern preferred species which differ in terms of quality and accessibility.



**Fig. 3.** Spatial distribution of the four main mollusc species, the most abundant annelid species, and the total macrobenthos collected in Yves Bay: the cockle *Cerastoderma edule*, the mud snail *Hydrobia ulvae*, the tellinid bivalve *Macoma balthica*, the peppery furrow shell *Scrobicularia plana*, and the polychaete *Nephtys hombergii*. Due to much higher densities for *H. ulvae* and the total biomass, the two maps on the left are presented with a distinct legend (in black), whereas other species are represented with a grey legend.

The available fraction for dunlin was always smaller than the available fraction for red knot when we considered only bivalve species abundances and biomass. Dunlin are more restricted by size and quality of their prey. Energy requirements of dunlin are smaller, since their body mass is less than half the body mass of red knot in the Pertuis Charentais (van de Kam et al., 2004).

Through the modelling of perceived habitat preferences of their main potential prey, we could highlight spatial trophic niches overlap, but models also showed potential segregation. We can hypothesise that trophic overlap carries over effects in terms of competition, particularly for very abundant and easily accessible species such as *H. ulvae*. However, the available fraction of *M. balthica* biomass and also *S. plana* numbers have highlighted distinct habitat preferences, and their distribution changed depending on the size of the fractions considered. Moreover, *N. hombergii* is a prey that is absent from the diet of red knot and could potentially constitute a sort of trophic way out for dunlin. Besides, *N. hombergii* could very well be a spatially segregative prey species for dunlin, as this prey was predicted in higher densities in lower ET and higher grain sizes in the north-western part of the bay, as opposed to nearly all other potential prey for the two shorebird species considered. Since dunlin have shown to experience trophic shifts depending on environmental conditions or seasons (Kuwaie et al., 2010; Martins et al., 2013) and were described successively as worm eaters (Bocher et al., 2014) or principally mollusc eaters in spatially close environments (Drouet, 2014), it would be interesting

to test whether this trophic shift demonstrated in the Pertuis Charentais is linked with the competition pressure between our two dominant shorebird species and translates into changing feeding areas in the Bay. Do dunlin feed more on worms and small *S. plana*, for instance, when red knot are found in very high numbers in the same area?

We underline the fact that the present study is a snapshot study. Models presented here should not be used to predict the distribution of species in distant spatial and temporal contexts as the distribution of species in a mudflat ecosystem has shown important inter-annual variability (van der Meer, 1999; Kraan et al., 2013). However, the study showed prey species distribution to be consistent with previous studies, particularly with studies of prey species distribution in other mudflats in the Pertuis Charentais in 2004 (Bocher et al., 2007; Compton et al., 2009).

On the small spatiotemporal scales (e.g. tidal scale, mudscale), knowledge of the distribution of MGS and ET in a mudflat of the Pertuis Charentais can help predict abundances of macrobenthos and can potentially affect directly the distribution of *Calidris alpina* and *Calidris canutus*. And it is very likely that shorebirds, especially *C. alpina* and *C. canutus*, would be foraging in areas with higher ET (i.e. on the upper intertidal areas) and progressively follow the water line with changing prey accessibility and availability. It is expected that shorebirds would change their foraging preferences according to environmental gradients influencing the distribution and biomass of their prey as it has been described for other

