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

Ponsero Alain [1], Sturbois Anthony [1,2], Desroy Nicolas [3,*], Le Mao Patrick [3], Jones Auriane [3], Fournier Jérôme [4,5]

[1] Réserve Naturelle de la Baie de Saint-Brieuc, site de l'étoile, 22120 Hillion, France
[2] VivArmor Nature, 10 boulevard de Sévigné, 22000 Saint-Brieuc, France
[3] IFREMER, Laboratoire Environnement et Ressources Bretagne nord, 38 rue du Port Blanc, BP 80108, 35801 Dinard Cedex, France
[4] CNRS, UMR 7208 BOREA, 61 rue Buffon, CP 53, 75231 Paris Cedex 05, France
[5] MNHN, Station de Biologie Marine, BP 225, 29182 Concarneau Cedex, France

* Corresponding author : Nicolas Desroy, email address : Nicolas.Desroy@ifremer.fr

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.

Graphical abstract
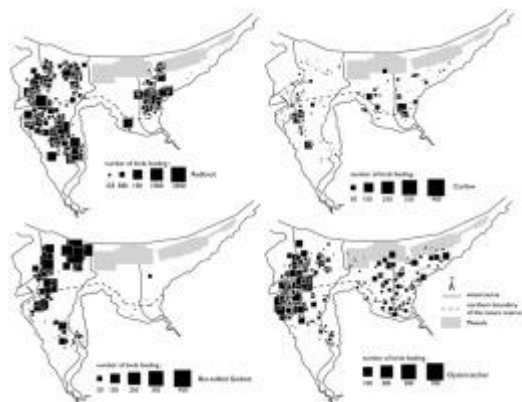
Highlights

► Total biomass of benthic macrofauna highly explains distribution of waders. ► Distribution patterns of waders differ significantly due to environmental factors. ► Spatial analysis of foraging waders should integrate the whole functional unit. ► Multi-scale approach is essential to study all factors influencing bird distribution.

Keywords : Waders, Benthos, Foraging behavior, Sandflat, Megatidal environment

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

33 foodwebs, in particular its nutritional importance for coastal birds (Goss-Custard, 1980; Baird et al.,

34 1985; Goss-Custard, 2006; De Smet et al., 2013). Waders present a spatial distribution strongly

35 connected to the local food supply (van de Kam et al., 2004). Consequently, they depend on benthic

36 assemblages characterized by specific species' composition presenting high biomasses (Evans et al.,

37 1984; McLusky and Elliott, 2004; Moreira, 1997; Newton, 1998) especially during migration (Piersma

38 and Jukema, 1990; Piersma et al., 1993) and cold periods (Kersten and Piersma, 1987; Piersma, 1990;

39 Degré, 2006). Under natural conditions, one of the difficulties in investigating such trophic

40 relationships is to clearly identify, at a given time, the resources and their exploitation modalities by

41 predators (Ponsero and Le Mao, 2011). Furthermore, nearby roosting sites also play a key role in the

42 presence of an abundant and diverse wader community in terms of species and of life cycle stages

43 (Triplet et al., 2003; Granadeiro et al., 2007; Le Corre et al., 2009).

44 Shorebirds feeding on intertidal areas are also highly mobile. Indeed, the wader prey are influenced by

45 the tide, consequently, a similar tidal rhythm can be observed in these birds' foraging activity.

46 (McLusky and Elliott, 2004). Each habitat has then a characteristic temporal pattern of use by

47 shorebirds related to tide time rather than feeding time as shown by Burger et al. (1977). The way

48 waders use space in terms of intensity is not only a function of the time during which the areas are

49 available, but also of the bird behaviour in relation to the advancing and receding tide (Granadeiro et

50 al., 2006). Trophic competitive exclusion may be avoided because species move from point to point

51 without fully exploiting the available food reserves (Recher, 1966). Folmer and Piersma (2012)

52 showed that the spatial distribution of foraging waders also depends on the endogenous social variable

53 of aggregation made up of the opposing mechanisms of conspecific attraction and repulsion. The

54 shorebird tendency to aggregate causes suitable habitat to remain unoccupied (Folmer et al., 2010;

55 Folmer and Piersma, 2012). Tidal cycles which cause cyclic spatial and temporal variability in their

56 feeding grounds, strongly constrain the foraging activity of estuarine species, and particularly of

57 waders (Fleischer, 1983; van de Kam et al., 2004; van Gils et al., 2005; Granadeiro et al., 2006; van

58 Gils et al., 2006). The presence of feeding waders in areas covered by a thin layer of surface water

59 (Palomo et al., 2003) or where the sediment is wet (Kelsey and Hassall, 1989), is frequently attributed

60 to a higher level of prey activity in such areas (Pienkowski, 1983). These conclusions were confirmed

61 by Rosa et al. (2007) which showed that sediment drainage and associated prey rhythms greatly

62 influenced wader foraging patterns on sediment flats. In a study carried out at a small spatial scale in

63 the Tagus estuary, Granadeiro et al. (2007) concluded that factors mostly affecting the shorebird's

64 distribution are the exposure period, the sediment type and the shell bank's extent. Unfortunately, most

65 of these papers examined the distribution of birds feeding in estuaries or bays only in relation to

66 environmental factors (Bryant, 1979; Symonds et al., 1984; Goss-Custard and Yates, 1992; Yates et al.,

67 1993; Moreira, 1993; Scheiffarth et al., 1996; Granadeiro et al., 2004, 2007; Rosa et al., 2007), without

68 considering the macrobenthic fauna. Preferably, such studies should be based on data collected over a

69 large fraction of the flats but resource and logistic constraints often force researchers to reduce
70 sampling (*e.g.* by concentrating the sampling effort near the coast line). Consequently, important
71 factors influencing shorebird broad-scale distribution patterns can be overlooked (Granadeiro et al.,
72 2007).

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

2. Material and methods

2.1 Study area

79 The field work was conducted in the bay of Saint-Brieuc (800 km² up to the isobaths 30 m, divided in
80 two parts by the bays of Yffiniac and Morieux), France (48°32N; 02°40W). The study area enclosed
81 about 2900 ha of tidal flats mainly dominated by fine to medium sands and under the influence of a
82 semi-diurnal megatidal regime (Figure 1). In this zone, tidal range varies between 4 m at neap tides
83 and nearly 13 m during spring tide. From 1998 to 2008, the bay of Saint-Brieuc was home to over
84 20,000 shorebirds during the winter months (Sturbois and Ponsero, 2014). Furthermore, four benthic
85 assemblages are distributed in belts along an inshore-offshore gradient of increasing grain-size
86 sediments [see Sturbois et al., 2015 for more details]. Benthic populations are particularly stable in this
87 area as shown for the cockle *Cerastoderma edule* (Ponsero et al., 2009). During overwintering, waders
88 represent one third of the total number of birds, and some species can reach more than 1% of the
89 overwintering national populations, according to the threshold defined in the Ramsar convention
90 (Delany et al., 2009). Waders are dominated by seven species: eurasian Oystercatcher *Haematopus*
91 *ostralegus*, eurasian Curlew *Numenius arquata*, grey Plover *Pluvialis arquata*, Redknot *Calidris*
92 *canutus*, Dunlin *Calidris alpina*, Sanderling *Calidris alba*, and Bar-tailed Godwit *Limosa lapponica*.
93 During cold winters, the site can be of international interest for Redknot and Bar-tail Godwit. Since
94 1998, 1140 ha of tidal flats are protected as a National Nature Reserve.

