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► To cite this version:

Céline Rolet, Nicolas Spilmont, Dominique Davoult, Eric Goberville, Christophe Luczak. Anthropogenic impact on macrobenthic communities and consequences for shorebirds in Northern France: a complex response. *Biological Conservation*, 2015, 184, pp.396-404. 10.1016/j.biocon.2015.02.016 . hal-01128368

HAL Id: hal-01128368

<https://hal.science/hal-01128368>

Submitted on 29 Sep 2015

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1 **Anthropogenic impact on macrobenthic communities and consequences for shorebirds**
2 **in Northern France: a complex response**

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34 21 Submitted to Biological Conservation

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36 22
37
38 23 Number of references: 80

39 24 Number of figures: 4

40 25 Number of tables: 1

41 26 Number of appendices: 3

42 27 Number of words in the abstract: 240

43 28 Number of words in the main text: 4826

30 **Abstract**

1
2 31 Shorebird populations are declining worldwide due to the combined effect of climate change
3 32 and anthropogenic forcing, the ongoing coastal urbanisation amplifying the alteration of their
4 33 habitat in both rate and magnitude. By focusing on a highly anthropogenically-influenced
5 34 region in Northern France, we studied the impact of a seawall construction on wintering
6 35 shorebird populations through potential alterations in the abundance and availability of their
7 36 food resources. We concurrently investigated changes in the spatial distribution of muddy-
8 37 sand beach macrobenthic communities between two periods of contrasting anthropogenic
9 38 impacts and examined year-to-year trends of wintering shorebirds. Our study reveals that the
10 39 seawall construction led to a major spatial reorganisation of the macrobenthic communities
11 40 with a drastic reduction of the muddy-sand community. However, no relation between
12 41 macrobenthic changes and shorebird abundances was detected. Fluctuations in shorebird
13 42 abundances appeared to be congruent with flyway population trends. This result suggests that
14 43 the response of shorebirds to human-induced perturbations is much more complex than
15 44 expected. While an assessment of potential disturbances induced by coastal engineering
16 45 constructions is needed, the pathways by which alterations could propagate through an
17 46 ecosystem are not linear and as such difficult to determine. Ecosystems appear as complex
18 47 adaptive systems in which macroscopic dynamics emerge from non-linear interactions at
19 48 entangled smaller/larger scales. Our results confirm that an in-depth knowledge of the local,
20 49 regional and global factors that influence trends of shorebirds and their habitat use is essential
21 50 for accurate and effective management and conservation strategies.

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27 51 **Keywords:** shorebirds, macrobenthic communities, anthropogenic impact, coastal
28 52 conservation, complexity
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54 **1. Introduction**

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2 55 The world's ocean shores, mainly dominated by sandy beaches (Schlacher et al., 2008),
3 56 represent an important component in processing large quantities of organic material and
4 57 recycling nutrients back to coastal waters (McLachlan and Brown, 2006). These zones also
5 58 provide permanent or transitory habitats for many invertebrates (zooplankton, benthic macro-
6 59 and meiofauna and insects) and vertebrates (fishes, turtles and shorebirds) for reproduction,
7 60 nurseries, migration or feeding (Schlacher et al., 2008; Defeo et al., 2009). In beach
8 61 ecosystems, primary and secondary consumers, mostly represented by benthic organisms
9 62 (Raffaelli and Hawkins, 1999), are consumed by top-predators such as shorebirds and fishes
10 63 (Dugan et al., 2003; McLachlan and Brown, 2006).

13
14 64 Because of low food resources compared to estuarine and wetlands systems (Spruzen et
15 65 al., 2008), sandy beaches are generally not considered as important feeding areas for
16 66 shorebirds. Since coastal wetlands have become scarce (Hubbard and Dugan, 2003), some
17 67 sandy beaches, especially those with muddy patches, may have become as attractive as
18 68 estuaries and wetlands systems for foraging shorebirds (Burger et al., 1997; McLusky and
19 69 Elliott, 2004; Van de Kam et al., 2004; Spruzen et al., 2008). However, previous studies have
20 70 shown that birds are the most abundant and diverse vertebrate species encountered in these
21 71 beaches (Burton, 2012). Buffer effect (Gill et al., 2001) and refuge during cold winter periods
22 72 in north-western Europe (Camphuysen et al., 1996; Marzec and Luczak, 2005) have been
23 73 suggested as potential factors influencing the use of these *a priori* low attractive habitats.

26
27 74 Beach areas provide a wide range of economical services for human settlements,
28 75 development and local subsistence (Defeo et al., 2009). As a result, more than 60% of the
29 76 world's population are currently living less than 60 km away from the sea (IPCC, 2007).
30 77 Urbanisation is thus becoming increasingly important and the growing human pressure on
31 78 beach ecosystems has significantly reduced both the number and the area of species habitats
32 79 (Schlacher et al., 2008). Both engineering constructions (e.g. dykes, pipelines, harbours...) and
33 80 recreational activities (e.g. swimming, camping, vehicles...) could induce drastic changes
34 81 in the distribution, diversity and abundance of macrobenthic species (Lewis et al., 2003;
35 82 Bertasi et al., 2007; Schlacher et al., 2008; Schlacher and Thompson, 2007, 2012). This
36 83 human fingerprint could directly and indirectly influence shorebird species (Goss-Custard and
37 84 Verboven, 1993) by disturbing their foraging behaviour (e.g. less time to feed; Thomas et al.,
38 85 2003), their breeding success as well as their nesting behaviour (Lord et al., 1997, 2001).
39 86 Global warming is another source of significant perturbation and climate-induced changes in
40 87 the physiology, phenology and biogeography of species, leading sometimes to ecosystem
41 88 reorganisations that have been already documented (Parmesan, 2006; Beaugrand et al., 2009;
42 89 Luczak et al., 2012). Temperature is a cardinal factor governing changes in both biological
43 90 and ecological systems from the individual to the community level (Goberville et al., 2014).
44 91 Sea-level rise and extreme climatic events could alter marine habitats by modifying coastal
45 92 landscapes and beach morphology (Harris et al., 2011).

