

How do macrobenthic resources concentrate foraging waders in large megatidal sandflats?



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ARTICLE INFO

Article history:

Received 9 October 2015

Received in revised form

7 March 2016

Accepted 31 May 2016

Available online 1 June 2016

Keywords:

Waders

Benthos

Foraging behavior

Sandflat

Megatidal environment

ABSTRACT

The relationship between foraging shorebirds, macrobenthos and sedimentary parameters has been widely studied across Western Europe. Megatidal areas have large zones uncovered when the water retreats. Consequently, in such cases, the tide also influences foraging activities. This paper examines the use of an intertidal space by waders to define how macrobenthic resource concentrates foraging activity of birds in a large megatidal sandflat. This approach combines accurate spatial distribution of waders (Oystercatcher, Eurasian curlew, Bar-tailed Godwit and Redknot) according to their activity with ecological/biological parameters. A differential exploitation of the flat is clearly shown, with macrobenthic biomass appearing as one of the main explanatory factor for the four species considered on the western part of the bay and altitude (shore elevation) in the eastern part. The novelty of this study relates to the large area, also presumed to be a functional unit, while considering at the same time the singularities of the different parts of the flat. This multi-scale approach identifies important factors influencing the differential distribution patterns observed. The different selected parameters present an important variability in their contribution, underlining the complexity of explaining the distribution of foraging birds. Consequently, the study of such complex phenomena needs to consider additional variables to improve the relevance of explanatory models.

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1. Introduction

The macrobenthos is an essential element for the functioning of estuarine and intertidal ecosystems. Many authors have highlighted the predominant function of this compartment in benthic and pelagic foodwebs, in particular its nutritional importance for coastal birds (Goss-Custard, 1980; Goss-Custard et al., 2006; Baird et al., 1985; De Smet et al., 2013). Waders present a spatial distribution strongly connected to the local food supply (van de Kam et al., 2004). Consequently, they depend on benthic assemblages characterized by specific species' composition presenting high biomasses (Evans et al., 1984; McLusky and Elliott, 2004; Moreira, 1997; Newton, 1998) especially during migration (Piersma and

Jukema, 1990; Piersma et al., 1993) and cold periods (Kersten and Piersma, 1987; Piersma, 1990; Degré, 2006). Under natural conditions, one of the difficulties in investigating such trophic relationships is to clearly identify, at a given time, the resources and their exploitation modalities by predators (Ponsoero and Le Mao, 2011). Furthermore, nearby roosting sites also play a key role in the presence of an abundant and diverse wader community in terms of species and of life cycle stages (Triplet et al., 2003; Granadeiro et al., 2007; Le Corre et al., 2009).

Shorebirds feeding on intertidal areas are also highly mobile. Indeed, the wader prey are influenced by the tide, consequently, a similar tidal rhythm can be observed in these birds' foraging activity. (McLusky and Elliott, 2004). Each habitat has then a characteristic temporal pattern of use by shorebirds related to tide time rather than feeding time as shown by Burger et al. (1977). The way waders use space in terms of intensity is not only a function of the time during which the areas are available, but also of the bird

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behavior in relation to the advancing and receding tide (Granadeiro et al., 2006). Trophic competitive exclusion may be avoided because species move from point to point without fully exploiting the available food reserves (Recher, 1966). Folmer and Piersma (2012) showed that the spatial distribution of foraging waders also depends on the endogenous social variable of aggregation made up of the opposing mechanisms of conspecific attraction and repulsion. The shorebird tendency to aggregate causes suitable habitat to remain unoccupied (Folmer et al., 2010; Folmer and Piersma, 2012). Tidal cycles which cause cyclic spatial and temporal variability in their feeding grounds, strongly constrain the foraging activity of estuarine species, and particularly of waders (Fleischer, 1983; van de Kam et al., 2004; van Gils et al., 2005; Granadeiro et al., 2006; van Gils et al., 2006). The presence of feeding waders in areas covered by a thin layer of surface water (Palomo et al., 2003) or where the sediment is wet (Kelsey and Hassall, 1989), is frequently attributed to a higher level of prey activity in such areas (Pienkowski, 1983). These conclusions were confirmed by Rosa et al. (2007) which showed that sediment drainage and associated prey rhythms greatly influenced wader foraging patterns on sediment flats. In a study carried out at a small spatial scale in the Tagus estuary, Granadeiro et al. (2007) concluded that factors mostly affecting the shorebird's distribution are the exposure period, the sediment type and the shell bank's extent. Unfortunately, most of these papers examined the distribution of birds feeding in estuaries or bays only in relation to environmental factors (Bryant, 1979; Symonds et al., 1984; Goss-Custard and Yates, 1992; Yates et al., 1993; Moreira, 1993; Scheiffarth et al., 1996; Granadeiro et al., 2004, 2007; Rosa et al., 2007), without considering the macrobenthic fauna. Preferably, such studies should be based on data collected over a large fraction of the flats but resource and logistic constraints often force researchers to reduce sampling (e.g. by concentrating the sampling effort near the coast line). Consequently, important factors influencing shorebird broad-scale distribution patterns can be overlooked (Granadeiro et al., 2007).

In this study, we examine, inside a presumed functional unit, how waders use intertidal space. The goal is to define how macrobenthic resources influence birds foraging activity in a large megatidal sandflat. This approach is based on the combination of accurate spatial distribution of waders depending on their activity and ecological/biological parameters.

2. Material and methods

2.1. Study area

The field work was conducted in the bay of Saint-Brieuc (800 km² up to the isobaths 30 m, divided in two parts by the bays of Yffiniac and Morieux), France (48°32'N; 02°40'W). The study area enclosed about 2900 ha of tidal flats mainly dominated by fine to medium sands and under the influence of a semi-diurnal megatidal regime (Fig. 1). In this zone, tidal range varies between 4 m at neap tides and nearly 13 m during spring tide. From 1998 to 2008, the bay of Saint-Brieuc was home to over 20,000 shorebirds during the winter months (Sturbois and Ponsero, 2014). Furthermore, four benthic assemblages are distributed in belts along an inshore-offshore gradient of increasing grain-size sediments [see Sturbois et al., 2015 for more details]. Benthic populations are particularly stable in this area as shown for the cockle *Cerastoderma edule* (Ponsero et al., 2009). During overwintering, waders represent one third of the total number of birds, and some species can reach more than 1% of the overwintering national populations, according to the threshold defined in the Ramsar convention (Delany et al., 2009). Waders are dominated by seven species: eurasian Oystercatcher *Haematopus ostralegus*, eurasian Curlew

Numenius arquata, grey Plover *Pluvialis arquata*, Redknot *Calidris canutus*, Dunlin *Calidris alpina*, Sanderling *Calidris alba*, and Bar-tailed Godwit *Limosa lapponica*. During cold winters, the site can be of international interest for Redknot and Bar-tail Godwit. Since 1998, 1140 ha of tidal flats are protected as a National Nature Reserve.