**Table 2**

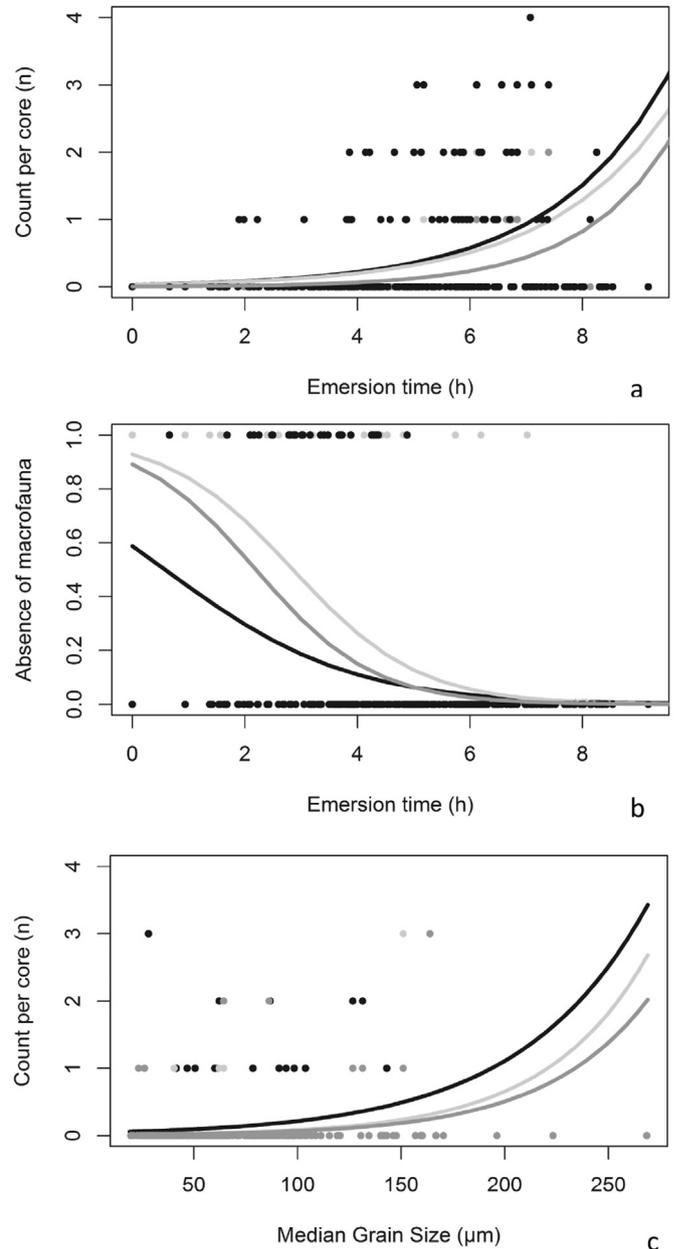
Selection of the minimal adequate model (bold) based on AIC values ( $\Delta AIC > 2$ ) for the most occurring prey in the system and in the diets of shorebirds, in counts (n), biomass (b), or presence/absence (P/A) depending on the species. Six models are compared; the 'Full' model represents the interaction of ET and MGS and their quadratic terms. Distribution family of the data is detailed, 'NB' for negative binomial, 'B' for binomial, 'G' for Gaussian. Abbreviations refer to Table 1.