50
51 93 Along the French coast of the Southern Bight of the North Sea, the "Hemmes de Marck"
52 94 is the only major muddy-sand beach representing an attractive feeding area for shorebirds
53 95 (Marzec and Luczak, 2005; Spilmont et al., 2009). However, the Calais harbour extension and
54 96 a seawall construction in 1984 induced the destruction of two main habitats: a pond/marsh
55 97 area and the aerial dunes as well as a high modification of the hydro-sedimentary dynamics
56 98 and processes in this area (Richard et al., 1980; Hequette and Aernouts, 2010). In the present
57 99 study, we investigated spatio-temporal changes in both muddy-sand beach communities and
58 100 potential consequences on staging wintering shorebird populations. First, we compared the

101 spatial distribution of the macrobenthic communities between the year 1982 (i.e. two years
1 102 before the harbour extension) and the year 2010 (i.e. 26 years later). We then evaluated year-
2 103 to-year changes in shorebird abundances from 1980 to 2012 to identify a possible relationship
3 104 with changes in their food resources (i.e. macrobenthic communities). Finally, we discussed
4 105 the implementation of management plans for effective shorebird conservation strategies.

6 7 106 **2. Materials and methods**

8 9 107 *2.1. Study site*

10
11 108 Highly impacted by anthropogenic activities, the French coast of the Southern Bight of the
12 109 North Sea has three important harbours: Boulogne-sur-Mer (fishing activities), Calais
13 110 (passenger travels) and Dunkerque (freight transport), constructions which have caused a
14 111 decrease in habitat availability for many species (Richard et al., 1980). This part of the coast
15 112 is mainly constituted by small estuarine areas and dissipative beaches (Rolet et al., 2014).
16 113 Among these dissipative beaches, “The Hemmes de Marck” beach, located less than 5
17 114 kilometres east from Calais harbour (Northern France; Fig. 1), is of great importance for
18 115 wintering and staging shorebirds because of its broad intertidal zone (up to 1500 meters
19 116 width), its muddy-sand patches and its location on the East Atlantic flyway, a biogeographic
20 117 entity encompassing the Atlantic coasts of Europe (Greenland included) and West Africa
21 118 (Marzec and Luczak, 2005; Delany et al., 2009). The tidal regime is semi-diurnal and
22 119 macrotidal, the tidal range decreasing from 6.4 m in Calais to 5.6 m in Dunkerque (SHOM,
23 120 1968). Due to sand supply generated by the onshore migration and coastal welding of a
24 121 nearshore sand bank, this site is the only in significant accretion in the region (Reichmuth and
25 122 Anthony, 2007; Hequette and Aernouts, 2010).

26 27 28 29 30 123 *2.2. Sampling strategy*

31
32 124 Sampling was carried out in autumn 1982 and 2010. To avoid potential biases due to any
33 125 sampling changes, we used the same sampling strategy in 2010 than in 1982. For both
34 126 periods, 17 stations (with three replicates per station) were sampled. Samples were collected
35 127 with a corer (1/40 m² down to a depth of 0.25 m) and washed through a 1 mm mesh sieve.
36 128 After sieving, all samples were immediately fixed and preserved in an 8% formaldehyde-
37 129 seawater solution. At each station, one sediment core was sampled for granulometry analysis.

40 130 *2.3. Laboratory work*

41
42 131 In the laboratory, the sieved samples were sorted and macrobenthic organisms were
43 132 counted and identified to the species level, except for Oligochaetes, Nematodes and some
44 133 damaged amphipods (which represent 1% and 2% of the total abundance in both 1982 and
45 134 2010). Faunal densities were expressed as the number of individuals per m² (ind.m⁻²).
46 135 Biomass was determined as ash free dry weight (g of AFDW.m⁻² after 6h drying at 520°C) for
47 136 each station (ICES, 1986). Granulometry was analysed by dry sieving through a nested series
48 137 of sieves with mesh sizes decreasing from 5 to 0.05 mm. Sediment grain size was grouped
49 138 into six categories according to the Larsson classification (1977): mud (< 0.05 mm), fine
50 139 sands (≥ 0.05-0.2 mm), medium sands (≥ 0.2-0.5 mm), coarse sands (≥ 0.5-2 mm), fine
51 140 gravels (≥ 2-5 mm) and coarse gravels (≥ 5-20 mm).

52 141 *2.4. Statistical analysis and mapping of macrobenthic communities*

53
54
55 142 For each sampling year (1982 and 2010), macrobenthic assemblages were identified
56 143 following the methods recommended by Clarke and Warwick (2001). Average agglomerative
57 144 clustering and non-metric multidimensional scaling (MDS) analyses were computed on Bray-

145 Curtis similarity matrices after 4th root transformation of species abundances to moderate the
146 influence of dominant species (Clarke and Warwick, 2001). ANOSIM randomisation test
147 (Clarke and Green, 1988) was performed to test the statistical significance of the groups
148 obtained from the previous classification within each year. Discriminating species, which
149 significantly ($p < 0.05$) contributed to segregate the different groups, were identified using the
150 similarity percentage routine (SIMPER). A non-parametric (permutational; 999 permutations)
151 multivariate analysis of variance (PERMANOVA; Anderson, 2001) was used to test
152 hypothesis about macrobenthic assemblage differences between the two sampling years (1982
153 and 2010). All analyses were performed with the Plymouth Routines in Multivariate Research
154 (PRIMER[®]) software version v6 (Clarke and Gorley, 2006). Macrobenthic communities
155 identified by multivariate analyses (cluster and MDS) were then combined with the ‘Direct
156 Field Observation’ (DFO) method proposed by Godet et al. (2009) and habitats were
157 determined using the EUNIS classification (Davies et al., 2004; Connor et al., 2004). The
158 different habitats obtained were then mapped in both 1982 and 2010, using aerial photographs
159 (© Ortho Littorale 2000) coupled with a Geographic Information System (ArcGIS 10[®]). From
160 this mapping and for both years, surfaces of each macrobenthic communities were calculated
161 based on the beach surface during low waters of spring tides. Mann-Whitney-Wilcoxon and
162 Kruskal-Wallis tests (Zar, 2014) were respectively used to test temporal (1982 *versus* 2010)
163 and spatial (within 1982 and 2010) differences ($p < 0.05$) in densities, biomasses and species
164 richness for each macrobenthic community.