2.2. Distribution of macrobenthic resources and sediment analysis

The macrofaunal distribution was assessed during a survey conducted in October 2010 (Fig. 1). At this date, 131 stations (located inside and outside of the reserve) covering 2900 ha of intertidal area were sampled according to a regular sampling network (see Godet et al., 2009a). At each station, three 25 cm deep sediment samples were collected for macrobenthic analysis, using a 17.6 cm² cylindrical handcorer. The content of the cores were gently sieved on site using a 1-mm square mesh sieve. The retained material was preserved for analysis in 5% buffered formaldehyde with added rose Bengal. A visual description of the sediment type was recorded. The macrofauna were identified to the highest possible taxonomic separation (usually species) and counted. The energetic value (biomass) of each taxon was determined as g of AFDW per 0.1 m² (loss of weight of dry organisms after 6 h at 520 °C). Two samples of sediment (surface of 3.2 cm², depth of 5 cm) were collected from additional cores and subsequently analyzed for grain size distribution and organic matter content. Sediment samples were cleaned with water and left to settle for 48 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; Salonen, 1979). Additionally, the sediment shear stress resistance was measured with a scissometer at a depth of 10 cm as a proxy for cohesion (Grabowski et al., 2011). All replicates were collected at a maximal distance of 2 m from each station, using GPS position-fixing (GPS Etrex Garmin).

2.3. Bird counts and localization of foraging areas

Considering the large scale of the study area, observations were carried out during winters 2010/11 and 2011/12 in the bays of Yffiniac and Morieux respectively (Fig. 1). A particular focus was made on four of the most abundant wader species identified as main consumers on the station and present in sufficiently large numbers for adequate statistical analyses: eurasian Oystercatcher, eurasian Curlew, Bar-tailed Godwit, Redknot (Ponsero and Le Mao, 2011).

Birds were counted regularly during daytime during the months of January and February 2010, 2011 and 2012, using a telescope (Kite SP-ED 80). The number of feeding birds was recorded during a total of 54 tidal cycles, under conditions varying from neap to spring tides. For each bird group, the species, the total number of feeding and roosting individuals and the observation time was noted. The localization of a bird group was calculated using a trigonometric formula based on the observer's geographical position (determined with a Global Positioning System) and measures of the bird group distance and its angle with the North:

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

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

Distance to observers and viewing angle with the North were provided using laser range-finding binoculars (Newcon LRB 3000 pro, 7 × 40). The binocular model used was able to measure a distance up to 700 m which limited the disturbance of birds.

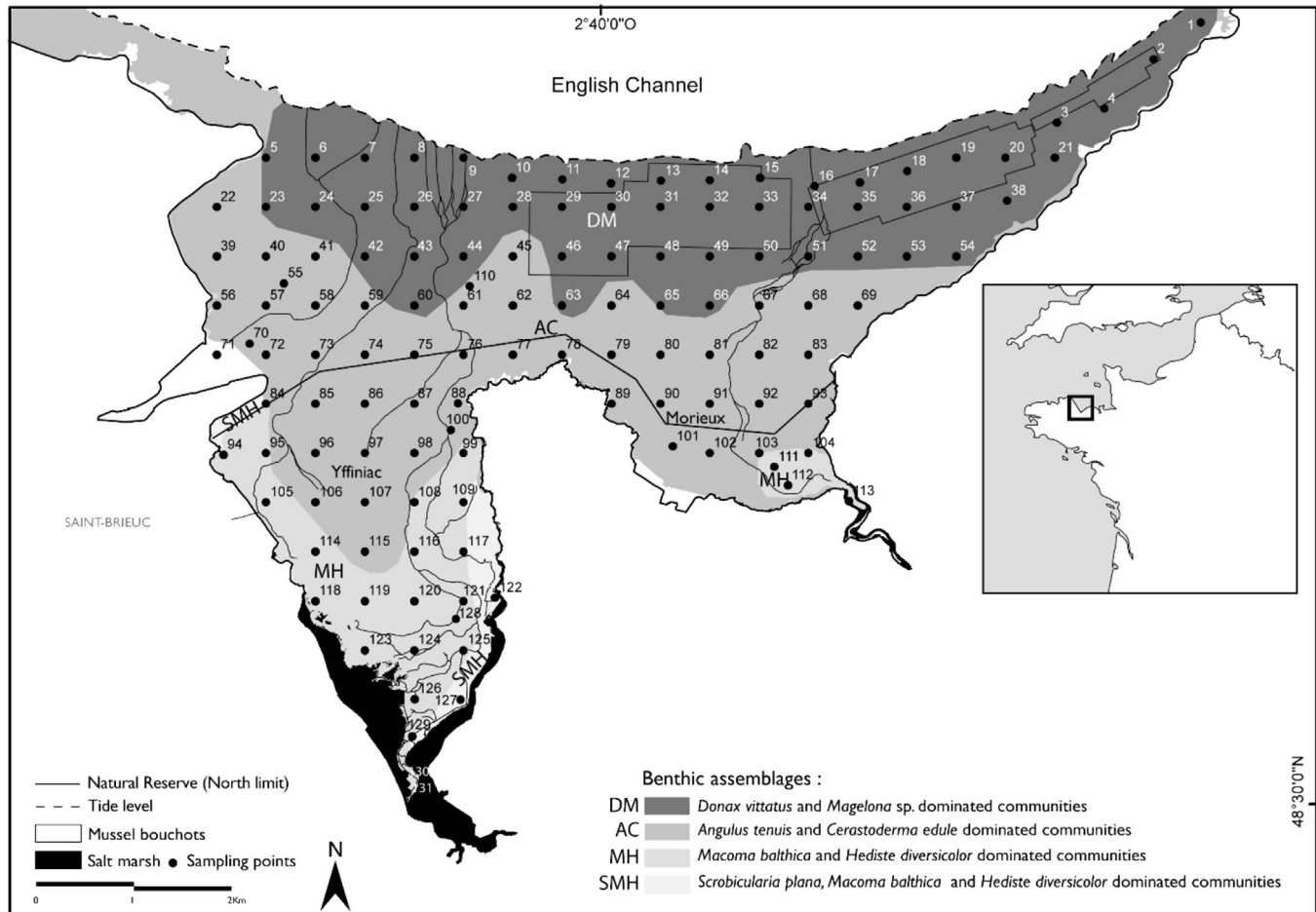


Fig. 1. Benthic intertidal assemblages identified in the bay of Saint-Brieuc. Points correspond to the 131 stations of the regular sampling network.

2.4. Data analysis

All the statistical analysis was performed with R v. 3.1.2 (R Development Core Team, 2015). The statistical description of sediments, based on grain-size distributions, was computed with the R package 'G2Sd' (see Fournier et al., 2014). Linear regression models were used to test the putative effect of the altitude (shore elevation) on the distribution of sedimentary parameters such as median grain size, mean, shear stress resistance of sediment or mud (<40 μm) content. The normality of residuals was checked with a Shapiro-Wilk test.

The mean values of the number of species (S), total abundance (N), Shannon diversity (H'), Simpson diversity (D'), Pielou evenness (J) were computed for all stations. Macrobenthic assemblages were defined previously in Sturbois et al. (2015) and presented in Fig. 1. The relationship between richness, abundance, total biomass, diversity indices (Shannon index, Simpson Index, Pielou evenness) of the benthic macrofauna and environmental parameters were analyzed with multiple linear regression models. The best linear models were selected using the 'regsubsets' function of the R package 'leaps', which plots a measure of fit against subset size (see Miller, 2002). The 'regsubsets' algorithm enables to select the optimal combination of factors that best 'explains' the variance of a variable.