<b>Total resource</b>							
<b>(1) HYD- (b)</b>		<b>(2) MAC - (b)</b>		<b>(3) CER - (n)</b>		<b>(4) NHO - (n)</b>	
Family	NB	Family	G	Family	NB	Family	NB
Model	$\Delta AIC$	Model	$\Delta AIC$	Model	$\Delta AIC$	Model	$\Delta AIC$
<b>Full</b>	<b>0</b>	<b>ET</b>	<b>0</b>	<b>MGS</b>	<b>0</b>	<b>ET × MGS</b>	<b>0</b>
ET	30.88	ET + MGS	0.35	ET + MGS	1.46	Full	0
ET + MGS	30.15	ET × MGS	0.89	ET	4.12	MGS	14.38
ET × MGS	32.07	Full	1.23	ET × MGS	3.42	ET + MGS	15.25
MGS	141.32	Null	7.69	Full	3.42	Null	21.69
Null	144.69	MGS	9.66	Null	6.2	ET	23.68
<b>(5) SCR - (n)</b>		<b>(6) MAC - (n)</b>		<b>(7) Benthos - P/A</b>			
Family	NB	Family	NB	Family	B		
Model	$\Delta AIC$	Model	$\Delta AIC$	Model	$\Delta AIC$		
<b>ET + MGS</b>	<b>0</b>	<b>ET</b>	<b>0</b>	<b>ET</b>	<b>0</b>		
ET × MGS	1.00	ET + MGS	1.95	ET + MGS	1.78		
Full	1.00	ET × MGS	3.87	ET × MGS	0.92		
ET	18.46	Full	3.87	Full	0.92		
MGS	30.30	Null	30.88	MGS	19.06		
Null	35.93	MGS	30.17	Null	23.18		
<b>Available resource for <i>C. alpina</i></b>							
<b>(1) HYH - (b)</b>		<b>(2) MAC - (b)</b>		<b>(3) CER - (n)</b>		<b>(4) NHO - (n)</b>	
Family	NB	Family	G	Family	NB	Family	NB
Model	$\Delta AIC$	Model	$\Delta AIC$	Model	$\Delta AIC$	Model	$\Delta AIC$
<b>Full</b>	<b>0</b>	<b>ET + MGS</b>	<b>0</b>	<b>MGS</b>	<b>0</b>	<b>ET × MGS</b>	<b>0</b>
ET	30.88	ET × MGS	1.62	ET	1.85	Full	0
ET + MGS	30.15	Full	0.57	ET + MGS	1.50	MGS	14.92
ET × MGS	32.07	MGS	4.51	Null	3.13	ET + MGS	16.19
MGS	141.32	ET	4.64	ET × MGS	3.48	Null	19.36
Null	144.69	Null	17.36	Full	3.48	ET	21.35
<b>(5) SCR - (n)</b>		<b>(6) MAC - (n)</b>		<b>(7) Benthos - P/A</b>			
Family	NB	Family	NB	Family	B		
Model	$\Delta AIC$	Model	$\Delta AIC$	Model	$\Delta AIC$		
<b>ET + MGS</b>	<b>0</b>	<b>ET</b>	<b>0</b>	<b>ET</b>	<b>0</b>		
ET	2.2	ET + MGS	0.49	ET + MGS	1.83		
ET × MGS	1.85	ET × MGS	2.19	ET × MGS	3.83		
Full	1.85	Full	2.19	Full	3.83		
Null	7.73	MGS	16.26	MGS	50.02		
MGS	8.69	Null	19.63	Null	61.24		
<b>Available resource for <i>C. canutus</i></b>							
<b>(1) HYD - (b)</b>		<b>(2) MAC - (b)</b>		<b>(3) CER - (n)</b>		<b>(4) NHO - (n)*</b>	
Family	NB	Family	G	Family	NB	Family	NB
Model	$\Delta AIC$	Model	$\Delta AIC$	Model	$\Delta AIC$	Model	$\Delta AIC$
<b>Full</b>	<b>0</b>	<b>ET</b>	<b>0</b>	<b>MGS</b>	<b>0</b>	-	-
ET	30.88	ET + MGS	0.14	ET	1.13	-	-
ET + MGS	30.15	ET × MGS	2.04	ET + MGS	0.26	-	-
ET × MGS	32.07	Full	2.29	ET × MGS	2.25	-	-
MGS	141.32	Null	8.23	Full	2.25	-	-
Null	144.69	MGS	10.23	Null	4.95	-	-
<b>(5) SCR - (n)</b>		<b>(6) MAC - (n)</b>		<b>(7) Benthos - P/A</b>			
Family	NB	Family	NB	Family	B		
Model	$\Delta AIC$	Model	$\Delta AIC$	Model	$\Delta AIC$		
<b>ET</b>	<b>0</b>	<b>ET</b>	<b>0</b>	<b>ET</b>	<b>0</b>		
ET + MGS	1.23	ET + MGS	2.00	ET + MGS	0.93		
ET × MGS	0.54	ET × MGS	4.00	ET × MGS	1.73		
Full	0.54	Full	4.00	Full	1.73		
Null	5.03	Null	27.93	MGS	66.85		
MGS	6.29	MGS	26.43	Null	71.94		

\*Species not ingested by *C. canutus*.