2.5. Long-term changes in shorebird populations

166 Changes in coastal shorebird abundances in the studied area were investigated using data
167 from annual reports of the wintering shorebirds monitoring programme (mid-January counts)
168 conducted from 1980 to 2012 (except in 2006 and 2007) in the context of the European
169 wetland bird survey (Wetlands International; Mahéo, 1980 to 2012). Because rare species
170 may reflect stochastic sampling effects (Poos and Jackson, 2012), decrease the signal-to-noise
171 ratio (Borcard et al., 2011) and cause analytical issues (Legendre and Legendre, 2012), only
172 shorebirds with a presence $> 2\%$ over the period 1980-2012 were selected (99% of the total
173 abundance; supplementary material appendix A; in bold). This procedure allowed the
174 selection of 5 species: Red knot *Calidris canutus islandica*, Sanderling *Calidris alba*, Dunlin
175 *Calidris alpina*, Oystercatcher *Haematopus ostralegus* and Grey plover *Pluvialis squatarola*
176 (supplementary material appendix A; in bold). Since species abundance data (number of
177 shorebirds counted during the period) exhibited skewed distributions, data were log-
178 transformed before performing further analysis (Jolliffe, 2005).

179 To extract major long-term changes in both the abundance and composition of coastal
180 shorebird populations in the “Hemmes de Marck” beach from 1980 to 2012, a standardised
181 principal component analysis (PCA for table with missing data; Bouvier, 1977) was
182 performed on the correlation matrix (30 years \times 5 species) and the first two principal
183 components were retained for further examination. This approach allowed in a single analysis
184 (1) the characterisation of the main long-term pattern in species, (2) the examination of
185 synchronicity (the correlation between each species and the principal components) and (3) the
186 detection of potential temporal discontinuity (Legendre and Legendre, 2012).

187 As a complement, individual species trends were tested using a non-parametric Spearman
188 rank correlation (ρ) between observations and time. Significance was evaluated with 1000
189 permutations (Legendre and Legendre, 2012). Analyses were performed with the “trend.test”
190 function of the R package “Pastecs” (Grosjean and Ibanez, 2002).

191 2.6. *Shorebirds spatial distribution*

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3 192 To identify feeding areas of shorebirds in the tidal flat, the study area was visited 10 times
4 193 during January following macrobenthos sampling (i.e. 1983 and 2011) at low tide +/- 2h.
5 194 During each visit, all the feeding birds were mapped. Birds were observed through a 40x
6 195 (Kowa TS-1 in 1983) and 20-60x zoom (Leica apo-televid in 2011) by a single observer from
7 196 a vantage point 50-1000 m from the birds, and level with or above it.

9
10 197 The synthesis of the feeding areas data were mapped for both 1983 and 2011 winter
11 198 periods using the mapping software ArcGIS 10[®] and overlaid on macrobenthic data
12 199 independently obtained.

13
14 200 **3. Results**

15
16 201 3.1. *Distribution of macrobenthic communities before the harbour extension (in*
17 202 *1982)*

18
19 203 Three macrobenthic assemblages were distinguished in 1982 by the cluster and MDS
20 204 analyses (MDS stress 0.13; ANOSIM 0.78; $p < 0.001$; supplementary material appendix B.1).

21
22 205 The first assemblage was the Polychaetes/Bivalves community dominated by muddy-sand
23 206 (A2.24 according to the EUNIS classification). Located in the upper intertidal part of the
24 207 entire study site and in the mid shore in the centre of the study area (in yellow; Fig. 2a), this
25 208 community covered 4.72 km² of the intertidal area in 1982 (Table 1). It was dominated by the
26 209 amphipod *Corophium arenarium* (68%) and the gastropod *Peringia ulvae* (28%).

27
28 210 The second community was located in the mid shore (in blue; Fig. 2a), covered 3.53 km²
29 211 of the studied beach (Table 1) and corresponded to the Amphipods and *Scolecopsis spp.* in
30 212 littoral medium-fine sand community (A2.223). The main species were the isopods *Eurydice*
31 213 *spp.* (28%), the amphipods *Bathyporeia spp.* (19%) and the polychaete *Scolecopsis squamata*
32 214 (8%).

33
34 215 The third assemblage, the Polychaetes/Amphipods dominated fine sand shores community
35 216 (A2.23), was located in the lower shore of the study site (in green; Fig. 2a) and covered a
36 217 surface of 8.14 km² (Table 1). It was dominated by the amphipods *Bathyporeia spp.* (15%),
37 218 *Haustorius arenarius* (17%) and *Urothoe brevicornis* (9%), and the polychaete *Nephtys*
38 219 *cirrosa* (5%).

39
40 220 These three macrobenthic communities had similar densities and biomasses (Table 1).
41 221 After application of a Kruskal-Wallis test (threshold $p < 0.05$), we only detected a significant
42 222 difference between sandy community species richness (A2.23; 9.0 ± 3.2 species; Table 1) and
43 223 muddy-sand community species richness (A2.24; 4.7 ± 1.9 species; Table 1).

44
45 224 The strandline (A2.21), located along the dunes, was determined using the DFO method
46 225 as no benthic sampling was performed in this area (in orange; Fig. 2a). This community
47 226 covered an area of 0.26 km² (Table 1).

48
49 227 3.2. *Distribution of macrobenthic communities 28 years later (in 2010)*

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51 228 While the cluster and MDS analyses applied for data sampled in 2010 revealed the same
52 229 EUNIS communities as those identified in 1982 (i.e. A2.24, A2.223 and A2.23; MDS stress
53 230 0.12; ANOSIM 0.53; $p < 0.001$; supplementary material appendix B.2), the multivariate

231 analysis performed on macrobenthic assemblages displayed a significant effect of years
1 232 (PERMANOVA: Pseudo- $F = 2.3214$; $p < 0.05$).

2
3 233 Indeed, the Polychaetes/Amphipods dominated fine sand community appeared more
4 234 dispersed in the MDS than 28 years before (supplementary material appendix B.2). Similar
5 235 patterns were found, but to a lesser extent, for the Amphipods and *Scolecopsis spp.* in littoral
6 236 medium-fine sand community. While the dominant species in each community were the same,
7 237 densities, biomasses and the distribution of communities were highly modified.