We used a Poisson generalized regression modeling approach to evaluate the relation between the cumulated presence of wader species during the 54 headcounts between January 2010 and

February 2012 and environmental [mean grain size (MEA), median grain size (MED), altitude (shore elevation) (ALT), shear stress resistance of sediment (STR), organic matter of sediment (MOR), water content of sediment (H2O)] and ecologic parameters [richness (RICH), total abundance (ABUN), total biomass of benthic macrofauna (BIOT), biomass of *Cerastoderma edule* (<10 mm) (BIOC1), biomass of *Cerastoderma edule* (15–25 mm) (BIOC2), biomass of other bivalves (BIOB) and biomass of other benthic organisms (BIOO)]. *C. edule* was considered separately regarding the high biomass value (56.3% of total biomass) measured in the mudflat. Maximum likelihood (r2ML) and Cragg and Uhler's (r2CU) Pseudo- R^2 were calculated with the R package 'pscl' (see Jackman, 2015). We used a logistic regression modeling approach to evaluate the spatial exploitation modalities of the different wader species (McCullagh and Nelder, 1989). McFadden (r2MF) Pseudo- R^2 coefficient was calculated with the R package 'pscl' (Jackman, 2015).

3. Results

3.1. Sediment distribution

A significant effect of the altitude (shore elevation) on several sedimentary parameters was demonstrated using linear regression models, but the low R^2 value reflects a high level of variation. The mean grain size ($F_{(1, 127)} = 7.866, p < 0.01, R^2 = 0.05$), the median grain size ($F_{(1, 127)} = 7.486, p < 0.01, R^2 = 0.05$) and the shear stress resistance ($F_{(1, 127)} = 31.31, p < 0.01, R^2 = 0.14$) tend to decrease in

relation to the altitude (shore elevation). The mud content increases with the altitude (shore elevation) ($F_{(1, 127)} = 7.891, p < 0.01, R^2 = 0.05$). A multiple linear regression shows that shear stress resistance seems to decrease significantly with altitude (shore elevation), median grain size and water content of sediment ($F_{(6, 122)} = 5.933, p < 0.001, R^2 = 0.18$).

3.2. Biomass distribution

The mean biomass value in the whole study area is $5.03 \text{ g m}^{-2} \pm 8.09$ and it is strongly correlated with bivalve biomass ($S = 121,270; p < 0.001$). Biomass values are significantly higher in Yffiniac ($7.85 \text{ g m}^{-2} \pm 9.96$) than in Morieux bay ($1.56 \text{ g m}^{-2} \pm 1.81$) ($F_{(1,127)} = 23.46, p < 0.001$). Difference is mainly due to *Cerastoderma edule* ($5.02 \text{ g m}^{-2} \pm 7.61$ and $0.16 \text{ g m}^{-2} \pm 0.58$) and in a lesser extent to the others bivalves ($1.12 \text{ g m}^{-2} \pm 4.61$ and $0.40 \text{ g m}^{-2} \pm 0.78$) and annelids ($1.71 \text{ g m}^{-2} \pm 4.43$ and 1.01 ± 1.38).

3.3. Relation between biological variables and environmental parameters

The total richness is positively correlated with median grain size ($F_{(3, 125)} = 22.58, p < 0.001$). The global abundance is positively correlated with the sorting of sediment ($F_{(6, 122)} = 6.642, p < 0.001$) and negatively correlated with the sediment median grain size ($p < 0.05$). The total biomass is positively correlated with the sediment organic matter content ($F_{(3, 122)} = 11.99, p < 0.001$) and the sediment median grain size ($p < 0.01$). Finally, the diversity (Shannon index) is positively correlated with the sediment median grain size ($F_{(4, 124)} = 19.7, p < 0.001$) and negatively correlated with the altitude (shore elevation) ($p < 0.001$).

3.4. Relation between waders and environmental and biological parameters

The factors most explaining the Oystercatcher presence are the altitude (shore elevation) ($p < 0.05$), the organic matter content ($p < 0.01$), the macrobenthos total biomass ($p < 0.001$) and the benthic macrofauna biomass excluding bivalves (Null deviance: 340.66 on 128 df; Residual deviance: 265.46 on 115 df. AIC: 546.25. r2ML: 44%, r2CU: 44% see Table 1).

Table 1

Result of the Poisson regression for the Oystercatcher. $0 < p < 0.001$ (***); $0.001 < p < 0.01$ (**); $0.01 < p < 0.05$ (*); $0.05 < p < 0.1$ (.). Null deviance: 340.66 on 128 df; Residual deviance: 265.46 on 115 df. AIC: 546.25. r2ML: 44%, r2CU: 44%. MEA: mean grain-size of sediment; MED: median grain size; ALT: altitude (shore elevation); STR: shear stress resistance; MOR: organic matter of sediment; H2O: water content of sediment; RICH: richness; ABUN: total abundance; BIOT: total biomass of benthic macrofauna; BIOB: total biomass of bivalves except *Cerastoderma edule*; BIOC: total biomass of benthic macrofauna except bivalves; BIOC1: total biomass of *C. edule* (<10 mm); BIOC2: total biomass of *C. edule* (15–25 mm).

	Estimate	Std. error	z value ²	Pr(>r)
(Intercept)	-0.3197565	1.1179183	-0.286	0.77486
MEA	0.0000438	0.0010195	0.043	0.96573
MED	0.0123173	0.0063370	1.944	0.05193.
ALT	0.0785106	0.0310502	2.529	0.01145 *
STR	0.0034907	0.0834056	0.042	0.96662
MOR	-2.0117009	0.7728592	-2.603	0.00924 **
H2O	0.0031136	0.0126700	0.246	0.80588
RICH	-0.0160452	0.0190788	-0.841	0.40035
ABUN	-0.0001926	0.0001284	-1.500	0.13366
BIOT	0.0487339	0.0080401	6.061	1.35e-09 ***
BIOB	-0.0512041	0.0483713	-1.059	0.28980
BIOC	-0.0608961	0.0233600	-2.607	0.00914 **
BIOC1	-2.5403100	2.9671243	-0.856	0.39191
BIOC2	0.1637277	0.3160671	0.518	0.60445

The factors most explaining the Bar-tailed Godwit presence are the mean grain size ($p < 0.05$), the shear stress resistance ($p < 0.01$), the sediment water content ($p < 0.05$), the richness ($p < 0.01$), the macrobenthos total biomass ($p < 0.001$), the macrobenthos biomass excluding bivalves ($p < 0.001$) and the small common cockle biomass (*Cerastoderma edule*) ($p < 0.01$) (Null deviance: 273.96 on 128 df; Residual deviance: 168.27 on 115 df. AIC: 306.32. r2ML: 56%, r2CU: 59% see Table 2).

The factors most explaining the Redknot presence are the sediment median grain size ($p < 0.01$), the altitude (shore elevation) ($p < 0.001$), the sediment organic matter content ($p < 0.01$), the total abundance ($p < 0.05$), the total macrobenthos biomass ($p < 0.001$), the benthic macrofauna biomass excluding bivalves ($p < 0.05$), the biomass of small common cockles (*Cerastoderma edule*, $p < 0.01$) and the biomass of large common cockles ($p < 0.05$) (Null deviance: 326.26 on 128 df; Residual deviance: 226.33 on 115 df. AIC: 463.46. r2ML: 54%, r2CU: 54% see Table 3).

The factors most explaining the presence of the eurasian Curlew are the altitude (shore elevation) ($p < 0.01$), the sediment organic matter content ($p < 0.05$) and the macrobenthos total biomass ($p < 0.001$) (Null deviance: 297.28 on 128 df; Residual deviance: 241.23 on 115 df. AIC: 509.71. r2ML: 35%, r2CU: 35% see Table 4).