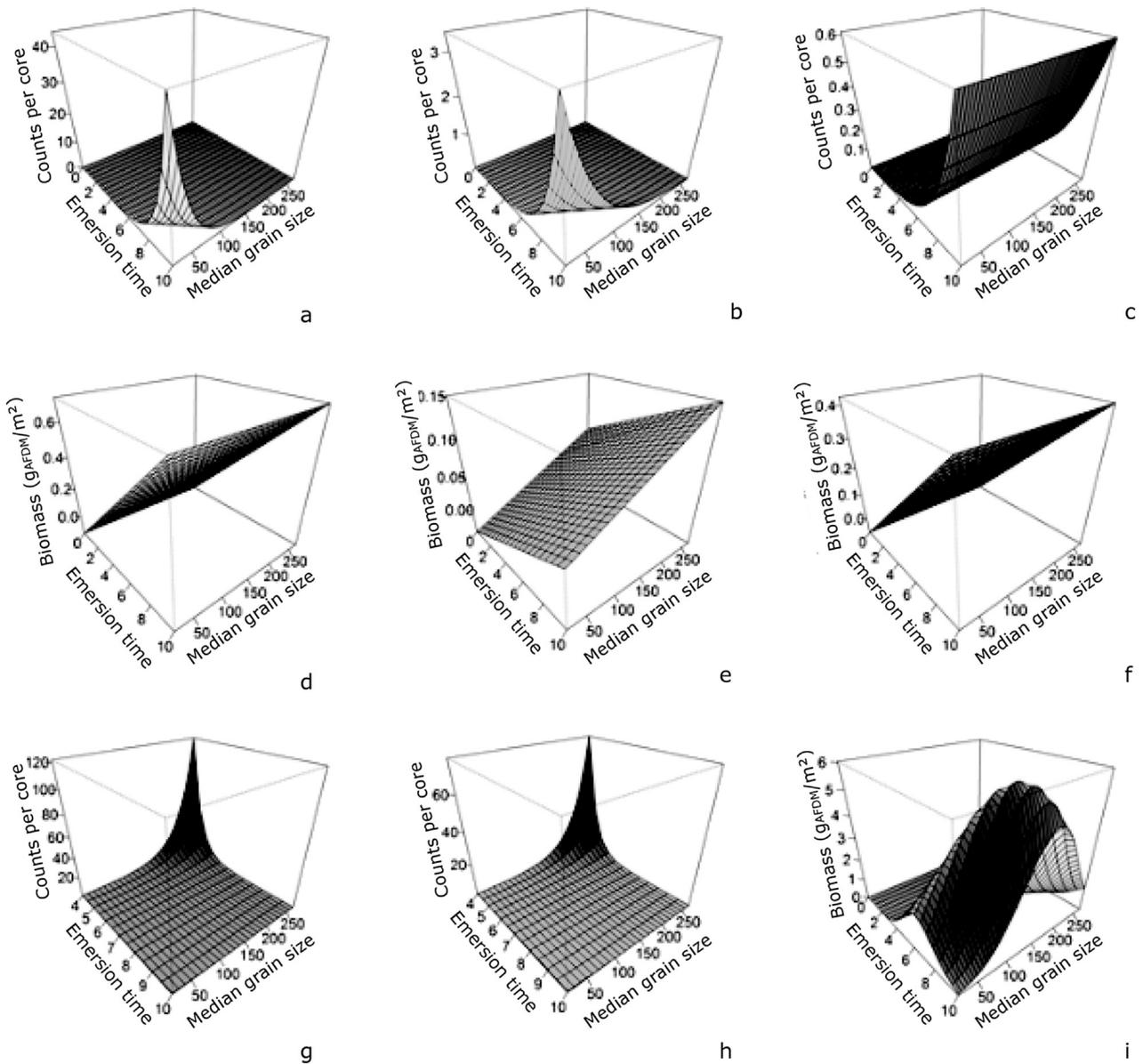
waterbirds (Takekawa et al., 2009).

