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

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## Abstract

Shorebird populations are declining worldwide due to the combined effect of climate change and anthropogenic forcing, the ongoing coastal urbanisation amplifying the alteration of their habitat in both rate and magnitude. By focusing on a highly anthropogenically-influenced region in Northern France, we studied the impact of a seawall construction on wintering shorebird populations through potential alterations in the abundance and availability of their food resources. We concurrently investigated changes in the spatial distribution of muddy-sand beach macrobenthic communities between two periods of contrasting anthropogenic impacts and examined year-to-year trends of wintering shorebirds. Our study reveals that the seawall construction led to a major spatial reorganisation of the macrobenthic communities with a drastic reduction of the muddy-sand community. However, no relation between macrobenthic changes and shorebird abundances was detected. Fluctuations in shorebird abundances appeared to be congruent with flyway population trends. This result suggests that the response of shorebirds to human-induced perturbations is much more complex than expected. While an assessment of potential disturbances induced by coastal engineering constructions is needed, the pathways by which alterations could propagate through an ecosystem are not linear and as such difficult to determine. Ecosystems appear as complex adaptive systems in which macroscopic dynamics emerge from non-linear interactions at entangled smaller/larger scales. Our results confirm that an in-depth knowledge of the local, regional and global factors that influence trends of shorebirds and their habitat use is essential for accurate and effective management and conservation strategies.

**Keywords:** shorebirds, macrobenthic communities, anthropogenic impact, coastal conservation, complexity

## 1. Introduction

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

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

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

Along the French coast of the Southern Bight of the North Sea, the "Hemmes de Marck" is the only major muddy-sand beach representing an attractive feeding area for shorebirds (Marzec and Luczak, 2005; Spilmont et al., 2009). However, the Calais harbour extension and a seawall construction in 1984 induced the destruction of two main habitats: a pond/marsh area and the aerial dunes as well as a high modification of the hydro-sedimentary dynamics and processes in this area (Richard et al., 1980; Hequette and Aernouts, 2010). In the present study, we investigated spatio-temporal changes in both muddy-sand beach communities and potential consequences on staging wintering shorebird populations. First, we compared the spatial distribution of the macrobenthic communities between the year 1982 (i.e. two years before the harbour extension) and the year 2010 (i.e. 26 years later). We then evaluated year-to-year changes in shorebird abundances from 1980 to 2012 to identify a possible relationship with changes in their food resources (i.e. macrobenthic communities). Finally, we discussed the implementation of management plans for effective shorebird conservation strategies.

## 2. Materials and methods

### *2.1. Study site*

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

### *2.2. Sampling strategy*

Sampling was carried out in autumn 1982 and 2010. To avoid potential biases due to any sampling changes, we used the same sampling strategy in 2010 than in 1982. For both periods, 17 stations (with three replicates per station) were sampled. Samples were collected with a corer (1/40 $m^2$ down to a depth of 0.25 m) and washed through a 1 mm mesh sieve. After sieving, all samples were immediately fixed and preserved in an 8% formaldehyde-seawater solution. At each station, one sediment core was sampled for granulometry analysis.

### *2.3. Laboratory work*

In the laboratory, the sieved samples were sorted and macrobenthic organisms were counted and identified to the species level, except for Oligochaetes, Nematodes and some damaged amphipods (which represent 1% and 2% of the total abundance in both 1982 and 2010). Faunal densities were expressed as the number of individuals per $m^2$ ($ind.m^{-2}$). Biomass was determined as ash free dry weight (g of $AFDW.m^{-2}$ after 6h drying at 520°C) for each station (ICES, 1986). Granulometry was analysed by dry sieving through a nested series of sieves with mesh sizes decreasing from 5 to 0.05 mm. Sediment grain size was grouped into six categories according to the Larsonneur classification (1977): mud (< 0.05 mm), fine sands (≥ 0.05-0.2 mm), medium sands (≥ 0.2-0.5 mm), coarse sands (≥ 0.5-2 mm), fine gravels (≥ 2-5 mm) and coarse gravels (≥ 5-20 mm).

### *2.4. Statistical analysis and mapping of macrobenthic communities*

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

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

### *2.5. Long-term changes in shorebird populations*

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

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

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

### 2.6. *Shorebirds spatial distribution*

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

The synthesis of the feeding areas data were mapped for both 1983 and 2011 winter periods using the mapping software ArcGIS 10® and overlaid on macrobenthic data independently obtained.