2.2 Distribution of macrobenthic resources and sediment analysis

96 The macrofaunal distribution was assessed during a survey conducted in October 2010 (Figure 1). At
97 this date, 131 stations (located inside and outside of the reserve) covering 2900 ha of intertidal area
98 were sampled according to a regular sampling network (see Godet et al., 2009a). At each station, three
99 25 cm deep sediment samples were collected for macrobenthic analysis, using a 17.6 cm² cylindrical
100 handcorer. The content of the cores were gently sieved on site using a 1-mm square mesh sieve. The
101 retained material was preserved for analysis in 5% buffered formaldehyde with added rose Bengal. A
102 visual description of the sediment type was recorded. The macrofauna were identified to the highest
103 possible taxonomic separation (usually species) and counted. The energetic value (biomass) of each

104   taxon was determined as g of AFDW per 0.1 m² (loss of weight of dry organisms after 6 h at 520°C).

105   Two samples of sediment (surface of 3.2 cm², depth of 5 cm) were collected from additional cores and

106   subsequently analysed for grain size distribution and organic matter content. Sediment samples were

107   cleaned with water and left to settle for 48 h. Sediments were then dried at 70°C for 24 h and sieved

108   through AFNOR standard sieves, and weighed. The dried samples were combusted at 540°C for 4 h in

109   order to determine the organic content (Hedges and Stern, 1984 ; Salonen, 1979). Additionally, the

110   sediment shear stress resistance was measured with a scissometer at a depth of 10 cm as a proxy for

111   cohesion (Grabowski et al., 2011). All replicates were collected at a maximal distance of 2 m from

112   each station, using GPS position-fixing (GPS Etrex Garmin).
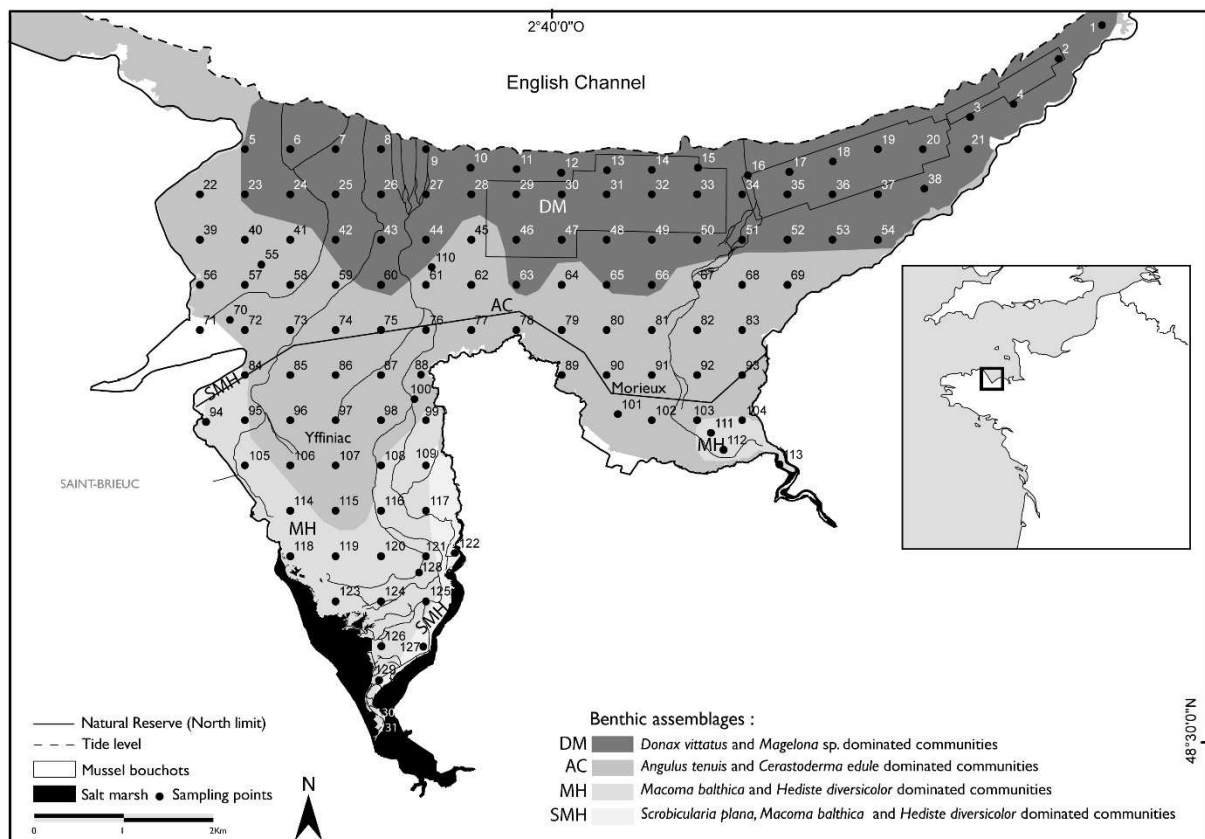
114   Figure 1. Benthic intertidal assemblages identified in the bay of Saint-Brieuc. Points correspond to the

115   131 stations of the regular sampling network.

2.3 Bird counts and localization of foraging areas

117   Considering the large scale of the study area, observations were carried out during winters 2010/11

118   and 2011/12 in the bays of Yffiniac and Morieux respectively (Figure 1). A particular focus was made

119   on four of the most abundant wader species identified as main consumers on the station and present in

120   sufficiently large numbers for adequate statistical analyses: eurasian Oystercatcher, eurasian Curlew,

121   Bar-tailed Godwit, Redknot (Ponsero and Le Mao, 2011).

122 Birds were counted regularly during daytime during the months of January and February 2010, 2011

123 and 2012, using a telescope (Kite SP-ED 80). The number of feeding birds was recorded during a total

124 of 54 tidal cycles, under conditions varying from neap to spring tides. For each bird group, the species,

125 the total number of feeding and roosting individuals and the observation time was noted. The

126 localization of a bird group was calculated using a trigonometric formula based on the observer's

127 geographical position (determined with a Global Positioning System) and measures of the bird group

128 distance and its angle with the North:

129 $$X \text{ bird} = X \text{ observer} + \sin (\text{angle}) \times \text{distance, with } X = \text{longitude}$$

130 $$Y \text{ bird} = Y \text{ observer} + \cos (\text{angle}) \times \text{distance, with } Y = \text{latitude}$$

131 Distance to observers and viewing angle with the North were provided using laser range-finding

132 binoculars (Newcon LRB 3000 pro,7×40). The binocular model used was able to measure a distance

133 up to 700 m which limited the disturbance of birds.

2.4 Data analysis

135 All the statistical analysis was performed with R v. 3.1.2 (R Development Core Team, 2015). The

136 statistical description of sediments, based on grain-size distributions, was computed with the R

137 package 'G2Sd' (see Fournier et al., 2014). Linear regression models were used to test the putative

138 effect of the altitude (shore elevation) on the distribution of sedimentary parameters such as median

139 grain size, mean, shear stress resistance of sediment or mud ($<40\mu m$) content. The normality of

140 residuals was checked with a Shapiro-Wilk test.

141 The mean values of the number of species (*S*), total abundance (*N*), Shannon diversity (*H'*), Simpson

142 diversity (*D'*), Pielou eveness (*J*) were computed for all stations. Macrobenthic assemblages were

143 defined previously in Sturbois et al. (2015) and presented in Figure 1. The relationship between

144 richness, abundance, total biomass, diversity indices (Shannon index, Simpson Index, Pielou eveness)

145 of the benthic macrofauna and environmental parameters were analyzed with multiple linear

146 regression models. The best linear models were selected using the 'regsubsets' function of the R

147 package 'leaps', which plots a measure of fit against subset size (see Miller, 2002). The 'regsubsets'

148 algorithm enables to select the optimal combination of factors that best 'explains' the variance of a

149 variable.