8
9
10 238 The Polychaetes/Bivalves dominated muddy-sand community (in yellow) showed higher
11 239 densities in 2010 (Mann-Whitney-Wilcoxon test, $p < 0.05$; Table 1) and its biomass increased
12 240 by a factor of 7 between 1982 and 2010, due to high densities of both *Peringia ulvae* and
13 241 *Corophium arenarium* (80% and 14% of the total abundance, respectively). Densities and
14 242 biomasses were significantly higher in this muddy-sand community than in the two other
15 243 sandy communities identified in 2010 (Kruskall-Wallis test, $p < 0.05$). The amphipod
16 244 *Bathyporeia pilosa* (42%), the polychaete *Pygospio elegans* (23%) and the isopods *Eurydice*
17 245 *spp.* (10%) dominated the Amphipods and *Scolecopsis spp.* in littoral medium-fine sand
18 246 community (in blue). The Polychaetes/Amphipods dominated fine sand shores community (in
19 247 green) was dominated by the polychaetes *Scolecopsis squamata* and *Nephtys cirrosa* (29% of
20 248 the total abundance), the crustaceans *Eurydice spp.* (15%) and *Bathyporeia pelagica* (6%).

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23
24 249 A major spatial reorganisation of benthic communities occurred between 1982 and 2010
25 250 (Fig. 2): the muddy-sand community dominated by Polychaetes and Bivalves lost 56% of its
26 251 surface (2.08 km² in 2010 *versus* 4.72 km² in 1982) whereas coverages of other communities
27 252 increased (65% for the strandline, 55% for the Amphipods and *Scolecopsis spp.* in littoral
28 253 medium-fine sand community and 7% for the Polychaetes/Amphipods dominated fine sand
29 254 shores community; Table 1). The muddy-sand community disappeared, firstly from the
30 255 western part of the studied area, replaced by the Polychaetes/Amphipods dominated fine sand
31 256 shores community, and secondly from the highest tidal levels replaced by the strandline and
32 257 the Amphipods and *Scolecopsis spp.* in littoral medium-fine sand community.

36 258 3.3. Long-term changes in shorebird abundances

37
38 259 Year-to-year changes in the first principal component (PC1; 41% of the total variability)
39 260 of the PCA applied on shorebird abundances showed low values (mostly negative) of the
40 261 component from 1980 to the mid-90's, followed by a rapid increase in the trend and relatively
41 262 high values (mostly positive) from 1996 until 2012 (Fig. 3a). Examination of the first
42 263 eigenvector indicated that Sanderling (*Calidris alba*), Oystercatcher (*Haematopus ostralegus*)
43 264 and, to a lesser extent, Red knot (*Calidris canutus islandica*) were positively correlated to the
44 265 PC1 (Fig. 3b), suggesting an increase in their abundances. In contrast, Grey plover (*Pluvialis*
45 266 *squatarola*) and Dunlin (*Calidris alpina*) were negatively correlated to this component (Fig.
46 267 3b), indicating a decline in their abundances over the last 30 years. The second principal
47 268 component (PC2; 27% of the total variability) appeared more affected by episodic events and
48 269 no major trend was detected (supplementary material appendix C.1). Long-term changes in
49 270 the PC2 showed low values of the component from 1980 to the mid-90's, followed by an
50 271 alternation between positive and negative values. Examination of the second eigenvector
51 272 indicated that Red knot and Dunlin predominantly contributed to changes, revealing a
52 273 significant reduction in their abundances in 1998-1999 and 2003-2004 (supplementary
53 274 material appendix C.2).

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59 275 Looking at each species trend for the period 1980-2012, Red knot, Sanderling and
60 276 Oystercatcher abundances significantly increased (Spearman rank correlation ρ of 0.35 ($p <$

0.05), 0.56 ($p < 0.01$) and 0.42 ($p < 0.05$), respectively; Fig. 4a-c), while Grey plover significantly decreased ($\rho = -0.50$, $p < 0.005$; Fig. 4d). No significant trend was noted for Dunlin (Fig. 4e) and the total shorebird abundances (Fig. 4f). Looking at each species trend before and after 1997 (i.e. change detected by examination of the first principal component; Fig. 3a), Sanderling was the only species with a significant increasing trend ($\rho = 0.41$, $p < 0.05$) between 1980 and 1996 (Fig. 4b). No significant trend was observed for the 1997-2012 period.

3.4. Associations between shorebirds and macrobenthic communities

For the two years, feeding shorebirds were located in the high and mid shore in the centre of the study area (Fig. 2). They were also found in the high shore of the western part of the beach in 1982 (Fig. 2a).

In 1982, 56% of the area used by shorebirds was located in the muddy-sand community dominated by Polychaetes and Bivalves, 31% in the Amphipods and *Scolecopsis spp.* in littoral medium-fine sand community, 11% in the fine sand community dominated by Polychaetes and Amphipods and only 2% in the strandline.

In 2010, concurrent with changes in macrobenthic communities (i.e. in densities, biomasses and spatial distribution), our results revealed changes in shorebird feeding zones (Fig. 2b): 48% of the feeding area was located in the muddy-sand community dominated by Polychaetes and Bivalves, 51% in the Amphipods and *Scolecopsis spp.* in littoral medium-fine sand community and 1% in the strandline. No bird was observed feeding or foraging in the fine sand community dominated by Polychaetes and Amphipods.

4. Discussion

In a preliminary study of the potential impact of the Calais harbour extension, Richard et al. (1980) speculated on a spatial modification of sediment characteristics with a huge reduction in muddy sediments. This predicted reduction occurred rapidly (Luczak and Dewarumez, pers. obs.). However, this anthropogenic forcing does not appear to influence all the regions of the French coast of the Southern Bight of the North Sea. For instance, the Gravelines beach, located 10 kilometres east from the Hemmes de Marck and characterised by the same four macrobenthic communities as those determined in our study site (Rolet et al., 2014), was not consistently impacted over the period 1978-2013 (Dewarumez, 1978 to 2013). This statement raised the following questions: Did the harbour extension influence the distribution of macrobenthic communities in the Hemmes de Marck beach? Did this anthropogenic perturbation propagate through the food web to influence top-predators such as wintering shorebirds?

The first hypothesis was supported by analyses that the harbour extension led to a drastic reduction in the muddy-sand community and a spatial reorganisation of macrobenthic communities. However, the second hypothesis was partially supported. No direct causal relation between food availability and changes in shorebird abundances was detected. Ecological processes that influence shorebird populations appear more complex than expected.