3.5. Spatial distribution of foraging waders

Spatial analysis of the bird distribution shows the existence of two main patches, one in the western (Yffiniac) and the other in the eastern (Morieux) part of the Saint-Brieuc bay, with a deficit of foraging birds in Morieux especially for Bar-tailed Godwit (only 0.65% of the total foraging birds are observed in Morieux), Oystercatcher (16.28%) and in a lesser extent for Redknot (26.95%). The distribution of Curlew is more balanced. The distribution of Bar-tailed Godwit and Redknot looks patchy and the distribution of eurasian Curlew and Oystercatcher is patchy in Yffiniac and more diffuse in Morieux (Fig. 2).

3.6. Co-exploitation of the flat by waders

The sandflat is not evenly used by the different wader species. Results of the logistic regression (Null deviance: 156.40 on 128 df; Residual deviance: 66.02 on 125 df; AIC: 74.02; $\chi^2_{(3)} = 90.7$;

Table 2

Result of the Poisson regression for the Bar-tailed Godwit. $0 < p < 0.001$ (***); $0.001 < p < 0.01$ (**); $0.01 < p < 0.05$ (*); $0.05 < p < 0.1$ (.). Null deviance: 273.96 on 128 df; Residual deviance: 168.27 on 115 df. AIC: 306.32. r2ML: 56%, r2CU: 59%. MEA: mean grain-size of sediment; MED: median grain size; ALT: altitude (shore elevation); STR: shear stress resistance; MOR: organic matter of sediment; H2O: water content of sediment; RICH: richness; ABUN: total abundance; BIOT: total biomass of benthic macrofauna; BIOB: total biomass of bivalves except *Cerastoderma edule*; BIOC: total biomass of benthic macrofauna except bivalves; BIOC1: total biomass of *C. edule* (<10 mm); BIOC2: total biomass of *C. edule* (15–25 mm).

	Estimate	Std. error	z value ²	Pr(>r)
(Intercept)	-0.0087997	2.2261730	-0.004	0.996846
MEA	-0.0035123	0.0017364	-2.023	0.043102 *
MED	0.0187538	0.0099972	1.876	0.060668.
ALT	0.1206525	0.0617671	1.953	0.050779.
STR	-0.4378411	0.1691989	-2.588	0.009661 **
MOR	-1.4463169	1.3644583	-1.060	0.289148
H2O	-0.0875412	0.0399573	-2.191	0.028461 *
RICH	0.1010384	0.0325173	3.107	0.001889 **
ABUN	-0.0001773	0.0002070	-0.857	0.391585
BIOT	0.0814475	0.0132128	6.164	7.08e-10 ***
BIOB	0.0213667	0.0364459	0.586	0.557702
BIOC	-0.0952007	0.0281146	-3.386	0.000709 ***
BIOC1	9.3714129	3.1204585	3.003	0.002671 **
BIOC2	-0.9236862	0.4771441	-1.936	0.052884.

Table 3

Result of the Poisson regression for the Redknot. $0 < p < 0.001$ (***) ; $0.001 < p < 0.01$ (**); $0.01 < p < 0.05$ (*) ; $0.05 < p < 0.1$ (.). Null deviance: 326.26 on 128 df; Residual deviance: 226.33 on 115 df. AIC: 463.46. r2ML: 54%, r2CU: 54%. MEA: mean grain-size of sediment; MED: median grain size; ALT: altitude (shore elevation); STR: shear stress resistance; MOR: organic matter of sediment; H2O: water content of sediment; RICH: richness; ABUN: total abundance; BIOT: total biomass of benthic macrofauna; BIOB: total biomass of bivalves except *Cerastoderma edule*; BIOC: total biomass of benthic macrofauna except bivalves; BIOC1: total biomass of *C. edule* (<10 mm); BIOC2: total biomass of *C. edule* (15–25 mm).

	Estimate	Std. error	z value ²	Pr(> r)
(Intercept)	-1.6941008	1.2873507	-1.316	0.188188
MEA	-0.0012881	0.0012185	-1.057	0.290451
MED	0.0213185	0.0074194	2.873	0.004062 **
ALT	0.1318445	0.0379411	3.475	0.000511 ***
STR	-0.1028163	0.0999419	-1.029	0.303592
MOR	-3.0537988	0.9759913	-3.129	0.001754 **
H2O	0.0147721	0.0115074	1.284	0.199246
RICH	-0.0036629	0.0221951	-0.165	0.868918
ABUN	-0.0003203	0.0001585	-2.021	0.043278 *
BIOT	0.0622807	0.0091535	6.804	1.02e-11 ***
BIOB	0.0084376	0.0325122	0.260	0.795233
BIOC	-0.0558689	0.0230024	-2.429	0.015148 *
BIOC1	6.7335521	2.1764525	3.094	0.001976 **
BIOC2	-0.6578962	0.3053595	-2.154	0.031201 *

Table 4

Result of the Poisson regression for the eurasian Curlew. $0 < p < 0.001$ (***) ; $0.001 < p < 0.01$ (**); $0.01 < p < 0.05$ (*) ; $0.05 < p < 0.1$ (.). Null deviance: 297.28 on 128 df; Residual deviance: 241.23 on 115 df. AIC: 509.71. r2ML: 35%, r2CU: 35%. MEA: mean grain-size of sediment; MED: median grain size; ALT: altitude (shore elevation); STR: shear stress resistance; MOR: organic matter of sediment; H2O: water content of sediment; RICH: richness; ABUN: total abundance; BIOT: total biomass of benthic macrofauna; BIOB: total biomass of bivalves except *Cerastoderma edule*; BIOC: total biomass of benthic macrofauna except bivalves; BIOC1: total biomass of *C. edule* (<10 mm); BIOC2: total biomass of *C. edule* (15–25 mm).

	Estimate	Std. error	z value ²	Pr(> r)
(Intercept)	-0.4230010	1.2293700	-0.344	0.7308
MEA	-0.0016402	0.0011857	-1.383	0.1666
MED	0.0135974	0.0071422	1.904	0.0569.
ALT	0.1033964	0.0332944	3.106	0.0019 **
STR	-0.0327893	0.0897975	-0.365	0.7150
MOR	-2.0910867	0.8417232	-2.484	0.0130 *
H2O	0.0010671	0.0125864	0.085	0.9324
RICH	-0.0055788	0.0202596	-0.275	0.7830
ABUN	-0.0001548	0.0001218	-1.271	0.2038
BIOT	0.0449887	0.0090429	4.975	6.52e-07 ***
BIOB	0.0146128	0.0238827	0.612	0.5406
BIOC	-0.0421487	0.0231803	-1.818	0.0690.
BIOC1	1.1491195	2.4134586	0.476	0.6340
BIOC2	-0.1027113	0.2822657	-0.364	0.7159

$p < 0.001$; r2MF = 57%) show that the Oystercatcher presence is positively related to the Bar-tailed Godwit (OP = 8.18; $p < 0.05$) and the eurasian Curlew (OP = 68.42; $p < 0.001$). No effect was found with the Redknot.

The Bar-tailed Godwit presence (*L. lapponica*) is positively and significantly (Null deviance: 159.74 on 128 df; Residual deviance: 118.35 on 125 df; AIC: 126.35; $\chi^2_{(3)} = 41.39$; $p < 0.001$; r2MF = 26%) related to the Redknot (OP = 11.53; $p < 0.001$). No effect was found with other wader species.

The Redknot presence is positively and significantly (Null deviance: 175.40 on 128 df; Residual deviance: 135.11 on 125 df; AIC: 143.11; $\chi^2_{(3)} = 40.28$; $p < 0.001$) related to the Bar-tailed Godwit (OP = 11.47; $p < 0.001$; r2MF = 23%). No effect was found with other wader species.