Can the potential trophic niche described here be directly linked with the spatial distribution of shorebirds in the field? One study



**Fig. 4.** (A) *M. balthica* abundances distribution predicted along ET gradient, (b) benthic macrofauna absence probability modelled along ET gradient, and (c) *C. edule* abundances modelled distribution depending on MGS. Lines indicate the predictions and dots indicate the original data. In black the distribution for the total resource, in grey the resources available for dunlin, and in lighter grey the resources available for red knot.

could directly link sediment characteristics to bird densities (Yates et al., 1993), and another succeeded in linking habitat loss to shorebird densities (Kraan et al., 2009). In the latter study, a solution to link benthic resource with bird distribution was developed using intake rates based on a functional response model to assess variations in suitable foraging area due to cockles dredging, and not directly using environmental variables. Such studies cannot be generalised and are based on local peculiarities. On a small spatial scale, for predicting foraging areas, one needs to assess prey preference through the analysis of quality (van Gils et al., 2006). Difficulties appear when we want to predict bird densities in time and



**Fig. 5.** (A) *S. plana* abundances modelled distribution along two environmental gradients for total resource, (b) resources available for dunlin, and (c) depending on ET for red knot; (d) *M. balthica* biomass modelled distribution along ET gradient for the total resource, (e) along ET and MGS for dunlin, and (f) only ET for red knot; (g) *N. hombergii* abundances modelled distribution along two environmental gradients, MGS and ET, for the total resource and (h) for the resources available for dunlin; (i) *H. ulvae* modelled distribution along two environmental gradients, MGS and ET, for the total resource, the resources available for dunlin, and the resources available for red knot.

space. Such models cannot deal with complex interspecific and intraspecific interactions (Folmer et al., 2012), as well as flyway population trends (Rolet et al., 2015).

Anthropogenic causes to this north-south strong granulometric gradient described in this study is plausible and can be the consequence of beach replenishment given north south longshore drift together with beach replenishment since the late 1980's, this gradient can be the consequence of increased erosion, with long shore transport also directed from north to south (Schoeman et al., 2004). Multiple studies have addressed the issue of human activity (e.g. dredging, aquaculture, and coastal management) directly impacting mudflat macrofauna through hydrodynamics and sediment characteristics (Leguerrier et al., 2004; Kraan et al., 2007; Masero et al., 2008; Compton et al., 2009). Few studies have integrated higher trophic levels into the picture, and revealed the

potential of macrobenthos as a bioindicator of habitat characteristics as well as an indicator of available food resources of top-predators or densities of shorebirds (Yates et al., 1993; Newton, 1998; Kraan et al., 2009). However our study could not directly connect beach replenishment, to macrobenthos density and shorebird distribution on the mudflat; this link could only be tested by reiterating the same field and laboratory effort in the future.

However, the present study emphasises the integrative potential of macrobenthic fauna to assess the impacts of habitat change (e.g. dikes, storms, land use) on intertidal and/or estuarine mudflat ecological functioning and approach the complex interactions among physical gradients, prey habitat preferences, and potential niche of two dominant shorebird species. We aim at supporting the idea that any change in the habitat (e.g. in grain size distribution, inundation time, or hydrodynamics) implies direct changes in

benthic abundances and biomass (Cozzoli et al., 2014) and could cascade up to the highest trophic levels (e.g. shorebirds distribution and densities, in our case). However, insufficient data were available to our knowledge for our study site concerning the temporal evolution of the gradients and the spatial distribution of shorebirds in the bay to conduct an integrative study. Local or national conservation measures for shorebird populations should not rely only on total feeding resource estimates or single-species carrying capacity calculations. Shorebirds experience competition and flexible foraging behaviour, and as migratory species, their population is affected by a large set of variables (van de Kam et al., 2004). Protecting these long distance migrants supposes a thorough understanding of their behaviour and long-term monitoring of the ecosystems they inhabit.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.ecss.2016.03.013>.