4.1. Changes in the spatial distribution of intertidal macrobenthic communities

Substantial changes in the spatial distribution of macrobenthic communities were detected in the “Hemmes de Marck” beach between 1982 and 2010. In 1982, before the Calais harbour

320 extension and the seawall construction (in 1984), a muddy-sand community dominated by
1 321 Polychaetes and Bivalves, occupied the major part of the intertidal area, whereas between
2 322 1982 and 2010, the Amphipods and *Scolecopsis spp.* in littoral medium-fine sand community
3 323 nearly doubled its surface. Hequette and Aernouts (2010) recently suggested an influence of
4 324 the Calais harbour wall on both the shoreline dynamic and the sedimentary environment in the
5 325 beach east of Calais. While mud constituted 12% of the sediment in this area in 1982, it only
6 326 represented 0.03% in 2010. These changes in sediment grain size induced a spatial
7 327 reorganisation and a turn-over in macrobenthic fauna: species living in muddy-sand sediment
8 328 disappeared from the eastern and western parts of the area (i.e. *Corophium arenarium* and
9 329 *Pygospio elegans*) and were replaced by sand affinity species (i.e. *Scolecopsis squamata* and
10 330 *Nephtys cirrosa*) or opportunistic species such as Oligochaeta and Nematoda. This result is in
11 331 accordance with Ahn and Choi (1998) who observed an increase in coarse sediments and a
12 332 shift in species dominance in an intertidal sandflat on the west coast of Korea after a seawall
13 333 construction. At the same time, the surface of the littoral medium-fine sand community
14 334 dominated by Amphipods and *Scolecopsis spp.* increased by 56% in surface area and its faunal
15 335 composition appeared more heterogeneous in 2010 than in 1982. This pattern is the
16 336 consequence of an ecosystem reorganisation which is characteristic of a complex adaptive
17 337 system (Levin, 1999; Frontier et al., 2008). Our study suggests that the seawall construction
18 338 caused major changes in hydrological conditions and sedimentary composition that directly
19 339 impacted the spatial distribution of macrobenthic communities in the “Hemmes de Marck”
20 340 beach. Such alteration, by propagation through the food web, should be expected to influence
21 341 higher trophic levels (e.g. fishes, shorebirds; Van de Kam et al., 2004).

27 342 4.2. Long-term changes in shorebird abundances and interactions with 28 343 macrobenthic communities 29 344

30 345 While a patent influence of the seawall construction was observed on macrobenthic
31 346 species, leading to a spatial reorganisation of these communities, no major change in overall
32 347 shorebird abundances was detected. Total shorebird abundances remained stable
33 348 (approximately 1000 shorebirds; mean 1045 ± 504), but with higher fluctuations post-1997.
34 349 During the period 1982-2010, the trends in wintering shorebird abundances matched with
35 350 those observed at larger scales at the species level (Delany et al., 2009; Wetlands
36 351 International, 2014).

37 352 Since the last decade, the study site has hosted increasingly important Knot numbers.
38 353 Even if no fluctuation with any clear trend was measured on long-term at the global flying
39 354 population (Wetlands International, 2014), recent increases in Red knot were also observed in
40 355 the U.K and the Netherlands over the ten seasons prior to 2006-2007 (Thaxter et al., 2010;
41 356 Hornman et al., 2011; Balmer et al., 2013). *Macoma balthica*, *Cerastoderma edule* and
42 357 *Peringia ulvae* are the mollusc species that dominate the diet of the Knot across Western
43 358 Europe (Quaintenne et al., 2010). *Peringia ulvae* appeared particularly abundant in the
44 359 muddy-sand community (A2.24) and might therefore represent a safe and predictable stock
45 360 for this molluscivore shorebird (Quaintenne et al., 2013).

46 361 Trends observed for Dunlin, Grey plover and Sanderling in the study site were congruent
47 362 with the pattern observed at the global flyway populations (Wetlands International, 2014). We
48 363 stress that the rise of Sanderling is locally related to the spatial extension of the “Amphipods
49 364 and *Scolecopsis spp.* in littoral-medium fine sand community” (+55% between 1982 and 2010).
50 365 This benthic community hosted a higher number of shorebirds in 2010 (+32%) and provided
51 366 an important food resource for this shorebird species: e.g. *Bathyporeia spp.* and *Scolecopsis
52 367 squamata* (Smit & Wolf, 1981; Vanermen et al., 2009). This pattern is the synergistic result of
53 368

367 a cross-scale interaction (Frontier et al., 2008): a local evolution of macrobenthic
1 368 communities that turns out to be a huge food resource area in the context of an overall
2 369 increase in the Sanderling flyway population. A closer examination of time series of Grey
3 370 plover revealed an evolution similar to that observed in U.K.: wintering number increased
4 371 from the 1980's to the mid-90's and has since declined. At a larger spatial scale, it remains
5 372 unclear whether these changes reflect a large-scale redistribution in response to climate
6 373 change (Maclean et al., 2008) or a population decline (Delany et al., 2009).

9 374 While a long-term decline in Oystercatcher occurred at the flyway population at large
10 375 scale (-1.6% *p.a.* 1983-2007; Wetlands International, 2014), a significant increase in this
11 376 species occurred during the overall period in the "Hemmes de Marck" beach. This feature
12 377 may be related to fluctuations among regions (Austin et al., 2000). As part of a refuge zone in
13 378 Northern France (Marzec and Luczak, 2005), the "Hemmes de Marck" beach holds a
14 379 substantial number of wintering Eurasian Oystercatcher during severe winter conditions
15 380 (Camphuysen et al., 1996) as observed in 1996/1997 (Marzec and Luczak, 2005).
16 381 Biogeographic movements in response to cold weather appear an important climate-related
17 382 driving force behind interannual changes at this site scale (Maclean et al., 2008) with a
18 383 longer-time consistent change that could be explained by a buffer effect at a regional scale
19 384 (Gill et al., 2001; Marzec and Luczak, 2005; Maclean et al., 2008; Dolman, 2012). In this
20 385 context, mussel cultivation close to the "Hemmes de Marck" beach might be an attractive
21 386 factor for this species (Goss-Custard, 1996; Caldow et al., 2003; Roycroft et al., 2004).