The eurasian Curlew presence is positively and significantly (Null deviance: 164.221 on 128 df; Residual deviance: 83.748 on 125 df; AIC: 91.748; $\chi^2_{(3)} = 80.47$; $p < 0.001$; r2MF = 49%) related to

the Oystercatcher (OP = 65.39; $p < 0.001$). No effect was found with other wader species.

4. Discussion

Our aim was to study the use of intertidal space by waders by combining spatial distribution data with ecological/biological parameters.

4.1. Relation between benthic resources and environmental parameters

Regarding environmental parameters, the bay of Saint-Brieuc is homogeneous, except for two muddy stations, located in the upstream part of Yffiniac and Morieux bays. Sedimentary parameters depend on the altitude (shore elevation), and the mean grain-size. Median grain size and shear stress resistance values decrease with the altitude (shore elevation). The upper shore sheltered character, with reduced hydrodynamic conditions, facilitates the silting process and is responsible for these lower sedimentary values. In the Morieux bay, the high shear stress resistance observed at low bathymetric levels may be linked to the presence of mussel bouchots and the associated circulation of vehicles on the flats.

In the bay of Saint-Brieuc, total macrobenthic specific richness increases along an inshore-offshore gradient, from 7 species in the upper to 43 in the lower parts as already shown by Sturbois et al. (2015). This gradient is characterized by the increase of the median grain size and of the emersion time. The total richness of benthic macrofauna is dramatically constraint by several parameters such as emersion time, temperature/salinity variations and anoxic conditions in most silted areas (Gray and Elliott, 2009). Among the benthic species collected in the flat, *Bathyporeia sarsi* and *Pygospio elegans* mainly occur in the upper levels, *Angulus tenuis* and *Cerastoderma edule* in the intermediate levels and *Donax vittatus* in the lowest part of the shore. The last three species constitute important prey for waders, as largely demonstrated in other European sites (Folmer et al., 2010; Dekinga and Piersma, 1993; Zwarts and Blomert, 1992; Boere and Smit, 1981). Biomass values are five times more elevated in Yffiniac bay than at the Morieux site. The heterogeneous distribution of the biomass corresponds to a heterogeneous distribution of foraging birds.

4.2. Waders and environmental/biological parameters

The explained deviance resulting from our global analysis ranged from 35% to 59%, which allowed us to validate the model. As reported by Granadeiro et al. (2004) from studies carried out in intertidal areas, generalized linear models are relevant in providing accurate shorebird occurrence predictions using physical and biological characteristics. The most relevant environmental/biological factors in explaining the shorebird occurrence are the total biomass (strongly dependent of bivalves) and the altitude (shore elevation) (Godet et al., 2009b). More generally, similar studies have revealed that the distribution of shorebirds in intertidal zones largely depends on the occurrence patterns of their invertebrate prey (Tagus estuary, Granadeiro et al., 2004; Granadeiro et al., 2006) and of annelids and *C. edule* (Wash embayment, West et al., 2007). For the Oystercatcher and the Bar-tailed Godwit, our results are in accordance with conclusions obtained by Folmer et al. (2010) in the Dutch Wadden sea which emphasized the significant influence of food as a predictor. For the eurasian Curlew, our conclusions diverge from Folmer et al. (2010) for which, in the Dutch Wadden Sea (mesotidal regime), biomass parameters are not the exclusive predictors for explaining the presence of this species.

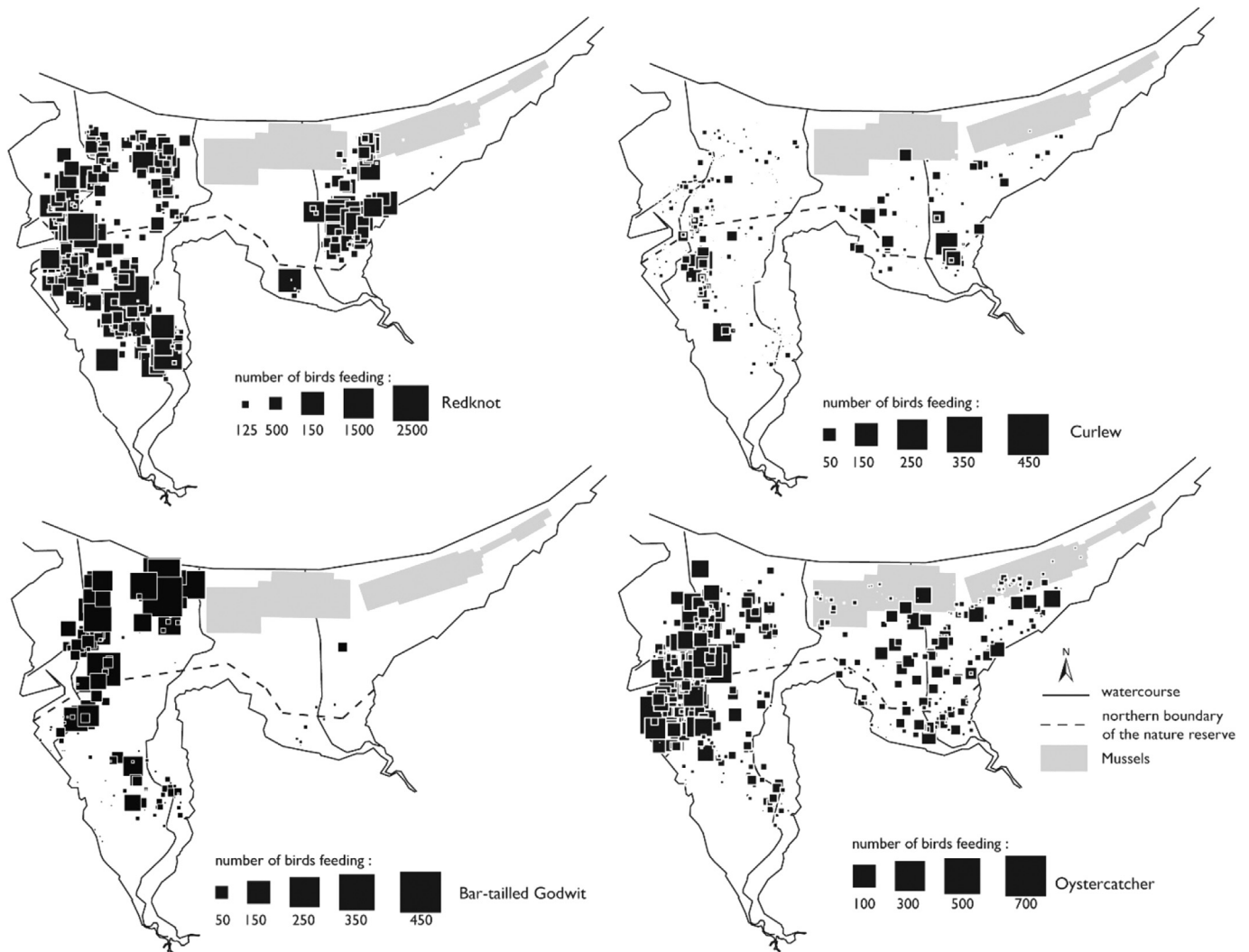


Fig. 2. Foraging area used by Redknot, Curlew, Bar-tailed Godwit, and Oystercatcher in the bay of Saint-Brieuc.