150 We used a Poisson generalized regression modeling approach to evaluate the relation between the

151 cumulated presence of wader species during the 54 headcounts between January 2010 and February

152 2012 and environmental [mean grain size (MEA), median grain size (MED), altitude (shore elevation)

153 (ALT), shear stress resistance of sediment (STR), organic matter of sediment (MOR), water content of

154 sediment (H20)] and ecologic parameters [richness (RICH), total abundance (ABUN), total biomass of

155 benthic macrofauna (BIOT), biomass of *Cerastoderma edule* (< 10 mm) (BIOC1), biomass of

156 *Cerastoderma. edule* (15-25 mm) (BIOC2), biomass of other bivalves (BIOB) and biomass of other

157 benthic organisms (BIOO)]. *C. edule* was considered separately regarding the high biomass value

158 (56.3% of total biomass) measured in the mudflat. Maximum likelihood (r2ML) and Cragg and

159 Uhler's (r2CU) Pseudo-R² were calculated with the R package 'pscl' (see Jackman, 2015). We used a

160 logistic regression modeling approach to evaluate the spatial exploitation modalities of the different

161 wader species (McCullagh and Nelder, 1989). McFadden (r2MF) Pseudo-R² coefficient was calculated

162 with the R package 'pscl' (Jackman, 2015).

3. Results

164 *Sediment distribution*

165 A significant effect of the altitude (shore elevation) on several sedimentary parameters was

166 demonstrated using linear regression models, but the low R² value reflects a high level of variation.

167 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, $p < 0.01$,

168 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

169 to the altitude (shore elevation). The mud content increases with the altitude (shore elevation) ($F_{(1,}$

170 $_{127)}$=7.891, $p < 0.01$, R^2=0.05). A multiple linear regression shows that shear stress resistance seems to

171 decrease significantly with altitude (shore elevation), median grain size and water content of sediment

172 ($F_{(6, 122)}$=5.933, $p < 0.001$, R^2=0.18).

173 *Biomass distribution*

174 The mean biomass value in the whole study area is 5.03 g.m⁻² ± 8.09 and it is strongly correlated with

175 bivalve biomass (S=121270; $p<0.001$). Biomass values are significantly higher in Yffiniac (7.85 g.m⁻²

176 ± 9.96) than in Morieux bay (1.56 g.m⁻² ± 1.81) ($F_{(1,127)}$= 23.46, $p<0.001$). Difference is mainly due to

177 *Cerastoderma edule* (5.02 g.m⁻² ± 7.61 and 0.16 g.m⁻² ± 0.58) and in a lesser extent to the others

178 bivalves (1.12 g.m⁻² ± 4.61 and 0.40 g.m⁻² ± 0.78) and annelids (1.71 g.m⁻² ± 4.43 and 1.01 ± 1.38).

179 *Relation between biological variables and environmental parameters*

180 The total richness is positively correlated with median grain size ($F_{(3, 125)}$ = 22.58, $p<0.001$) . The

181 global abundance is positively correlated with the sorting of sediment ($F_{(6, 122)}$ = 6.642, $p<0.001$) and

182 negatively correlated with the sediment median grain size ($p<0.05$). The total biomass is positively

183 correlated with the sediment organic matter content ($F_{(3, 122)}$ = 11.99, $p<0.001$) and the sediment

184 median grain size ($p<0.01$). Finally, the diversity (Shannon index) is positively correlated with the

185 sediment median grain size ($F_{(4, 124)}$ = 19.7, $p<0.001$) and negatively correlated with the altitude (shore

186 elevation) ($p<0.001$).

187 *Relation between waders and environmental and biological parameters*

188 The factors most explaining the Oystercatcher presence are the altitude (shore elevation) ($p<0.05$), the

189 organic matter content ($p<0.01$), the macrobenthos total biomass ($p<0.001$) and the benthic macrofau-

190 na biomass excluding bivalves (Null deviance: 340.66 on 128 *df*; Residual deviance: 265.46 on 115 *df*.

191 AIC: 546.25. r2ML: 44%, r2CU: 44% see Table 1).

192 The factors most explaining the Bar-tailed Godwit presence are the mean grain size (*p*<0.05), the

193 shear stress resistance (*p*<0.01), the sediment water content (*p*<0.05), the richness (*p*<0.01), the mac-

194 robenthos total biomass (*p*<0.001), the macrobenthos biomass excluding bivalves (*p*<0.001) and the

195 small common cockle biomass (*Cerastoderma edule*) (*p*<0.01) (Null deviance: 273.96 on 128 *df*; Re-

196 sidual deviance: 168.27 on 115 *df*. AIC: 306.32. r2ML: 56%, r2CU: 59% seeTable 2).

197 The factors most explaining the Redknot presence are the sediment median grain size (*p*<0.01), the

198 altitude (shore elevation) (*p*<0.001), the sediment organic matter content (*p*<0.01), the total abun-

199 dance (*p*<0.05), the total macrobenthos biomass (*p*<0.001), the benthic macrofauna biomass exclud-

200 ing bivalves (*p*<0.05), the biomass of small common cockles (*Cerastoderma edule*, *p*<0.01) and the

201 biomass of large common cockles (*p*<0.05) (Null deviance: 326.26 on 128 *df*; Residual deviance:

202 226.33 on 115 *df*. AIC: 463.46. r2ML: 54%, r2CU: 54% see Table 3).

203 The factors most explaining the presence of the eurasian Curlew are the altitude (shore elevation)

204 (*p*<0.01), the sediment organic matter content (*p*<0.05) and the macrobenthos total biomass (*p*<0.001)

205 (Null deviance: 297.28 on 128 *df*; Residual deviance: 241.23 on 115 *df*. AIC: 509.71. r2ML: 35%,

206 r2CU: 35% see Table 4).

207 *Spatial distribution of foraging waders*

208 Spatial analysis of the bird distribution shows the existence of two main patches, one in the western

209 (Yffiniac) and the other in the eastern (Morieux) part of the Saint-Brieuc bay, with a deficit of foraging

210 birds in Morieux especially for Bar-tailed Godwit (only 0.65 % of the total foraging birds are observed

211 in Morieux), Oystercatcher (16.28 %) and in a lesser extent for Redknot (26.95 %). The distribution of

212 Curlew is more balanced. The distribution of Bar-tailed Godwit and Redknot looks patchy and the

213 distribution of eurasian Curlew and Oystercatcher is patchy in Yffiniac and more diffuse in Morieux

214 (Figure 2).