26 387 In our study, we did not detect an immediate response of shorebirds to modifications in
27 388 macrobenthic communities. The distribution and availability of food resources did not appear
28 389 to be the main driver of shorebird populations during the period 1980-2012 in our study site,
29 390 i.e. at a local spatial scale. However, our results revealed a major modification in shorebird
30 391 abundances *circa* 1996-1997, a change already observed at larger spatial scale for Grey
31 392 plover, Oystercatcher and Knot. A concomitant abrupt change in the mid-90's has already
32 393 been observed in both terrestrial and marine realms: e.g. short-distance migratory raptors at
33 394 the European scale (Jaffré et al., 2013), trophic network in the Northeast Atlantic from
34 395 zooplankton to Balearic Shearwater (*Puffinus mauretanicus*; Luczak et al., 2011), or a
35 396 pronounced abrupt change in the North Sea ecosystem from sea to land with respect to larvae
36 397 and adults swimming crabs and one of their main predator, lesser black-backed Gull (*Larus*
37 398 *fuscus graelsii*; Luczak et al., 2012, 2013; Schwemmer et al., 2013).

41 399 These patterns of synchronous pulsed short-period modification exhibit a close parallelism
42 400 with large scale climate-induced temperature events (Reid and Beaugrand, 2012; Goberville
43 401 et al., 2014). Even if not noticed by the authors, this sudden change appeared in the
44 402 Community Temperature Index (CTI) calculated on shorebird assemblages wintering in
45 403 France (Godet et al., 2011; see their Fig. 1a), suggesting not a gradual, but an abrupt shift
46 404 northwards in wintering areas (Maclean et al., 2008).

49 405 A major question remains however unanswered: why the cascading effect of
50 406 anthropogenic perturbation did not impact wintering shorebirds? Food usually appears to be
51 407 the main factor driving the distribution of shorebirds, and a general relationship between the
52 408 density of birds in an intertidal area and the amount of food available for a given species
53 409 exists (Prater, 1981). In the Mont-Saint-Michel bay, of prime importance for wintering
54 410 shorebirds in France, Eybert et al. (2003) showed that the decrease in four shorebird species
55 411 (Oystercatcher, Dunlin, Red knot and Bar-tailed godwit (*Limosa lapponica*)), was related to
56 412 both a reduction in their preferred preys and an increase in human disturbances (mussel and
57 413 oyster farming). In the bay of Seine, the reduction by 20% of the mudflat area induced by the

414 “Le Havre” harbour extension could have influenced the mortality and body condition of
1 415 some shorebird species including Dunlins and Oystercatchers (Durell et al., 2005). Here, the
2 416 temporal stability in wintering bird number before/after disturbance, combined with a slight
3 417 modification in the spatial occupation by foraging shorebirds, suggested that (i) before
4 418 perturbation, the carrying capacity of the site was far from being reached, and (ii) the lower
5 419 food resource threshold has not been attained. In consequence, shorebird abundances in the
6 420 “Hemmes de Marck” beach did not appear affected by the Calais harbour extension.
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9 421 4.3. *Implications for management and conservation*

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11 422 Our results revealed that changes in high trophic level species at a local scale are not
12 423 necessarily a consequence of bottom-up effects propagating through a food web. Despite
13 424 drastic changes in macrobenthic communities, shorebird abundances in the “Hemmes de
14 425 Marck” beach appear more related to large-scale species trends (Maclean et al., 2008; Godet
15 426 et al., 2011). These results highlight the need to assess the extent to which wintering shorebird
16 427 assemblages could be impacted by the conjunction of local, regional and global influences.
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19 428 If future constructions are planned on coastal environments, some caution would be
20 429 required to alleviate potential consequences on intertidal areas and its benthic fauna. As we
21 430 showed, some direct consequences might be anticipated (e.g. changes in macrobenthic
22 431 communities). However, post-development consequences at the food web level (e.g. on top-
23 432 predators) appear harder or even impossible to predict accurately because of the multiple non-
24 433 linear interactions at entangled smaller/larger spatio-temporal scales (Levin, 1998, 2003;
25 434 Frontier et al., 2008).
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29 435 **Acknowledgments**

30
31 436 This work was carried out in the framework of the MACROFONE programme funded by the
32 437 region Nord - Pas-de-Calais and FRB. The authors are grateful to the Groupe Ornithologique
33 438 et Naturaliste du Nord – Pas-de-Calais (GON) for providing shorebirds data and to J.M.
34 439 Dewarumez, C. Maillard, J. Prygiel, J. Orange, D. Menu, V. Serreau, T. Luczak and M. Jaffré
35 440 for their help during benthic sampling. We are also grateful to the handling editor Vincent
36 441 Devictor and to the two anonymous referees for their helpful comments and suggestions,
37 442 which improved this paper.
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Figures

Anthropogenic impact on macrobenthic communities and consequences for shorebirds in Northern France: a complex response

Figures Legends:

Figure 1. Location of the study site.