4.3. Oystercatcher

In the bay of Saint-Brieuc, the Oystercatcher distribution is significantly dependent of total biomass, total biomass excluding bivalves and sediment organic matter. Foraging activity spatial analyses show a very patchy and a more diffuse distribution respectively in Yffiniac and Morieux bays. These differences could be shown by the presence, in Morieux, of 320 ha of bouchots on the lowest part of the flat. Swell and waste due to the bouchots exploitation generate a diffuse dispersal of *Mytilus edulis* on the outskirt of the culture area. As a consequence, Oystercatchers were mainly found in the lowest levels in Morieux bay (including bouchots), and their presence had no direct link with non-cultivated species biomass (in opposition with Yffiniac bay, Fig. 2). Mussels, not sampled in our study, are a well-known food for Oystercatchers (Le Rossignol et al., 2011; Nagarajan et al., 2002; Blomert et al., 1996; Norton-Griffiths, 1967; Goss-Custard and Yates, 1992).

4.4. Bar-tailed Godwit

The Bar-tailed Godwit distribution is explained by total biomass, total biomass excluding bivalves and small *C. edule* (<10 mm) biomass and, in a lesser extent, to sediment water content and

mean grain size. As a direct consequence of the sediment drainage, the largest groups of foraging Bar-tailed Godwit were found on the lowest parts of the sandflat, in opposition with other wader species (Fig. 2).

Discussions prevail in the literature on the existence of a tide following behavior in this species (Smith and Evans, 1973; Zwartz, 1988; Turpie, 1994; Tiedemann and Nehls, 1997; Both et al., 2003; Dias, 2008; Rosa et al., 2007; Catry et al., 2012; Duijns et al., 2014). Such behavior could however vary seasonally (as observed by Granadeiro et al. (2007) for several species) and according to the sex of the bird (Duijns et al., 2014).

In Morieux bay, various human activities, including the presence of mussel bouchots and associated circulation, could lead the birds (notably Bar-tailed Godwit) to avoid an exploitable foraging ground, as suggested by Taylor and Bester (1999).

4.5. Redknot

The Redknot patchy distribution is mainly explained by total biomass, altitude (shore elevation), median grain size and small common cockle biomass (Fig. 2). The link between this species and cockles confirms the finding of a recent study conducted in the bay of Saint-Brieuc by Sturbois et al. (2015). They also showed that

Mytilus edulis does not reach high global occurrence frequencies in droppings ($\approx 7.5\%$). Although this prey remains an opportunistic item, its frequency of occurrence increases from the upper to the lower flat because of the mussel predation coming from bouchots (Sturbois et al., 2015). The presence of foraging Redknot in the upper part of the shore may be the direct consequence of the avoidance of the bouchot area and the presence of great abundance of *Angulus tenuis* in the east upper part of the flat.

4.6. Eurasian Curlew

Total biomass and altitude (shore elevation) are the most important factors explaining the eurasian Curlew distribution. In the bay of Saint-Brieuc, the megatidal conditions offer to birds the possibility to forage on large sandflats. Consequently, the lowest levels, limited in surface and exposure time, are very attractive to foraging birds as already observed in the megatidal bay of the Mont Saint-Michel (De Smet et al., 2013). These low levels are characterized by clean medium to fine sands, contrasting with the muddy habitats studied by Folmer et al. (2010) in the Dutch Wadden Sea under mesotidal regime. This species is known to be sensitive to human activities as reported by Spaans et al. (1996), such as mussel culture which seems to be a disturbing activity (Fig. 2).

4.7. Specific exploitation of the flat

The presence on the same foraging ground (simultaneously or not) of the eurasian Curlew and of the Oystercatcher, are positively related. This confirms the concordant distribution patterns observed in the bay for these two species (Fig. 2). Similarly, the presence of Bar-tailed Godwits is positively related to the presence of Redknot and *vice versa*. No effect was found between the Bar-tailed Godwit and other wader species probably due to the tide following behavior of this species.

The unequal use of the flat by the four considered wader species confirms the conclusions of VanDusen et al. (2012), which stipulate that the habitat heterogeneity explains the non-random spatial distribution of foraging shorebirds. In the bay of Saint-Brieuc, only part of the flats benefit of a high protection level (National Nature Reserve). As suggested by Granadeiro et al. (2007) in the Tagus estuary, taking into account additional habitats neighboring the bay of Saint-Brieuc would help to better understand the overall value of this presumed functional unit for foraging shorebirds.

4.8. Alternative factors potentially affecting the bird distribution

According to the ideal free distribution model of Fretwell and Calver (1969), foragers are supposed to aggregate in patches where food is the most abundant. However, several studies have shown that other aspects (i. interference and conspecific attraction, ii. sediment characteristics; iii prey accessibility, iv. tidal regime and v. human disturbance) can influence the bird distribution and could help in the interpretation of the model unexplained variability.

- i The shorebird intrinsic behavior could explain the variability of their distribution in space and time. At a given time, spatial distribution of foraging waders in patchy resource areas also depends on the ability of species to aggregate (for interference and conspecific attraction, see Folmer and Piersma, 2012; Folmer et al., 2011). Consequently, conspecific attraction may lead to large areas with abundant food resources remaining unexploited (Folmer et al., 2011).
- ii The sediment grain-size may contribute to explain shorebird feeding distribution regarding its influence on benthic invertebrate prey. Depending on the sediment shear stress resistance,

the availability of the benthic prey can differ, independently of their abundances and could explain sandflat specific anomalies in shorebird usage (VanDusen et al., 2012).

- iii Estimation of prey availability based on 25 cm deep core samples provides a representative estimation of the accessible prey fraction for long-billed wader (Oystercatcher, Curlew, Bar-tailed Godwit). However, the biomass recorded using the core-sampler may overestimate the actual prey available to short-billed birds as Redknot (Zwarts and Wanink, 1991).
- iv Several studies have already shown the influence of tidal regime on shorebird foraging activities (Granadeiro et al., 2006; 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, benthic invertebrate assemblages are usually distributed along a continuum with regard to the bathymetric gradient (McLachan and Jaramillo, 1995). Consequently, the diet composition in heterogeneous areas can be expected to be more diversified.
- v Foraging birds are sensitive to various human activities, which can lead them to abandon usual foraging zones located on the flat (Mitchell et al., 1988; Hill et al., 1997; Burger et al., 2007; Yasué et al., 2008; Colwell, 2010; van den Hout et al., 2014; Rolet et al., 2015). When present, human activities alone can explain the bird distribution since they will look for safer foraging grounds, independently of the resources biomass.

Our paper underlines, as many others in the literature, the complexity of explaining the distribution of foraging birds (Sutherland, 1983; Thomas et al., 2003; Granadeiro et al., 2004; Folmer and Piersma, 2012; VanDusen et al., 2012). Such articles must integrate ecological/biological variables; intra- and interspecific interactions, prey accessibility, tidal conditions and impacting human activities to improve the relevance of the explanatory models. As much as possible, such approaches must be conducted on large areas, ideally at a functional unit scale for the considered species. However, the importance of the singularities of the different flat parts should not be excluded as they could influence significantly the wader distribution. Such lack of a multi-scale approach may fail to identify important factors influencing the differential distribution patterns of foraging birds.

Acknowledgements

We sincerely thank everyone who helped us in the field and laboratory. Special thanks go to Severine Kwiecien, Clara Morey Rubio, Alicia Simonin, and Emilie Bouchée.