## 3. Results

### 3.1. *Distribution of macrobenthic communities before the harbour extension (in 1982)*

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

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

The second community was located in the mid shore (in blue; Fig. 2a), covered 3.53 km$^2$ of the studied beach (Table 1) and corresponded to the Amphipods and *Scolelepis spp.* in littoral medium-fine sand community (A2.223). The main species were the isopods *Eurydice spp.* (28%), the amphipods *Bathyporeia spp.* (19%) and the polychaete *Scolelepis squamata* (8%).

The third assemblage, the Polychaetes/Amphipods dominated fine sand shores community (A2.23), was located in the lower shore of the study site (in green; Fig. 2a) and covered a surface of 8.14 km$^2$ (Table 1). It was dominated by the amphipods *Bathyporeia spp.* (15%), *Haustorius arenarius* (17%) and *Urothoe brevicornis* (9%), and the polychaete *Nephtys cirrosa* (5%).

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

The strandline (A2.21), located along the dunes, was determined using the DFO method as no benthic sampling was performed in this area (in orange; Fig. 2a). This community covered an area of 0.26 km$^2$ (Table 1).

### 3.2. *Distribution of macrobenthic communities 28 years later (in 2010)*

While the cluster and MDS analyses applied for data sampled in 2010 revealed the same EUNIS communities as those identified in 1982 (i.e. A2.24, A2.223 and A2.23; MDS stress 0.12; ANOSIM 0.53; $p < 0.001$; supplementary material appendix B.2), the multivariate analysis performed on macrobenthic assemblages displayed a significant effect of years (PERMANOVA: Pseudo-$F$ = 2.3214; $p < 0.05$).

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

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

A major spatial reorganisation of benthic communities occurred between 1982 and 2010 (Fig. 2): the muddy-sand community dominated by Polychaetes and Bivalves lost 56% of its surface (2.08 $km^2$ in 2010 *versus* 4.72 $km^2$ in 1982) whereas coverages of other communities increased (65% for the strandline, 55% for the Amphipods and *Scolelepis spp.* in littoral medium-fine sand community and 7% for the Polychaetes/Amphipods dominated fine sand shores community; Table 1). The muddy-sand community disappeared, firstly from the western part of the studied area, replaced by the Polychaetes/Amphipods dominated fine sand shores community, and secondly from the highest tidal levels replaced by the strandline and the Amphipods and *Scolelepis spp.* in littoral medium-fine sand community.

### 3.3. *Long-term changes in shorebird abundances*

Year-to-year changes in the first principal component (PC1; 41% of the total variability) of the PCA applied on shorebird abundances showed low values (mostly negative) of the component from 1980 to the mid-90's, followed by a rapid increase in the trend and relatively high values (mostly positive) from 1996 until 2012 (Fig. 3a). Examination of the first eigenvector indicated that Sanderling (*Calidris alba*), Oystercatcher (*Haematopus ostralegus*) and, to a lesser extent, Red knot (*Calidris canatus islandica*) were positively correlated to the PC1 (Fig. 3b), suggesting an increase in their abundances. In contrast, Grey plover (*Pluvialis squatarola*) and Dunlin (*Calidris alpina*) were negatively correlated to this component (Fig. 3b), indicating a decline in their abundances over the last 30 years. The second principal component (PC2; 27% of the total variability) appeared more affected by episodic events and no major trend was detected (supplementary material appendix C.1). Long-term changes in the PC2 showed low values of the component from 1980 to the mid-90's, followed by an alternation between positive and negative values. Examination of the second eigenvector indicated that Red knot and Dunlin predominantly contributed to changes, revealing a significant reduction in their abundances in 1998-1999 and 2003-2004 (supplementary material appendix C.2).