## References

- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Trans. Automatic Control* 19 (6), 716–723.
- Anderson, M.J., 2008. Animal-sediment relationships re-visited: characterising species' distributions along an environmental gradient using canonical analysis and quantile regression splines. *J. Exp. Mar. Biol. Ecol.* 366 (1), 16–27.
- Armonies, W., Hartke, D., 1995. Floating of mud snails *Hydrobia ulvae* in tidal waters of the Wadden Sea, and its implications in distribution patterns. *Helgoländer Meeresunters.* 49 (1–4), 529–538.
- Baker, M.C., Baker, A.E.M., 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. *Ecol. Monogr.* 43 (2), 193–212.
- Beukema, J., 1993. Successive changes in distribution patterns as an adaptive strategy in the bivalve *Macoma balthica* (L.) in the Wadden Sea. *Helgoländer Meeresunters.* 47 (3), 287–304.
- Bijleveld, A.I., van Gils, J.A., et al., 2012. Designing a benthic monitoring programme with multiple conflicting objectives. *Methods Ecol. Evol.* 3 (3), 526–536.
- Bocher, P., Piersma, T., et al., 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 (2), 577–594.
- Bocher, P., Robin, F., et al., 2014. Trophic resource partitioning within a shorebird community feeding on intertidal mudflat habitats. *J. Sea Res.* 92, 115–124.
- Burnham, K.P., Anderson, D.R., et al., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65 (1), 23–35.
- Compton, T.J., Troost, T.A., et al., 2008. Distributional overlap rather than habitat differentiation characterizes co-occurrence of bivalves in intertidal soft sediment systems. *Mar. Ecol. Prog. Ser.* 373, 25–35.
- Compton, T.J., Troost, T.A., et al., 2009. Repeatable sediment associations of burrowing bivalves across six European tidal flat systems. *Mar. Ecol. Prog. Ser.* 382, 87–98.
- Compton, T.J., Holthuijsen, S., et al., 2013. Distinctly variable mudscapes: distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. *J. Sea Res.* 82, 103–116.
- Cozzoli, F., Eelkema, M., et al., 2014. A mixed modeling approach to predict the effect of environmental modification on species distributions. *PLoS One* 9 (2).
- Creutzberg, F., Wapenaar, P., et al., 1984. Distribution and density of the benthic fauna in the southern North Sea in relation to bottom characteristics and hydrographic conditions. *Rapp. P.-v. Réun. Cons. Perm. Int. Explor. Mer.* 183, 101–110.
- Dankers, N., Beukema, J.J., 1981. Distributional patterns of macrozoobenthic species in relation to some environmental factors. In: *Invertebrates in the Wadden Sea*, Stichting Veth to Steun Aan Waddenonderzoek. N. Dankers, H. Kuhl and W. J. Wolff. Leiden.
- Delaney, S., Scott, D.A., et al., 2009. *An Atlas of Wader Populations in Africa and Western Eurasia*. International Wageningen, Wetlands.
- R: a language and environment for statistical computing. In: R Development Core Team (Ed.), 2015. R Foundation for Statistical Computing, Vienna, Austria.
- Drouet, S., 2014. Écologie trophique du bécasseau variable, *Calidris alpina*, en Baie de Bourgneuf (France): relation avec le microphytobenthos, Nantes, p. 254. PhD Thesis.
- Folmer, E.O., Olf, H., et al., 2012. The spatial distribution of flocking foragers: disentangling the effects of food availability, interference and conspecific attraction by means of spatial autoregressive modeling. *Oikos* 121 (4), 551–561.
- Fossette, S., Gleiss, A.C., et al., 2015. Current-oriented swimming by jellyfish and its role in bloom maintenance. *Curr. Biol.* 25 (3), 342–347.
- Gray, J.S., 1974. Animal-sediment relationships. *Oceanogr. Mar. Biol. Annu. Rev.* 12, 223–261.
- Guizien, K., Dupuy, C., et al., 2014. Microorganism dynamics during a rising tide: disentangling effects of resuspension and mixing with offshore waters above an intertidal mudflat. *J. Mar. Syst.* 129, 178–188.