References

- Baird, D., Evans, P.R., Milne, H., Pienkowski, M.W., 1985. Utilization by shorebirds of benthic invertebrate production in intertidal areas. *Oceanogr. Mar. Biol. Annu. Rev.* 23, 573–597.
- 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, 236–261.
- Blomert, A.M., Ens, B.J., Goss-Custard, D., Hulscher, J.B., Zwarts, L., 1996. Oystercatchers and their estuarine food supplies. *Ardea* 84A, 1–538.
- 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.
- Both, C., Edelaar, P., Renema, W., 2003. Interference between the sexes in foraging bar-tailed Godwits *Limosa lapponica*. *Ardea Wageningen*. 91, 268–273.
- Bryant, D.M., 1979. Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). *Estuar. Coast. Mar. Sci.* 9, 369–384.
- Burger, J., Carlucci, S.A., Jeitner, C.W., Niles, L., 2007. Habitat choice, disturbance, and management of foraging shorebirds and gulls at a migratory stopover. *J. Coast. Res.* 23, 1159–1166.
- Burger, J., Howe, M.A., Hahn, D.C., Chase, J., 1977. Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. *Auk* 94 (4),

- 743–758.
- Catry, T., Alves, J.A., Gill, J.A., Gunnarsson, T.G., Granadeiro, J.P., 2012. Sex promotes spatial and dietary segregation in a migratory shorebird during the non-breeding season. *PLoS ONE* 7, e33811.
- Colwell, M.A., 2010. *Shorebird Ecology, Conservation, and Management*. University of California Press.
- 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): *Limicola conchilega* serves as an oasis in the tidal flats. *Mar. Biol.* 160 (4), 751–761.
- Degré, D., 2006. Réseau trophique de l'anse de l'Aiguillon : Dynamique et structure spatiale de la macrofaune et des limicoles hivernants. Université de La Rochelle, p. 518.
- 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.
- Delany, S., Scott, D., Dodman, T., Stroud, D., 2009. An Atlas of Wader Populations in Africa and Western Eurasia. Wetlands International, Wageningen.
- Dias, M.A.F.P., 2008. Factors Affecting the Use of Estuarine Areas by Waders: Implications for Their Conservation. Universidade de Lisboa, p. 159.
- Duijns, S., Gils, J.A., Spaans, B., Horn, J., Brugge, M., Piersma, T., 2014. Sex specific winter distribution in a sexually dimorphic shorebird is explained by resource partitioning. *Ecol. Evol.* 4, 4009–4018.
- Evans, P.R., Goss-Custard, J.D., Hale, W.G., 1984. *Coastal Waders and Wildfowl in Winter*. Cambridge University Press, Cambridge.
- Fleischer, R.C., 1983. Relationships between tidal oscillations and Ruddy Turnstone flocking, foraging, and vigilance behavior. *Condor* 85, 22–29.
- Folmer, E.O., Olf, H., Piersma, T., 2010. How well do food distributions predict spatial distributions of shorebirds with different degrees of self-organization? *J. Animal Ecol.* 79, 747–756.
- Folmer, E.O., Olf, H., Piersma, T., 2011. 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.
- Folmer, E.O., Piersma, T., 2012. The contributions of resource availability and social forces to foraging distributions: a spatial lag modelling approach. *Anim. Behav.* 84 (6), 1371–1380.
- Fournier, J., Gallon, R.K., Paris, R., 2014. G2Sd: a new package for the statistical analysis of unconsolidated sediments. *Geomorphol. Relief Process. Environ.* 1, 73–78.
- Fretwell, S.D., Calver, J.S., 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta biotheor.* 19, 37–44.
- Godet, L., Fournier, J., Toupoint, N., Olivier, F., 2009a. Mapping and monitoring intertidal benthic habitats: a review of techniques and proposal of a new visual methodology for the European coasts. *Prog. Phys. Geogr.* 33 (3), 378–402.
- Godet, L., Toupoint, N., Fournier, J., Le Mao, P., Retière, C., Olivier, F., 2009b. Clams farmers and oystercatchers: effects of the degradation of *Limicola conchilega* beds on the spatial distribution of shorebirds. *Mar. Pollut. Bull.* 58 (4), 589–595.
- Goss-Custard, J.D., 1980. Competition for food and interference among waders. *Ardea* 68, 52.
- Goss-Custard, J.D., West, A.D., Yates, M.G., Pettifor, R., 2006. Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. *Biol. Rev.* 81 (4), 1–29.
- Goss-Custard, J.D., Yates, M.G., 1992. Towards predicting the effect of salt-marsh reclamation on feeding bird numbers on the Wash. *J. Appl. Ecol.* 29, 330–340.
- Grabowski, R.C., Droppo, I.G., Wharton, G., 2011. Erodibility of cohesive sediment: the importance of sediment properties. *Earth Sci. Rev.* 105, 101–120.
- Granadeiro, J.P., Andrade, J., Palmeirim, J.M., 2004. Modelling the distribution of shorebirds in estuarine areas using generalised additive models. *J. Sea Res.* 52, 227–240.
- 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.
- Granadeiro, J.P., Santos, C.D., Dias, M.P., Palmeirim, J.M., 2007. Environmental factors drive habitat partitioning in birds feeding in intertidal flats: implications for conservation. *Hydrobiologia* 587, 291–302.
- Gray, J., Elliott, M., 2009. *Ecology of Marine Sediments. From Science to Management*. Oxford University Press, Oxford.
- Hedges, J.I., Stern, J.H., 1984. Carbon and nitrogen determinations of carbonate-containing solids [In sediments, sediment trap materials and plankton]. *Limnol. Oceanogr.* 29.
- Hill, D., Hockin, D., Price, D., Tucker, G., Morris, R., Treweek, J., 1997. Bird disturbance: improving the quality and utility of disturbance research. *J. Appl. Ecol.* 275–288.
- Jackman, S., 2015. *Pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory*. Stanford University. Department of Political Science, Stanford University, Stanford, California. R package version 1.4.9. URL: <http://pscl.stanford.edu/>.
- Kelsey, M.G., Hassall, M., 1989. Patch selection by Dunlin on a heterogeneous mudflat. *Ornis Scand.* 20, 250–254.
- Kersten, M., Piersma, T., 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* 75, 175–187.
- Le Corre, N., Gélinaud, G., Brigand, L., 2009. Bird disturbance on conservation sites in Brittany (France): the standpoint of geographers. *J. Coast. Conserv.* 13, 109–118.
- Le Rossignol, A.P., Buckingham, S.G., Lea, S.E.G., Nagarajan, R., 2011. Breaking down the mussel (*Mytilus edulis*) shell: which layers affect Oystercatchers (*Haematopus ostralegus*) prey selection? *J. Exp. Mar. Biol. Ecol.* 405, 87–92.
- McCullagh, P., Nelder, J.A., 1989. *Generalized Linear Models*. Chapman and Hall London, p. 532.
- McLachlan, A., Jaramillo, E., 1995. Zonation on sandy beaches. *Oceanogr. Mar. Biol. An Annu. Rev.* 33, 305–335.
- McLusky, D.S., Elliott, M., 2004. *The Estuarine Ecosystem: Ecology, Threats, and Management*. Oxford University Press Oxford, UK.
- Miller, A., 2002. *Subset Selection in Regression*. Chapman & Hall/CRC Monographs on Statistics & Applied Probability, London.
- Mitchell, J.R., Moser, M.E., Kirby, J.S., 1988. Declines in midwinter counts of waders roosting on the Dee estuary. *Bird Study* 35, 191–198.
- Moreira, F., 1993. Patterns of use of intertidal estuarine areas by feeding bird assemblages: a study in the Tagus estuary (Portugal). *Ardeola* 40, 39–53.
- Moreira, F., 1997. The importance of shorebirds to energy fluxes in a food web of a South European estuary. *Estuar. Coast. Shelf Sci.* 44, 67–78.
- Nagarajan, R., Lea, S.E., Goss-Custard, J., 2002. Reevaluation of patterns of mussel (*Mytilus edulis*) selection by European oystercatchers (*Haematopus ostralegus*). *Can. J. Zool.* 80, 846–853.
- Newton, I., 1998. *Population Limitation in Birds*. Academic Press, London.
- Norton-Griffiths, M., 1967. Some ecological aspects of the feeding behaviour of the oystercatcher *Haematopus ostralegus* on the edible mussel *Mytilus edulis*. *Ibis* 109, 412–424.
- Palomo, G., Botto, F., Navarro, D., Escapa, M., Iribarne, O.O., 2003. Does the presence of the SW Atlantic burrowing crab *Chasmagnathus granulatus* Dana affect predator–prey interactions between shorebirds and polychaetes? *J. Exp. Mar. Biol. Ecol.* 290, 211–228.
- Pienkowski, M.W., 1983. Surface activity of some intertidal invertebrates in relation to temperature and the foraging behavior of their shorebird predators. *Mar. Ecol. Prog. Ser. Oldend.* 11, 141–150.
- Piersma, T., 1990. Pre-migratory 'fattening' usually involves more than the deposition of fat alone. *Ring. Migr.* 11, 113–115.
- 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., Jukema, J., 1990. Budgeting the flight of a long-distance migrant: changes in nutrient reserve levels of Bar-tailed Godwits at successive spring staging sites. *Ardea* 78, 315–337.
- Ponsoero, A., Dabouneau, L., Allain, J., 2009. Modelling of the Cockle (*Cerastoderma edule* L.) fishing grounds in a purpose of sustainable management of traditional harvesting. *Fish. Sci.* 75, 839–850.
- Ponsoero, A., Le Mao, P., 2011. Consommation de la macro-faune invertébrée benthique par les oiseaux d'eau en baie de Saint-Brieuc. *Revue d'Écol.* 66, 383–397.
- R Development Core Team, 2015. *A Language and Environment for Statistical Computing*. Available at: <http://www.R-project.org/>.
- Recher, H.F., 1966. Some aspects of the ecology of migrant shorebirds. *Ecology* 47 (3), 393–407.
- Rolet, C., Spilmont, N., Davout, D., Goberville, E., Luczak, C., 2015. Anthropogenic impact on macrobenthic communities and consequences for shorebirds in Northern France: a complex response. *Biol. Conserv.* 184, 396–404.
- 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.
- Salonen, K., 1979. The selection of temperature for high temperature combustion of carbon. *Acta Hydrochim. Hydrobiol.* 7 (6), 591–597.
- Scheiffarth, G., Nehls, G., Austen, I., 1996. Modelling distribution of shorebirds on tidal flats in the Wadden Sea and visualisation of results with the GIS IDRISI. In: Lorup, E., Strobl, J. (Eds.), IDRISI GIS 96. Geographische Materialien, Heft 25. Selbstverlag des Instituts für Geographie der Universität, Salzburg., Salzburger.
- Smith, P.C., Evans, P.R., 1973. *Studies of shorebirds at Lindisfarne, Northumberland. 1. Feeding ecology and behaviour of the Bar-tailed Godwit*. *Wildfowl* 24, 135–140.
- Spaans, B., Bruinzeel, L.W., Smit, C.J., 1996. Effecten van verstering door mensen op wadvogels in de Waddenzee en de Oosterschelde. Instituut voor Bos-en Natuuronderzoek (IBN-DLO).
- Sturbois, A., Ponsoero, A., 2014. Synthèse ornithologique de la baie de Saint-Brieuc, phénologie et évolution des effectifs sur la période 1970–2013. Réserve Naturelle Baie de Saint-Brieuc, p. 90.
- Sturbois, A., Ponsoero, A., Desroy, N., Le Mao, P., Fournier, J., 2015. Exploitation of intertidal feeding resources by the Redknot *Calidris canutus* under megatidal conditions. *J. Sea Res.* 96, 23–30.
- Sutherland, W.J., 1983. Aggregation and the ideal free distribution. *J. Animal Ecol.* 52 (3), 821–828.
- Symonds, F.L., Langslow, D.R., Pienkowski, M.W., 1984. Movements of wintering shorebirds within the Firth of Forth: species differences in usage of an intertidal complex. *Biol. Conserv.* 28, 187–215.
- Taylor, I.R., Bester, A., 1999. The response of foraging waders to human recreation disturbance at Rhyll, Phillip Island, Victoria. *Stilt* 35, 67.
- Thomas, K., Kvitek, R.G., Bretz, C., 2003. Effects of human activity on the foraging behavior of sanderlings *Calidris alba*. *Biol. Conserv.* 109, 67–71.
- Tiedemann, R., Nehls, G., 1997. Saisonale und tidale Variation in der Nutzung von Wattflächen durch nahrungssuchende Vögel. *J. für Ornithol.* 138, 183–198.
- Triplet, P., Mequin, N., Prevost, A., Erlinger, D., Sueur, F., 2003. Rythme d'activité

