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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.

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 (μm) and the percentage of silt (fraction < 63 μm) were determined using a Malvern Mastersizer 2000 diffraction laser (particle sizes analysed from 0.04 to 2000 μm). 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 Karpytchev, 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.