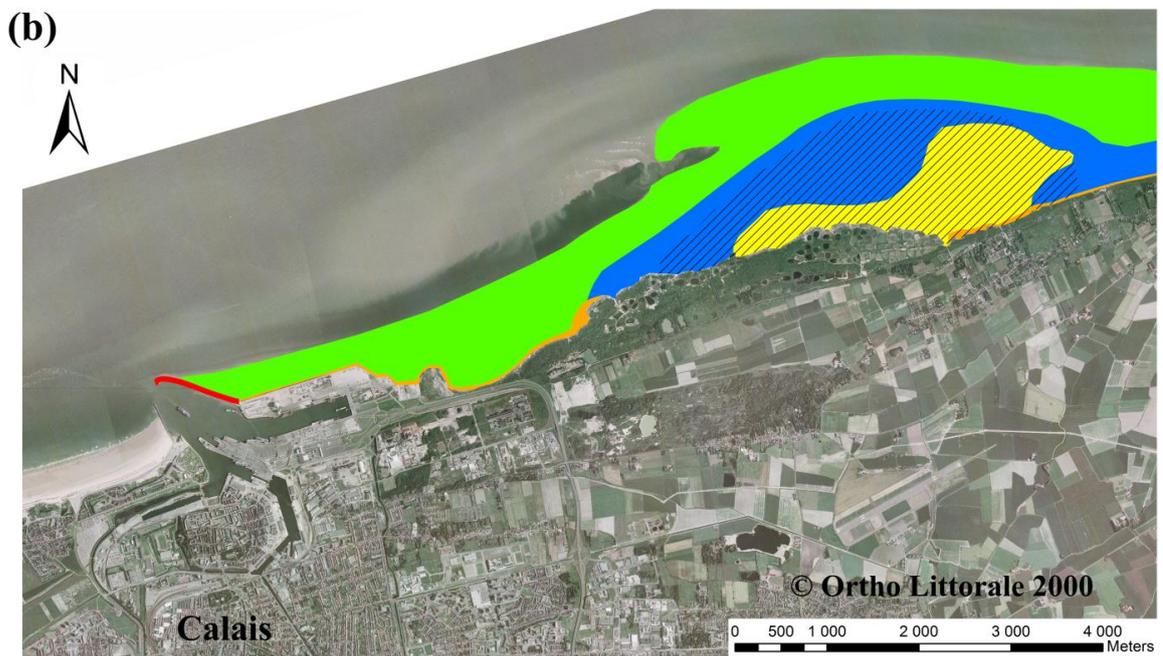
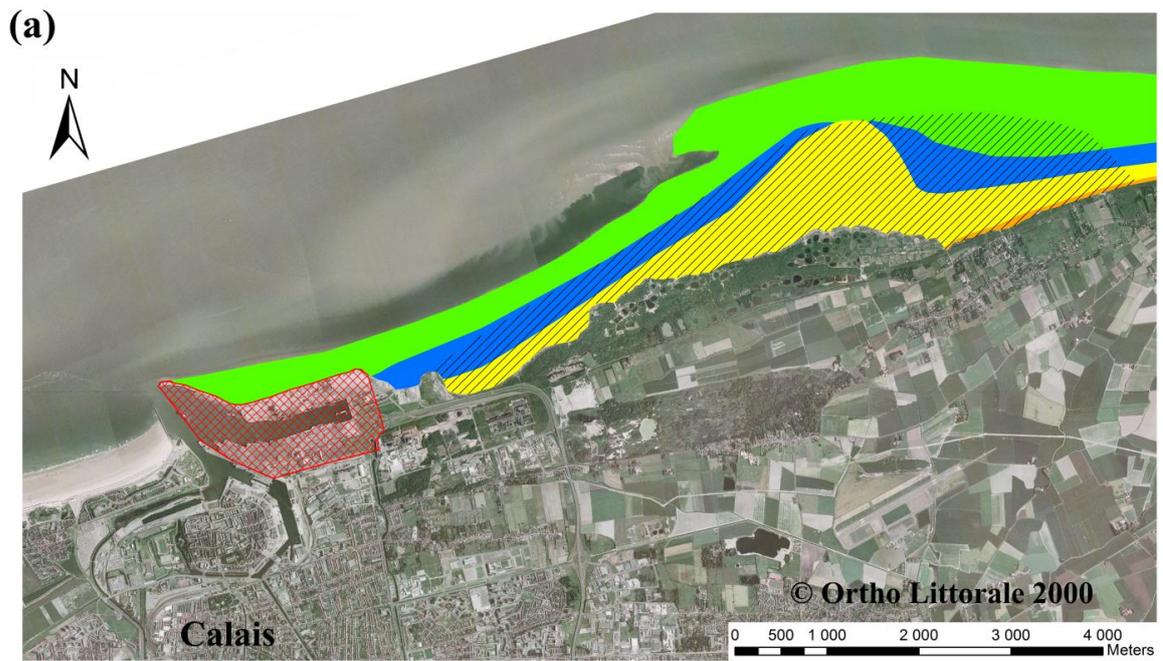
Figure 2. Spatial distribution of macrobenthic communities in the “Hemmes de Marck” beach according to the EUNIS classification (colored) and the main area of staging and wintering shorebirds (hatched): (a) in 1982 (i.e. two years before the Calais harbour extension) and (b) in 2010 (i.e. 26 years later). The hatched red area corresponds to the area of harbour extension and seawall construction, absent in 1982. The red line represents the seawall, built in 1984.

Figure 3. Long-term changes in coastal shorebird abundances in the “Hemmes de Marck” beach (1982 to 2012). (a) First principal component (PC1) calculated from a standardised Principal Component Analysis (PCA) performed on coastal shorebird abundances (41% of the total variability). The vertical dashed line separates periods before and after 1997. (b) First normalised eigenvectors. The width of the histogram represents the value of the eigenvector (positively in green and negatively in red). Arrows indicate the trend of each species in relation to the PC1.

Figure 4. Shorebird abundances in the “Hemmes de Marck” beach from 1980 to 2012 for: (a) Red knot, (b) Sanderling, (c) Oystercatcher, (d) Grey plover, (e) Dunlin and (f) the sum of all shorebird species. The vertical dashed line separates periods before and after 1997.