- diurne de l'Huïtrier-pie *Haematopus ostralegus*, du Courlis cendré *Numenius arquata* et du Bécasseau variable *Calidris alpina* en Baie de Somme. *Alauda* 71, 459–468.
- Turpie, J.K., 1994. Why do plovers have a stereotyped behaviour? *Wader Study Group Bull.* 75, 39.
- van de Kam, J., de Goeij, P.J., Piersma, T., Zwarts, L.I., 2004. *Shorebirds: An Illustrated Behavioural Ecology*. KNNV Publishers, Utrecht, Netherlands.
- 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 Redknots 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., 2005. Digestive bottleneck affects foraging decisions in Redknots *Calidris canutus*. II. Patch choice and length of working day. *J. Animal Ecol.* 74, 120–130.
- van Gils, J.A., Spaans, B., Dekinga, A., Piersma, T., 2006. Foraging in a tidally structured environment by Redknots (*Calidris canutus*): ideal, but not free. *Ecology* 87, 1189–1202.
- VanDusen, B.M., Fegley, S.R., Peterson, C.H., 2012. Prey Distribution, Physical Habitat Features, and Guild Traits Interact to Produce Contrasting Shorebird Assemblages among Foraging Patches. *PLoS One* 7, e52694.
- West, A.D., Yates, M.G., McGrorty, S., Stillman, R.A., 2007. Predicting site quality for shorebird communities: A case study on the Wash embayment, UK. *Ecol. Model.* 202, 527–539.
- Yasué, M., Dearden, P., Moore, A., 2008. An approach to assess the potential impacts of human disturbance on wintering tropical shorebirds. *Oryx* 42, 415.
- Yates, M.G., Goss-Custard, J.D., McGrorty, S., Lakhani, K.H., Durell, S.L.V.D., Clarke, R.T., Rispin, W.E., Moy, I., Yates, T.J., Plant, R.A., 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *J. Appl. Ecol.* 30, 599–614.
- Zwarts, L., 1988. Numbers and distribution of coastal waders in Guinea-Bissau. *Ardea* 76, 42–55.
- Zwarts, L., Blomert, A.M., 1992. Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. *Mar. Ecol. Prog. Ser.* 83, 113–128.
- Zwarts, L., Wanink, J.H., 1991. The macrobenthos fraction accessible to waders may represent marginal prey. *Oecologia* 87, 581–587.