- Haubois, A.-G., Guarini, J.-M., et al., 2002. Spatio-temporal differentiation in the population structure of *Hydrobia ulvae* on an intertidal mudflat (Marennes-Oléron Bay, France). *J. Mar. Biol. Assoc. U. K.* 82 (04), 605–614.
- Hervouet, J.-M., 2007. *Hydrodynamics of Free Surface Flows: Modelling with the Finite Element Method*. John Wiley & Sons.
- Hutchinson, G.E., 1957. Cold spring harbor symposium on quantitative biology. Concluding Remarks 22, 415–427.
- Hutchinson, G.E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* 145–159.
- Kraan, C., Piersma, T., et al., 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. J. du Conseil* 64 (9), 1735–1742.
- Kraan, C., van Gils, J.A., et al., 2009. Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *J. Animal Ecol.* 78 (6), 1259–1268.
- Kraan, C., Aarts, G., et al., 2010. The role of environmental variables in structuring landscape-scale species distributions in seafloor habitats. *Ecology* 91 (6), 1583–1590.
- Kraan, C., Aarts, G., et al., 2013. Temporal variability of ecological niches: a study on intertidal macrobenthic fauna. *Oikos* 122 (5), 754–760.
- Kuwaie, T., Kibe, E., et al., 2003. Effect of emersion and immersion on the porewater nutrient dynamics of an intertidal sandflat in Tokyo Bay. *Estuar. Coast. Shelf Sci.* 57 (5), 929–940.
- Kuwaie, T., Miyoshi, E., et al., 2010. Foraging mode shift in varying environmental conditions by dunlin *Calidris alpina*. *Mar. Ecol. Prog. Ser.* 406, 281–289.
- Leguerrier, D., Niquil, N., et al., 2004. Modeling the impact of oyster culture on a mudflat food web in Marennes-Oléron Bay (France). *Mar. Ecol. Prog. Ser.* 273, 147–161.
- M'Closkey, R.T., 1976. Community structure in sympatric rodents. *Ecology* 728–739.
- MacArthur, R.H., 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39 (4), 599–619.
- Martins, R.C., Catry, T., et al., 2013. Seasonal Variations in the diet and foraging behaviour of Dunlin *Calidris alpina* in a South European Estuary: improved feeding conditions for northward migrants. *PLoS One* 8 (12), e81174.
- Masero, J.A., Castro, M., et al., 2008. Evaluating impacts of shellfish and baitworm digging on bird populations: short-term negative effects on the availability of the mudsnail *Hydrobia ulvae* to shorebirds. *Biodivers. Conservation* 17 (4), 691–701.
- Moreira, F., 1997. The importance of shorebirds to energy fluxes in a food web of a south European estuary. *Estuar. Coast. Shelf Sci.* 44 (1), 67–78.
- Nebel, S., Thompson, G.J., 2011. The evolution of sexual bill-size dimorphism in shorebirds: a morphometric test of the resource partitioning hypothesis. *Evol. Ecol. Res.* 13 (1), 35–44.
- Newton, I., 1998. *Population Limitation in Birds*. Academic press.
- Nicolle, A., Karpytchev, M., 2007. Evidence for spatially variable friction from tidal amplification and asymmetry in the Pertuis Breton (France). *Cont. Shelf Res.* 27 (18), 2346–2356.
- Nicolle, A., Karpytchev, M., et al., 2009. Amplification of the storm surges in shallow waters of the Pertuis Charentais (bay of Biscay, France). *Ocean. Dyn.* 59 (6), 921–935.
- Multivariable geostatistics in S: the gstat package. In: Pebesma, E.J. (Ed.), *Comput. Geosciences* 30, 683–691.
- Piersma, T., Hoekstra, R., et al., 1993. Scale and intensity of intertidal habitat use by knot *Calidris canutus* in the Western Wadden Sea in relation to food, friends and foes. *Neth. J. Sea Res.* 31 (4), 331–357.
- Quaintenne, G., 2010. Sélection de l'habitat et des ressources trophiques chez le bécasseau maubèche *Calidris canutus*: distribution à l'échelle européenne et particularités des sites d'hivernage français, La Rochelle.
- Rhoads, D.C., Boyer, L.F., 1982. The Effects of Marine Benthos on Physical Properties of Sediments. *Animal-sediment Relations*. Springer, pp. 3–52.
- Rolet, C., Spilmont, N., et al., 2015. Anthropogenic impact on macrobenthic communities and consequences for shorebirds in Northern France: a complex response. *Biol. Conserv.* 184 (0), 396–404.