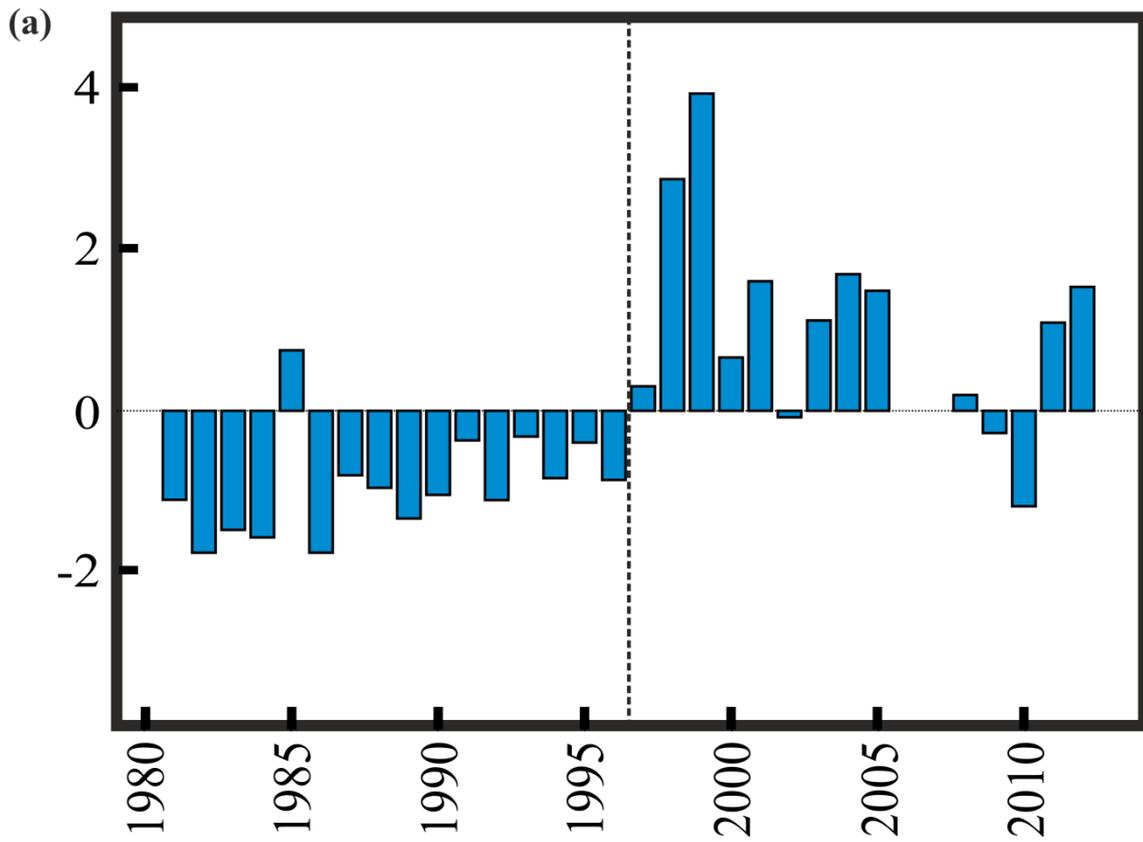


Figure 1
Rolet et al.



-  A2.21 Strandline
-  A2.24 Polychaetes/Bivalves dominated muddy-sand shores
-  A2.223 Amphipods and *Scolecipis spp.* in medium-fine sand
-  A2.23 Polychaetes/Amphipods dominated fine sand shores
-  Shorebirds feeding area
-  Harbour extension
-  Seawall constructed in 1984

Figure 2
Rolet et al.



(b)

Species	First eigenvectors	Long-term trends
Red knot <i>(Calidris canutus islandica)</i>	0.406	↗
Sanderling <i>(Calidris alba)</i>	0.618	↗
Oystercatcher <i>(Haematopus ostralegus)</i>	0.564	↗
Dunlin <i>(Calidris alpina)</i>	-0.656	↘
Grey plover <i>(Pluvialis squatarola)</i>	-0.864	↘

Figure 3
Rolet et al.

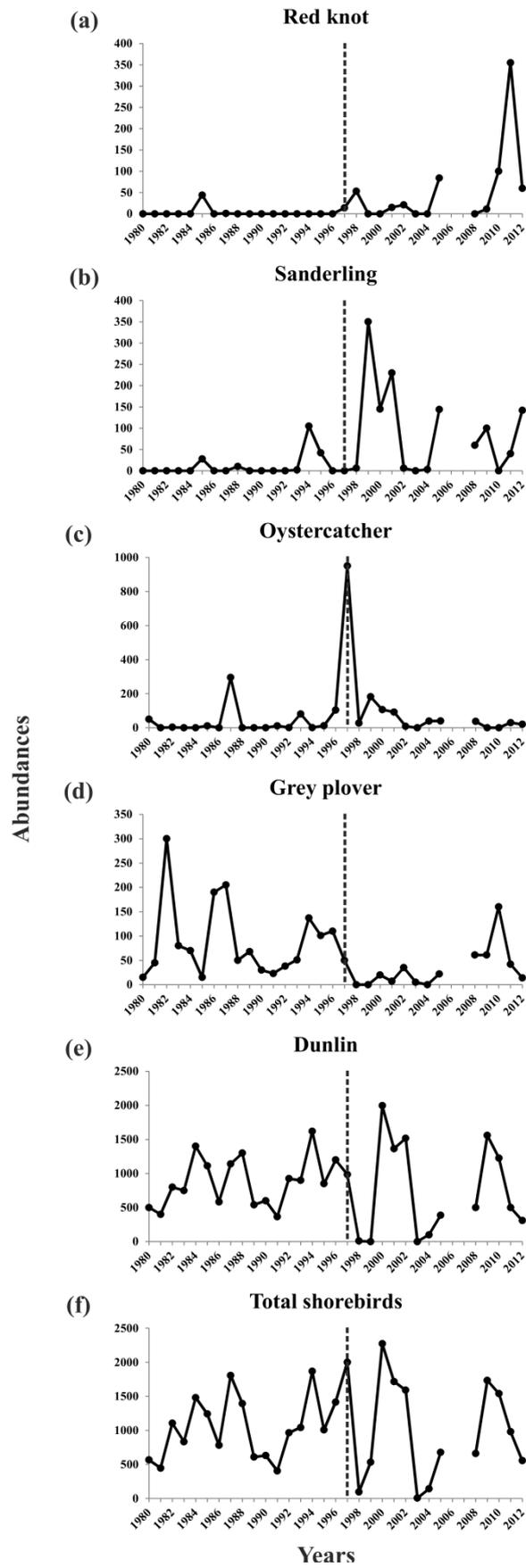


Figure 4
Rolet et al.

Table**Anthropogenic impact on macrobenthic communities and consequences for shorebirds in Northern France: a complex response****Table legend:**

Table 1. Mean density (ind.m⁻²), mean biomass (g.m⁻²), mean species richness and associated standard deviations (SD), and areas (in km²) for each macrobenthic community based on the EUNIS classification in 1982 and 2010. Changes in the area between the two periods are expressed in percentage (%).

Macrobenthic communities (EUNIS classification)	Mean density (ind.m ⁻²) ± SD		Mean biomass (g.m ⁻²) ± SD		Mean species richness ± SD		Area (km ²)		Evolution between 1982 and 2010	
	1982	2010	1982	2010	1982	2010	1982	2010		
A2.21 Strandline	NaN	NaN	NaN	NaN	NaN	NaN	0.26	0.43	65%	
A2.24 Polychaetes/Bivalves dominated muddy sand shores	3666 ± 5551	24335 ± 20902	1.56 ± 2.07	10.97 ± 8.59	4.7 ± 1.9	8.0 ± 3.0	4.72	2.08	56%	
A2.223 Amphipods and <i>Scolelepis spp.</i> in littoral medium-fine sand	392 ± 196	1727 ± 2898	1.21 ± 2.50	0.57 ± 0.70	6.2 ± 2.1	6.3 ± 2.1	3.53	5.46	55%	
A2.23 Polychaetes/Amphipods dominated fine sand shores	278 ± 120	184 ± 124	1.38 ± 1.70	0.17 ± 0.15	9.0 ± 3.2	6.8 ± 3.1	8.14	8.68	7%	

Table 1
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