215
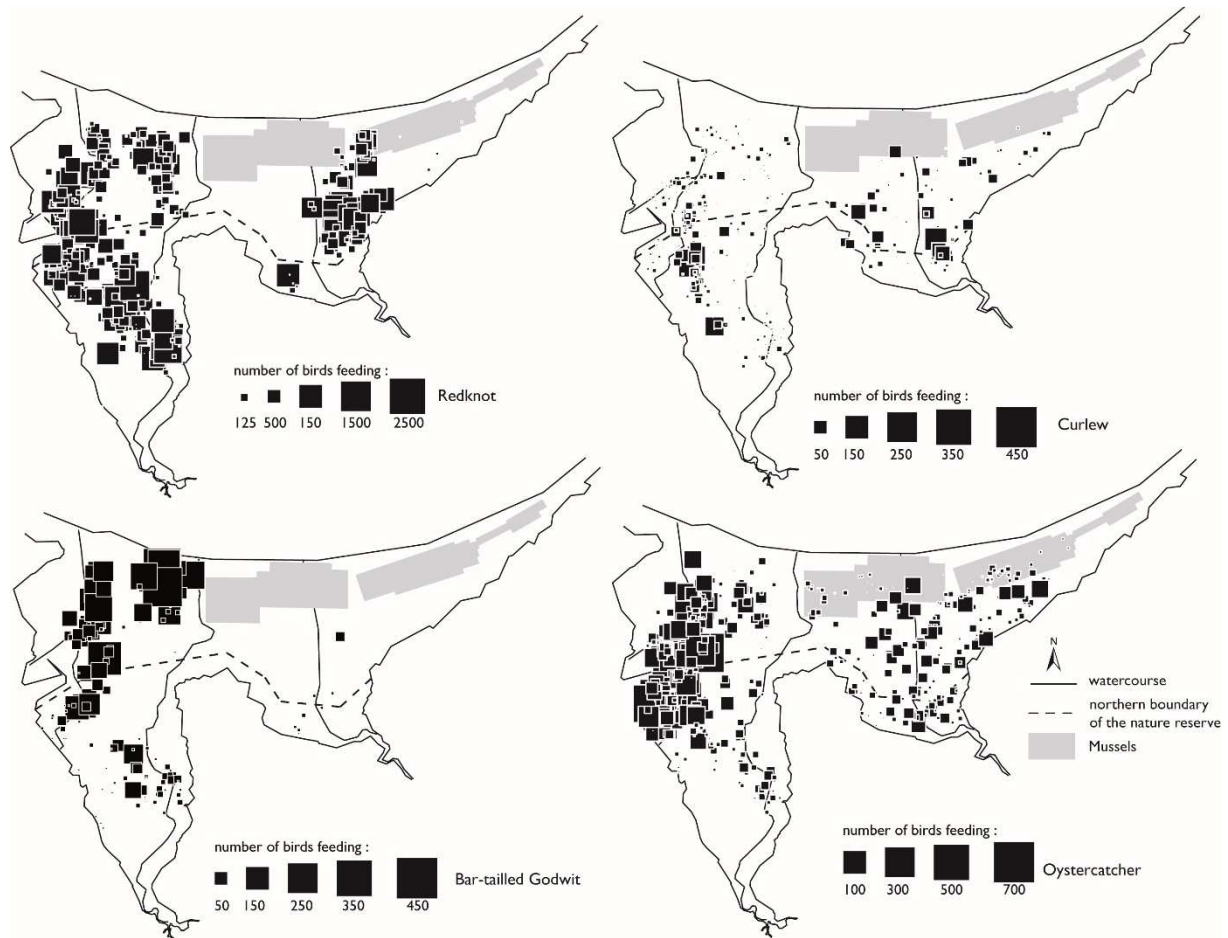
216
217 Figure 2. Foraging area used by Redknot, Curlew, Bar-tailed Godwit, and Oystercatcher in the bay of
218 Saint-Brieuc.

219 *Co-exploitation of the flat by waders*

220 The sandflat is not evenly used by the different wader species. Results of the logistic regression (Null
221 deviance: 156.40 on 128 *df*; Residual deviance: 66.02 on 125 *df*; AIC: 74.02; $\chi^2_{(3)}$=90.7; $p<0.001$;
222 r2MF=57%) show that the Oystercatcher presence is positively related to the Bar-tailed Godwit
223 (OP=8.18; $p< 0.05$) and the eurasian Curlew (OP=68.42; $p<0.001$). No effect was found with the
224 Redknot.

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

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

231 The eurasian Curlew presence is positively and significantly (Null deviance: 164.221 on 128 *df*; Re-
232 sidual deviance: 83.748 on 125 *df*; AIC: 91.748; $\chi^2_{(3)}$=80.47; $p<0.001$; r2MF=49%) related to the Oys-
233 tercatcher (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.

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.

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

269 conclusions diverge from Folmer et al. (2010) for which, in the Dutch Wadden Sea (mesotidal regime),

270 biomass parameters are not the exclusive predictors for explaining the presence of this species.

271 *Oystercatcher*

272 In the bay of Saint-Brieuc, the Oystercatcher distribution is significantly dependent of total biomass,

273 total biomass excluding bivalves and sediment organic matter. Foraging activity spatial analyses show

274 a very patchy and a more diffuse distribution respectively in Yffiniac and Morieux bays. These

275 differences could be shown by the presence, in Morieux, of 320 ha of bouchots on the lowest part of

276 the flat. Swell and waste due to the bouchots exploitation generate a diffuse dispersal of *Mytilus edulis*

277 on the outskirt of the culture area. As a consequence, Oystercatchers were mainly found in the lowest

278 levels in Morieux bay (including bouchots), and their presence had no direct link with non-cultivated

279 species biomass (in opposition with Yffiniac bay, Figure 2). Mussels, not sampled in our study, are a

280 well-known food for Oystercatchers (Le Rossignol et al., 2011; Nagarajan et al., 2002; Blomert et al.,

281 1996; Norton-Griffiths, 1967; Goss-Custard and Yates, 1992).

282 *Bar-tailed Godwit*

283 The Bar-tailed Godwit distribution is explained by total biomass, total biomass excluding bivalves and

284 small *C. edule* (<10 mm) biomass and, in a lesser extent, to sediment water content and mean grain

285 size. As a direct consequence of the sediment drainage, the largest groups of foraging Bar-tailed

286 Godwit were found on the lowest parts of the sandflat, in opposition with other wader species (Figure

287 2).

288 Discussions prevail in the literature on the existence of a tide following behavior in this species (Smith

289 and Evans, 1973; Zwarts, 1988; Turpie, 1994; Tiedemann and Nehls, 1997; Both et al., 2003; Dias,

290 2008; Rosa et al., 2007; Catry et al., 2012; Duijns et al., 2014). Such behavior could however vary

291 seasonally (as observed by Granadeiro et al. (2007) for several species) and according to the sex of the

292 bird (Duijns et al., 2014).

293 In Morieux bay, various human activities, including the presence of mussel bouchots and associated

294 circulation, could lead the birds (notably Bar-tailed Godwit) to avoid an exploitable foraging ground,

295 as suggested by Taylor and Bester (1999).

296 *Redknot*

297 The Redknot patchy distribution is mainly explained by total biomass, altitude (shore elevation),

298 median grain size and small common cockle biomass (Figure 2). The link between this species and

299 cockles confirms the finding of a recent study conducted in the bay of Saint-Brieuc by Sturbois et al.

300 (2015). They also showed that *Mytilus edulis* does not reach high global occurrence frequencies in

301 droppings (≈7.5%). Although this prey remains an opportunistic item, its frequency of occurrence

302 increases from the upper to the lower flat because of the mussel predation coming from bouchots

303 (Sturbois et al., 2015). The presence of foraging Redknot in the upper part of the shore may be the

304 direct consequence of the avoidance of the bouchot area and the presence of great abundance of

305 *Angulus tenuis* in the east upper part of the flat.

306 *Eurasian Curlew*

307 Total biomass and altitude (shore elevation) are the most important factors explaining the eurasian

308 Curlew distribution. In the bay of Saint-Brieuc, the megatidal conditions offer to birds the possibility

309 to forage on large sandflats. Consequently, the lowest levels, limited in surface and exposure time, are

310 very attractive to foraging birds as already observed in the megatidal bay of the Mont Saint-Michel

311 (De Smet et al., 2013). These low levels are characterized by clean medium to fine sands, contrasting

312 with the muddy habitats studied by Folmer et al. (2010) in the Duch Wadden Sea under mesotidal

313 regime. This species is known to be sensitive to human activities as reported by Spaans et al. (1996),

314 such as mussel culture which seems to be a disturbing activity (Figure 2).

315 *Specific exploitation of the flat*

316 The presence on the same foraging ground (simultaneously or not) of the eurasian Curlew and of the

317 Oystercatcher, are positively related. This confirms the concordant distribution patterns observed in

318 the bay for these two species (Figure 2). Similarly, the presence of Bar-tailed Godwits is positively

319 related to the presence of Redknot and *vice versa*. No effect was found between the Bar-tailed Godwit

320 and other wader species probably due to the tide following behavior of this species.