- Sanders, H.L., 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnol. Oceanogr.* 3 (3), 245–258.
- Santos, C.D., Granadeiro, J.P., et al., 2005. "Feeding ecology of dunlin *Calidris alpina* in a southern European estuary. *Ardeola* 52 (2), 235–252.
- Schoeman, P.K., Hoogewoning, S.E., et al., 2004. "Managing coastal erosion in Europe illustrated by 60 case studies. *Coast. Eng.* 3, 187.
- Schoener, T.W., 1965. The evolution of bill size differences among sympatric congeneric species of birds. *Evolution* 189–213.
- Schoener, T.W., 1974. Resource partitioning in ecological communities. *Science* 185 (4145), 27–39.
- Takekawa, J., Miles, A., et al., 2009. Dietary flexibility in three representative waterbirds across salinity and depth gradients in salt ponds of San Francisco Bay. *Hydrobiologia* 626 (1), 155–168.
- Thrush, S.F., Hewitt, J.E., et al., 2003. Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. *Mar. Ecol. Prog. Ser.* 263 (101), e112.
- Trainor, A.M., Schmitz, O.J., et al., 2014. Enhancing species distribution modeling by characterizing predator-prey interactions. *Ecol. Appl.* 24 (1), 204–216.
- van de Kam, J., Ens, B., et al., 2004. *Shorebirds: an Illustrated Behavioural Ecology*. Utrecht: KNNV Publishers.
- van der Meer, J., 1999. Keeping things in order: multivariate direct gradient analysis of a strongly fluctuating benthic community. *J. Sea Res.* 42 (4), 263–273.
- van Gils, J.A., Piersma, T., et al., 2006. "Shellfish dredging pushes a flexible avian top predator out of a marine protected area. *PLoS Biol.* 4, 12.
- Venables, W.N., Ripley, B.D. (Eds.), 2002. *Modern Applied Statistics with S*, fourth ed. Springer, New York.
- Wells, F.E., 1978. The relationship between environmental variables and the density of the mudsnail *Hydrobia totteni* in a Nova Scotia salt marsh. *J. Molluscan Stud.* 44, 120–129.
- Yates, M., Goss-Custard, J., et al., 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *J. Appl. Ecol.* 599–614.
- Ysebaert, T., Meire, P., et al., 2002. Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. *Mar. Ecol. Prog. Ser.* 225.
- Zwarts, L., 1986. Burying depth of the benthic bivalve *Scrobicularia plana* (da Costa) in relation to siphon-cropping. *J. Exp. Mar. Biol. Ecol.* 101 (1), 25–39.