321 The unequal use of the flat by the four considered wader species confirms the conclusions of

322 VanDusen et al. (2012), which stipulate that the habitat heterogeneity explains the non-random spatial

323 distribution of foraging shorebirds. In the bay of Saint-Brieuc, only part of the flats benefit of a high

324 protection level (National Nature Reserve). As suggested by Granadeiro et al. (2007) in the Tagus

325 estuary, taking into account additional habitats neighboring the bay of Saint-Brieuc would help to

326 better understand the overall value of this presumed functional unit for foraging shorebirds.

327 *Alternative factors potentially affecting the bird distribution*

328 According to the ideal free distribution model of Fretwell and Calver (1969), foragers are supposed to

329 aggregate in patches where food is the most abundant. However, several studies have shown that other

330 aspects (i. interference and conspecific attraction, ii. sediment characteristics; iii prey accessibility, iv.

331 tidal regime and v. human disturbance) can influence the bird distribution and could help in the

332 interpretation of the model unexplained variability.

333 i. The shorebird intrinsic behavior could explain the variability of their distribution in space and time.

334 At a given time, spatial distribution of foraging waders in patchy resource areas also depends on the

335 ability of species to aggregate (for interference and conspecific attraction, see Folmer and Piersma,

336 2012; Folmer et al., 2011). Consequently, conspecific attraction may lead to large areas with abundant

337 food resources remaining unexploited (Folmer et al., 2011).

338 ii. The sediment grain-size may contribute to explain shorebird feeding distribution regarding its

339 influence on benthic invertebrate prey. Depending on the sediment shear stress resistance, the

340 availability of the benthic prey can differ, independently of their abundances and could explain

341 sandflat specific anomalies in shorebird usage (VanDusen et al., 2012).

342 iii: Estimation of prey availability based on 25 cm deep core samples provides a representative

343 estimation of the accessible prey fraction for long-billed wader (Oystercatcher, Curlew, Bar-tailed

344 Godwit). However, the biomass recorded using the core-sampler may overestimate the actual prey

345 available to short-billed birds as Redknot (Zwarts and Wanink, 1991).

346 iv. Several studies have already shown the influence of tidal regime on shorebird foraging activities

347 (Granadeiro et al., 2006; van Gils et al., 2006). In intertidal flats with semi-diurnal mesotidal regimes,

348 as in the Dutch Wadden Sea, the habitats used by waders for foraging are relatively uniform

349 (Beukema, 1976). Flocks of birds forage on a few dominant prey species. *A contrario*, under megatidal

350 conditions, benthic invertebrate assemblages are usually distributed along a continuum with regard to

351 the bathymetric gradient (McLachlan and Jaramillo, 1995). Consequently, the diet composition in

352 heterogeneous areas can be expected to be more diversified.

353 v. Foraging birds are sensitive to various human activities, which can lead them to abandon usual

354 foraging zones located on the flat (Mitchell et al., 1988; Hill et al., 1997; Burger et al., 2007; Yasué et

355 al., 2008; Colwell, 2010; van den Hout et al., 2014; Rolet al., 2015). When present, human activities

356 alone can explain the bird distribution since they will look for safe foraging grounds, independently of

357 the resources biomass.

358 Our paper underlines, as many others in the literature, the complexity of explaining the distribution of

359 foraging birds (Sutherland, 1983; Thomas et al., 2003; Granadeiro et al., 2004; Folmer and Piersma,

360 2012; VanDusen et al., 2012). Such articles must integrate ecological/biological variables; intra- and

361 interspecific interactions, prey accessibility, tidal conditions and impacting human activities to

362 improve the relevance of the explanatory models. As much as possible, such approaches must be

363 conducted on large areas, ideally at a functional unit scale for the considered species. However, the

364 importance of the singularities of the different flat parts should not be excluded as they could influence

365 significantly the wader distribution. Such lack of a multi-scale approach may fail to identify important

366 factors influencing the differential distribution patterns of foraging birds.

367

368 **Acknowledgements**

371 **References**

372 Baird, D., Evans, P.R., Milne, H., Pienkowski, M.W., 1985. Utilization by shorebirds of benthic

373 invertebrate production in intertidal areas. Oceanography and Marine Biology Annual Review 23, 573-

374 597.

375 Beukema, J.J., 1976. Biomass and species richness of the macrobenthic animals living on the tidal

376 flats of the Dutch Wadden sea. Netherlands Journal of Sea Research 10, 236-261.

377 Blomert, A.M., Ens, B.J., Goss-Custard, D., Hulscher, J.B., Zwarts, L., 1996. Oystercatchers and their

378 estuarine food supplies. Ardea 84A, 1-538.

379 Boere, G.C., Smit, C.J., 1981. Knot (*Calidris canutus* L.) in: Smit, C.J., Wolff, W.J. (Ed.), Birds of the

380 Wadden Sea, Rotterdam, pp. 136-145.

381 Both, C., Edelaar, P., Renema, W., 2003. Interference between the sexes in foraging Bar-tailed

382 Godwits *Limosa lapponica*. Ardea-Wageningen 91, 268-273.

383 Bryant, D.M., 1979. Effects of prey density and site character on estuary usage by overwintering

384 waders (Charadrii). Estuarine and Coastal Marine Science 9, 369-384.

385 Burger, J., Carlucci, S.A., Jeitner, C.W., Niles, L., 2007. Habitat choice, disturbance, and management

386 of foraging shorebirds and gulls at a migratory stopover. Journal of Coastal Research 23, 1159-1166.

387 Burger, J., Howe, M.A., Hahn, D.C., Chase, J., 1977. Effects of tide cycles on habitat selection and

388 habitat partitioning by migrating shorebirds. The Auk, 743-758.

389 Catry, T., Alves, J.A., Gill, J.A., Gunnarsson, T.G., Granadeiro, J.P., 2012. Sex promotes spatial and

390 dietary segregation in a migratory shorebird during the non-breeding season. PLoS ONE 7, e33811.

391 Colwell, M.A., 2010. Shorebird ecology, conservation, and management. University of California

392 Press.

393 De Smet, B., Godet, L., Fournier, J., Desroy, N., Jaffré, M., Vincx, M., Rabaut, M., 2013. Feeding

394 grounds for waders in the Bay of the Mont Saint-Michel (France): the *Lanice conchilega* reef serves as

395 an oasis in the tidal flats. Marine Biology 160, 751-761.

396 Degré, D., 2006. Réseau trophique de l'anse de l'Aiguillon : Dynamique et structure spatiale de la

397 macrofaune et des limicoles hivernants. Université de La Rochelle, p. 518.

398 Dekinga, A., Piersma, T., 1993. Reconstructing diet composition on the basis of faeces in a

399 mollusceating wader, the Knot *Calidris canutus*. Bird Study 40, 144-156.

400 Delany, S., Scott, D., Dodman, T., Stroud, D., 2009. An atlas of wader populations in Africa and
401 Western Eurasia. Wetlands International, Wageningen.

402 De Smet, B., Godet, L., Fournier, J., Desroy, N., Jaffré, M., Vincx, M., Rabaut, M., 2013. Feeding
403 grounds for waders in the Bay of the Mont-Saint-Michel (France): *Lanice conchilega* serves as an
404 oasis in the tidal flats. Marine Biology 160(4), 751-761.

405 Dias, M.A.F.P., 2008. Factors affecting the use of estuarine areas by waders: implications for their
406 conservation. Universidade de Lisboa, p. 159p.

407 Duijns, S., Gils, J.A., Spaans, B., Horn, J., Brugge, M., Piersma, T., 2014. Sex specific winter
408 distribution in a sexually dimorphic shorebird is explained by resource partitioning. Ecology and
409 Evolution.

410 Evans, P.R., Goss-Custard, J.D., Hale, W.G., 1984. Coastal waders and wildfowl in winter. Cambridge
411 University Press, Cambridge.

412 Fleischer, R.C., 1983. Relationships between tidal oscillations and Ruddy Turnstone flocking,
413 foraging, and vigilance behavior. Condor 85, 22-29.

414 Folmer, E.O., Olff, H., Piersma, T., 2010. How well do food distributions predict spatial distributions
415 of shorebirds with different degrees of self-organization? Journal of Animal Ecology 79, 747-756.

416 Folmer, E.O., Olff, H., Piersma, T., 2011. The spatial distribution of flocking foragers: disentangling
417 the effects of food availability, interference and conspecific attraction by means of spatial
418 autoregressive modeling. Oikos.

419 Folmer, E.O., Piersma, T., 2012. The contributions of resource availability and social forces to
420 foraging distributions: a spatial lag modelling approach. Animal Behaviour.

421 Fournier, J., Gallon, R.K., Paris, R., 2014. G2Sd: a new package for the statistical analysis of
422 unconsolidated sediments. Géomorphologie: relief, processus, environnement 1, 73-78.

423 Fretwell, S.D., Calver, J.S., 1969. On territorial behavior and other factors influencing habitat
424 distribution in birds. Acta biotheoretica 19, 37-44.

425 Godet, L., Fournier, J., Toupoint, N., Olivier, F., 2009a. Mapping and monitoring intertidal benthic
426 habitats: a review of techniques and proposal of a new visual methodology fort the European coasts.
427 Progress in Physical Geography 33(3), 378-402.

428 Godet, L., Toupoint, N., Fournier, J., Le Mao, P., Retière, C., Olivier, F., 2009b. Clams farmers and
429 oystercatchers: effects of the degradation of *Lanice conchilega* beds on the spatial distribution of
430 shorebirds. Marine Pollution Bulletin 58(4), 589-595.

431 Goss-Custard, J.D., 1980. Competition for food and interference among waders. Ardea 68, 52.

432 Goss-Custard, J.D., 2006. Intake rates and the functional response in shorebirds (Charadriiformes)
433 eating macro-invertebrates. Biol. Rev., 1-29.

434 Goss-Custard, J.D., Yates, M.G., 1992. Towards predicting the effect of salt-marsh reclamation on
435 feeding bird numbers on the Wash. Journal of Applied Ecology, 330-340.

436 Grabowski, R.C., Droppo, I.G., Wharton, G., 2011. Erodibility of cohesive sediment: the importance
437 of sediment properties. Earth-Science Reviews 105, 101-120.

438 Granadeiro, J.P., Andrade, J., Palmeirim, J.M., 2004. Modelling the distribution of shorebirds in
439 estuarine areas using generalised additive models. Journal of Sea Research 52, 227-240.

440 Granadeiro, J.P., Dias, M.P., Martins, R.C., Palmeirim, J.M., 2006. Variation in numbers and behaviour
441 of waders during the tidal cycle: implications for the use of estuarine sediment flats. Acta Oecologica
442 29, 293-300.

443 Granadeiro, J.P., Santos, C.D., Dias, M.P., Palmeirim, J.M., 2007. Environmental factors drive habitat
444 partitioning in birds feeding in intertidal flats: implications for conservation. Hydrobiologia 587, 291-
445 302.

446 Gray, J., Elliott, M., 2009. Ecology of marine sediments. From science to management. Oxford
447 University Press, Oxford.

448 Hedges, J.I., Stern, J.H., 1984. Carbon and nitrogen determinations of carbonate-containing solids [In
449 sediments, sediment trap materials and plankton]. Limnology and Oceanography 29.

450 Hill, D., Hockin, D., Price, D., Tucker, G., Morris, R., Treweek, J., 1997. Bird disturbance: improving
451 the quality and utility of disturbance research. Journal of Applied Ecology, 275-288.

452 Jackman, S., 2015. pscl: Classes and Methods for R Developed in the Political Science Computational
453 Laboratory. Stanford University. Department of Political Science, Stanford University, Stanford,
454 California. R package version 1.4.9. URL http://pscl.stanford.edu/.

455 Kelsey, M.G., Hassall, M., 1989. Patch selection by Dunlin on a heterogeneous mudflat. Ornis
456 Scandinavica 20, 250-254.

457 Kersten, M., Piersma, T., 1987. High levels of energy expenditure in shorebirds: metabolic adaptations
458 to an energetically expensive way of life. Ardea 75, 175-187.

459 Le Corre, N., Gélinaud, G., Brigand, L., 2009. Bird disturbance on conservation sites in Brittany
460 (France): the standpoint of geographers. Journal of Coastal Conservation 13, 109-118.

461 Le Rossignol, A.P., Buckingham, S.G., Lea, S.E.G., Nagarajan, R., 2011. Breaking down the mussel
462 (*Mytilus edulis*) shell: Which layers affect Oystercatchers'(*Haematopus ostralegus*) prey selection?
463 Journal of Experimental Marine Biology and Ecology 405, 87-92.

464 McCullagh, P., Nelder, J.A., 1989. Generalized linear models. Chapman and Hall London.

465 McLachan, A., Jaramillo, E., 1995. Zonation on sandy beaches. Oceanography and Marine Biology:
466 An Annual Review 33, 305-335.

467 McLusky, D.S., Elliott, M., 2004. The estuarine ecosystem: ecology, threats, and management. Oxford
468 University Press Oxford (UK).

469 Miller, A., 2002. Subset selection in regression. Chapman & Hall/CRC Monographs on Statistics &
470 Applied Probability, London.

471 Mitchell, J.R., Moser, M.E., Kirby, J.S., 1988. Declines in midwinter counts of waders roosting on the
472 Dee estuary. Bird Study 35, 191-198.

473 Moreira, F., 1993. Patterns of use of intertidal estuarine areas by feeding bird assemblages: a study in
474 the Tagus estuary (Portugal). Ardeola 40, 39-53.

475 Moreira, F., 1997. The importance of shorebirds to energy fluxes in a food web of a South European
476 estuary. Estuarine, Coastal and Shelf Science 44, 67-78.

477 Nagarajan, R., Lea, S.E., Goss-Custard, J., 2002. Reevaluation of patterns of mussel (*Mytilus edulis*)
478 selection by European oystercatchers (*Haematopus ostralegus*). Canadian Journal of Zoology 80, 846-
479 853.

480 Newton, I., 1998. Population limitation in birds. Academic Press, London.

481 Norton-Griffiths, M., 1967. Some ecological aspects of the feeding behaviour of the oystercatcher
482 *Haematopus ostralegus* on the edible mussel *Mytilus edulis*. Ibis 109, 412-424.

483 Palomo, G., Botto, F., Navarro, D., Escapa, M., Iribarne, O.O., 2003. Does the presence of the SW
484 Atlantic burrowing crab *Chasmagnathus granulatus* Dana affect predator–prey interactions between
485 shorebirds and polychaetes? Journal of experimental marine biology and ecology 290, 211-228.

486 Pienkowski, M.W., 1983. Surface activity of some intertidal invertebrates in relation to temperature
487 and the foraging behavior of their shorebird predators. Marine Ecology Progress Series. Oldendorf 11,
488 141-150.

489 Piersma, T., 1990. Pre-migratory 'fattening' usually involves more than the deposition of fat alone.
490 Ringing & Migration 11, 113-115.

491 Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P., Wiersma, P., 1993. Scale
492 and intensity of intertidal habitat use by knots *Calidris canutus* in the Western Wadden Sea in relation
493 to food, friends and foes. Netherlands Journal of Sea Research 31, 331-357.

494 Piersma, T., Jukema, J., 1990. Budgeting the flight of a long-distance migrant: changes in nutrient
495 reserve levels of Bar-tailed Godwits at successive spring staging sites. Ardea 78, 315-337.

496 Ponsero, A., Dabouineau, L., Allain, J., 2009. Modelling of the Cockle (*Cerastoderma edule* L.)
497 fishing grounds in a purpose of sustainable management of traditional harvesting. Fisheries Science
498 75, 839-850.

499 Ponsero, A., Le Mao, P., 2011. Consommation de la macro-faune invertébrée benthique par les oiseaux
500 d'eau en baie de Saint-Brieuc. Revue d'Ecologie 66, 383-397.

501 R Development Core Team, 2015. A language and environment for statistical computing. Available at
502 http://www.R-project.org/.

503 Recher, H.F., 1966. Some aspects of the ecology of migrant shorebirds. Ecology, 393-407.

504 Rolet, C., Spilmont, N., Davoult, D., Goberville, E., Luczak, C., 2015. Anthropogenic impact on
505 macrobenthic communities and consequences for shorebirds in Northern France: A complex response.
506 Biological Conservation 184, 396-404.

507 Rosa, S., Granadeiro, J.P., Cruz, M., Palmeirim, J.M., 2007. Invertebrate prey activity varies along the
508 tidal cycle and depends on sediment drainage: Consequences for the foraging behaviour of waders.
509 Journal of Experimental Marine Biology and Ecology 353, 35-44.

510 Salonen, K., 1979. The selection of temperature for high temperature combustion of carbon. Acta
511 Hydrochim. Hydrobiol. 7(6), 591-597.

512 Scheiffarth, G., Nehls, G., Austen, I., 1996. Modelling distribution of shorebirds on tidal flats in the
513 Wadden Sea and visualisation of results with the GIS IDRISI, in: Lorup, E., Strobl, J. (Eds.), IDRISI
514 GIS 96. Geographische Materialien, Heft 25. Selbstverlag des Instituts für Geographie der Universität,
515 Salzburg., Salzburger.

516 Smith, P.C., Evans, P.R., 1973. Studies of shorebirds at Lindisfarne, Northumberland. 1. Feeding
517 ecology and behaviour of the Bar-tailed Godwit. Wildfowl 24, 135-140.

518 Spaans, B., Bruinzeel, L.W., Smit, C.J., 1996. Effecten van verstoring door mensen op wadvogels in
519 de Waddenzee en de Oosterschelde. Instituut voor Bos-en Natuuronderzoek (IBN-DLO).

520 Sturbois, A., Ponsero, A., 2014. Synthèse ornithologique de la baie de Saint-Brieuc, phénologie et
521 évolution des effectifs sur la période 1970-2013. Réserve Naturelle Baie de Saint-Brieuc, p. 90p.

522 Sturbois, A., Ponsero, A., Desroy, N., Le Mao, P., Fournier, J., 2015. Exploitation of intertidal feeding
523 resources by the Redknot *Calidris canutus* under megatidal conditions. Journal of Sea Research 96,
524 23-30.

525 Sutherland, W.J., 1983. Aggregation and the ideal free'distribution. The Journal of Animal Ecology,
526 821-828.

527 Symonds, F.L., Langslow, D.R., Pienkowski, M.W., 1984. Movements of wintering shorebirds within
528 the Firth of Forth: species differences in usage of an intertidal complex. Biological Conservation 28,
529 187-215.

530 Taylor, I.R., Bester, A., 1999. The response of foraging waders to human recreation disturbance at
531 Rhyll, Phillip Island, Victoria. The Stilt 35, 67.

532 Thomas, K., Kvitek, R.G., Bretz, C., 2003. Effects of human activity on the foraging behavior of
533 sanderlings *Calidris alba*. Biological Conservation 109, 67-71.

534 Tiedemann, R., Nehls, G., 1997. Saisonale und tidale Variation in der Nutzung von Wattflächen durch
535 nahrungssuchende Vögel. Journal für Ornithologie 138, 183-198.

536 Triplet, P., Mequin, N., Prevost, A., Erlinger, D., Sueur, F., 2003. Rythme d'activité diurne de
537 l'Huîtrier-pie *Haematopus ostralegus*, du Courlis cendré *Numenius arquata* et du Bécasseau variable
538 *Calidris alpina* en Baie de Somme. Alauda 71, 459-468.

539 Turpie, J.K., 1994. Why do plovers have a stereotyped behaviour? Wader Study Group Bulletin 75, 39.

540 van de Kam, J., de Goeij, P.J., Piersma, T., Zwarts, L.I., 2004. Shorebirds: an illustrated behavioural
541 ecology. Utrecht, Netherlands, KNNV Publishers.

542 van den Hout, P.J., van Gils, J.A., Robin, F., van der Geest, M., Dekinga, A., Piersma, T., 2014.
543 Interference from adults forces young Redknots to forage for longer and in dangerous places. Animal
544 Behaviour 88, 137-146.

545 van Gils, J.A., Dekinga, A., Spaans, B., Vahl, W.K., Piersma, T., 2005. Digestive bottleneck affects
546 foraging decisions in Redknots *Calidris canutus*. II. Patch choice and length of working day. Journal
547 of Animal Ecology 74, 120-130.

548 van gils, J.A., Spaans, B., Dekinga, A., Piersma, T., 2006. Foraging in a tidally structured environment
549 by Redknots (*Calidris canutus*): ideal, but not free. Ecology 87, 1189-1202.

550 VanDusen, B.M., Fegley, S.R., Peterson, C.H., 2012. Prey Distribution, Physical Habitat Features, and
551 Guild Traits Interact to Produce Contrasting Shorebird Assemblages among Foraging Patches. PLoS
552 ONE e 7, e52694.

553 West, A.D., Yates, M.G., McGrorty, S., Stillman, R.A., 2007. Predicting site quality for shorebird
554 communities: A case study on the Wash embayment, UK. Ecological Modelling 202, 527-539.

555 Yasué, M., Dearden, P., Moore, A., 2008. An approach to assess the potential impacts of human
556 disturbance on wintering tropical shorebirds. Oryx 42, 415.

557 Yates, M.G., Goss-Custard, J.D., McGrorty, S., Lakhani, K.H., Durell, S.L.V.D., Clarke, R.T., Rispin,
558 W.E., Moy, I., Yates, T.J., Plant, R.A., 1993. Sediment characteristics, invertebrate densities and
559 shorebird densities on the inner banks of the Wash. Journal of Applied Ecology, 599-614.

560 Zwarts, L., 1988. Numbers and distribution of coastal waders in Guinea-Bissau. Ardea 76, 42-55.

561 Zwarts, L., Blomert, A.M., 1992. Why knot *Calidris canutus* take medium-sized *Macoma balthica*
562 when six prey species are available. Marine Ecology Progress Series 83, 113-128.

563 Zwarts, L., Wanink, J.H., 1991. The macrobenthos fraction accessible to waders may represent
564 marginal prey. Oecologia 87, 581-587.

565

566

567 **Table captions**

568

569

570 Table 1. Result of the Poisson regression for the Oystercatcher. $0<p<0.001$ (***); $0.001<p<0.01$ (**);
571 $0.01<p<0.05$ (*); $0.05<p<0.1$ (.). Null deviance: 340.66 on 128 *df*; Residual deviance: 265.46 on 115
572 *df*. AIC: 546.25. r2ML: 44%, r2CU: 44%. MEA: mean grain-size of sediment; MED: median grain
573 size; ALT: altitude (shore elevation); STR: shear stress resistance; MOR: organic matter of sediment;
574 H2O: water content of sediment; RICH: richness: ABUN: total abundance; BIOT: total biomass of
575 benthic macrofauna; BIOB: total biomass of bivalves except *Cerastoderma edule*; BIOO: total bio-
576 mass of benthic macrofauna except bivalves; BIOC1: total biomass of *C. edule* (<10 mm); BIOC2:
577 total biomass of *C. edule* (15-25 mm)

578

579 Table 2. Result of the Poisson regression for the Bar-tailed Godwit. $0<p<0.001$ (***); $0.001<p<0.01$
580 (**); $0.01<p<0.05$ (*); $0.05<p<0.1$ (.). Null deviance: 273.96 on 128 *df*; Residual deviance: 168.27
581 on 115 *df*. AIC: 306.32. r2ML: 56%, r2CU: 59%. MEA: mean grain-size of sediment; MED: median
582 of sedigrain sizement; ALT: altitude (shore elevation); STR: shear stress resistance; MOR: organic
583 matter of sediment; H2O: water content of sediment; RICH: richness: ABUN: total abundance; BIOT:
584 total biomass of benthic macrofauna; BIOB: total biomass of bivalves except *Cerastoderma edule*;
585 BIOO: total biomass of benthic macrofauna except bivalves; BIOC1: total biomass of *C. edule* (<10
586 mm); BIOC2: total biomass of *C. edule* (15-25 mm)

587

588 Table 3. Result of the Poisson regression for the Redknot. $0<p<0.001$ (***); $0.001<p<0.01$ (**);
589 $0.01<p<0.05$ (*); $0.05<p<0.1$ (.). Null deviance: 326.26 on 128 *df*; Residual deviance: 226.33 on 115
590 *df*. AIC: 463.46. r2ML: 54%, r2CU: 54%. MEA: mean grain-size of sediment; MED: median grain
591 size; ALT: altitude (shore elevation); STR: shear stress resistance; MOR: organic matter of sediment;
592 H2O: water content of sediment; RICH: richness: ABUN: total abundance; BIOT: total biomass of

593 benthic macrofauna; BIOB: total biomass of bivalves except *Cerastoderma edule*; BIOO: total bio-

594 mass of benthic macrofauna except bivalves; BIOC1: total biomass of *C. edule* (<10 mm); BIOC2:

595 total biomass of *C. edule* (15-25 mm)

596

597 Table 4. Result of the Poisson regression for the eurasian Curlew. $0 < p < 0.001$ (***); $0.001 < p < 0.01$

598 (**); $0.01 < p < 0.05$ (*); $0.05 < p < 0.1$ (.). Null deviance: 297.28 on 128 *df*; Residual deviance: 241.23

599 on 115 *df*. AIC: 509.71. r2ML: 35%, r2CU: 35%. MEA: mean grain-size of sediment; MED: median

600 grain size; ALT: altitude (shore elevation); STR: shear stress resistance; MOR: organic matter of sedi-

601 ment; H2O: water content of sediment; RICH: richness: ABUN: total abundance; BIOT: total biomass

602 of benthic macrofauna; BIOB: total biomass of bivalves except *Cerastoderma edule*; BIOO: total bi-

603 omass of benthic macrofauna except bivalves; BIOC1: total biomass of *C. edule* (<10 mm); BIOC2:

604 total biomass of *C. edule* (15-25 mm)

605

606 **Figure captions**

607 Figure 1. Benthic intertidal assemblages identified in the bay of Saint-Brieuc. Points correspond to the

608 131 stations of the regular sampling network.

609

610 Figure 2. Foraging area used by Redknot, Curlew, Bar-tailed Godwit, and Oystercatcher in the bay of

611 Saint-Brieuc.

612

TABLES

613
614
615
616   Table 1
617   Result of the Poisson regression for the Oystercatcher. $0<p<0.001$ (***); $0.001<p<0.01$ (**); $0.01<$
618    $p<0.05$ (*); $0.05< p<0.1$ (.). Null deviance: 340.66 on 128 *df*; Residual deviance: 265.46 on 115 *df*.
619   AIC: 546.25. r2ML: 44%, r2CU: 44%.
620   MEA: mean grain-size of sediment; MED: median grain size; ALT: altitude (shore elevation); STR:
621   shear stress resistance; MOR: organic matter of sediment; H2O: water content of sediment; RICH:
622   richness: ABUN: total abundance; BIOT: total biomass of benthic macrofauna; BIOB: total biomass of
623   bivalves except *Cerastoderma edule*; BIOO: total biomass of benthic macrofauna except bivalves;
624   BIOC1: total biomass of *C. edule* (<10 mm); BIOC2: total biomass of *C. edule* (15-25 mm)

	Estimate	*Std. Error*	*z value²*	*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
BIOO	-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

625
626

627 Table 2

628 Result of the Poisson regression for the Bar-tailed Godwit. $0<p<0.001$ (***); $0.001< p<0.01$ (**);

629 $0.01< p<0.05$ (*); $0.05< p<0.1$ (.). Null deviance: 273.96 on 128 *df*; Residual deviance: 168.27 on 115

630 *df*. AIC: 306.32. r2ML: 56%, r2CU: 59%.

631 MEA: mean grain-size of sediment; MED: median grain size; ALT: altitude (shore elevation); STR:

632 shear stress resistance; MOR: organic matter of sediment; H2O: water content of sediment; RICH:

633 richness: ABUN: total abundance; BIOT: total biomass of benthic macrofauna; BIOB: total biomass of

634 bivalves except *Cerastoderma edule*; BIOO: total biomass of benthic macrofauna except bivalves;

635 BIOC1: total biomass of *C. edule* (<10 mm); BIOC2: total biomass of *C. edule* (15-25 mm)

	Estimate	*Std. Error*	*z value²*	*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
BIOO	-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 .

636

637

638 Table 3
639 Result of the Poisson regression for the Redknot. 0<p<0.001 (***); 0.001<p<0.01 (**); 0.01<p<0.05
640 (*); 0.05<p<0.1 (.). Null deviance: 326.26 on 128 *df*; Residual deviance: 226.33 on 115 *df*. AIC:
641 463.46. r2ML: 54%, r2CU: 54%.
642 MEA: mean grain-size of sediment; MED: median grain size; ALT: altitude (shore elevation); STR:
643 shear stress resistance; MOR: organic matter of sediment; H2O: water content of sediment; RICH:
644 richness: ABUN: total abundance; BIOT: total biomass of benthic macrofauna; BIOB: total biomass of
645 bivalves except *Cerastoderma edule*; BIOO: total biomass of benthic macrofauna except bivalves;
646 BIOC1: total biomass of *C. edule* (<10 mm); BIOC2: total biomass of *C. edule* (15-25 mm)

	Estimate	Std. Error	z value²	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
BIOO	-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 *

647
648

649 Table 4

650 Result of the Poisson regression for the eurasian Curlew. 0 <p< 0.001 (***); 0.001< p<0.01 (**);

651 0.01< p< 0.05 (*); 0.05< p<0.1 (.). Null deviance: 297.28 on 128 *df*; Residual deviance: 241.23 on 115

652 *df*. AIC: 509.71. r2ML: 35%, r2CU: 35%.

653 MEA: mean grain-size of sediment; MED: median grain size; ALT: altitude (shore elevation); STR:

654 shear stress resistance; MOR: organic matter of sediment; H2O: water content of sediment; RICH:

655 richness: ABUN: total abundance; BIOT: total biomass of benthic macrofauna; BIOB: total biomass of

656 bivalves except *Cerastoderma edule*; BIOO: total biomass of benthic macrofauna except bivalves;

657 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
BIOO	-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

658
659