Looking at each species trend for the period 1980-2012, Red knot, Sanderling and Oystercatcher abundances significantly increased (Spearman rank correlation $\rho$ 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 *Scolelepis 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 *Scolelepis 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 extension and the seawall construction (in 1984), a muddy-sand community dominated by Polychaetes and Bivalves, occupied the major part of the intertidal area, whereas between 1982 and 2010, the Amphipods and *Scolelepis spp.* in littoral medium-fine sand community nearly doubled its surface. Hequette and Aernouts (2010) recently suggested an influence of the Calais harbour wall on both the shoreline dynamic and the sedimentary environment in the beach east of Calais. While mud constituted 12% of the sediment in this area in 1982, it only represented 0.03% in 2010. These changes in sediment grain size induced a spatial reorganisation and a turn-over in macrobenthic fauna: species living in muddy-sand sediment disappeared from the eastern and western parts of the area (i.e. *Corophium arenarium* and *Pygospio elegans*) and were replaced by sand affinity species (i.e. *Scolelepis squamata* and *Nephtys cirrosa*) or opportunistic species such as Oligochaeta and Nematoda. This result is in accordance with Ahn and Choi (1998) who observed an increase in coarse sediments and a shift in species dominance in an intertidal sandflat on the west coast of Korea after a seawall construction. At the same time, the surface of the littoral medium-fine sand community dominated by Amphipods and *Scolelepis spp.* increased by 56% in surface area and its faunal composition appeared more heterogeneous in 2010 than in 1982. This pattern is the consequence of an ecosystem reorganisation which is characteristic of a complex adaptive system (Levin, 1999; Frontier et al., 2008). Our study suggests that the seawall construction caused major changes in hydrological conditions and sedimentary composition that directly impacted the spatial distribution of macrobenthic communities in the “Hemmes de Marck” beach. Such alteration, by propagation through the food web, should be expected to influence higher trophic levels (e.g. fishes, shorebirds; Van de Kam et al., 2004).

### *4.2. Long-term changes in shorebird abundances and interactions with macrobenthic communities*

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

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

Trends observed for Dunlin, Grey plover and Sanderling in the study site were congruent with the pattern observed at the global flyway populations (Wetlands International, 2014). We stress that the rise of Sanderling is locally related to the spatial extension of the “Amphipods and *Scolelepis spp.* in littoral-medium fine sand community” (+55% between 1982 and 2010). This benthic community hosted a higher number of shorebirds in 2010 (+32%) and provided an important food resource for this shorebird species: e.g. *Bathyporeia spp.* and *Scolelepis squamata* (Smit & Wolf, 1981; Vanermen et al., 2009). This pattern is the synergistic result of a cross-scale interaction (Frontier et al., 2008): a local evolution of macrobenthic communities that turns out to be a huge food resource area in the context of an overall increase in the Sanderling flyway population. A closer examination of time series of Grey plover revealed an evolution similar to that observed in U.K.: wintering number increased from the 1980's to the mid-90's and has since declined. At a larger spatial scale, it remains unclear whether these changes reflect a large-scale redistribution in response to climate change (Maclean et al., 2008) or a population decline (Delany et al., 2009).

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

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

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

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

"Le Havre" harbour extension could have influenced the mortality and body condition of some shorebird species including Dunlins and Oystercatchers (Durell et al., 2005). Here, the temporal stability in wintering bird number before/after disturbance, combined with a slight modification in the spatial occupation by foraging shorebirds, suggested that *(i)* before perturbation, the carrying capacity of the site was far from being reached, and *(ii)* the lower food resource threshold has not been attained. In consequence, shorebird abundances in the "Hemmes de Marck" beach did not appear affected by the Calais harbour extension.

### *4.3. Implications for management and conservation*

Our results revealed that changes in high trophic level species at a local scale are not necessarily a consequence of bottom-up effects propagating through a food web. Despite drastic changes in macrobenthic communities, shorebird abundances in the "Hemmes de Marck" beach appear more related to large-scale species trends (Maclean et al., 2008; Godet et al., 2011). These results highlight the need to assess the extent to which wintering shorebird assemblages could be impacted by the conjunction of local, regional and global influences.

If future constructions are planned on coastal environments, some caution would be required to alleviate potential consequences on intertidal areas and its benthic fauna. As we showed, some direct consequences might be anticipated (e.g. changes in macrobenthic communities). However, post-development consequences at the food web level (e.g. on top-predators) appear harder or even impossible to predict accurately because of the multiple non-linear interactions at entangled smaller/larger spatio-temporal scales (Levin, 1998, 2003; Frontier et al., 2008).

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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.**

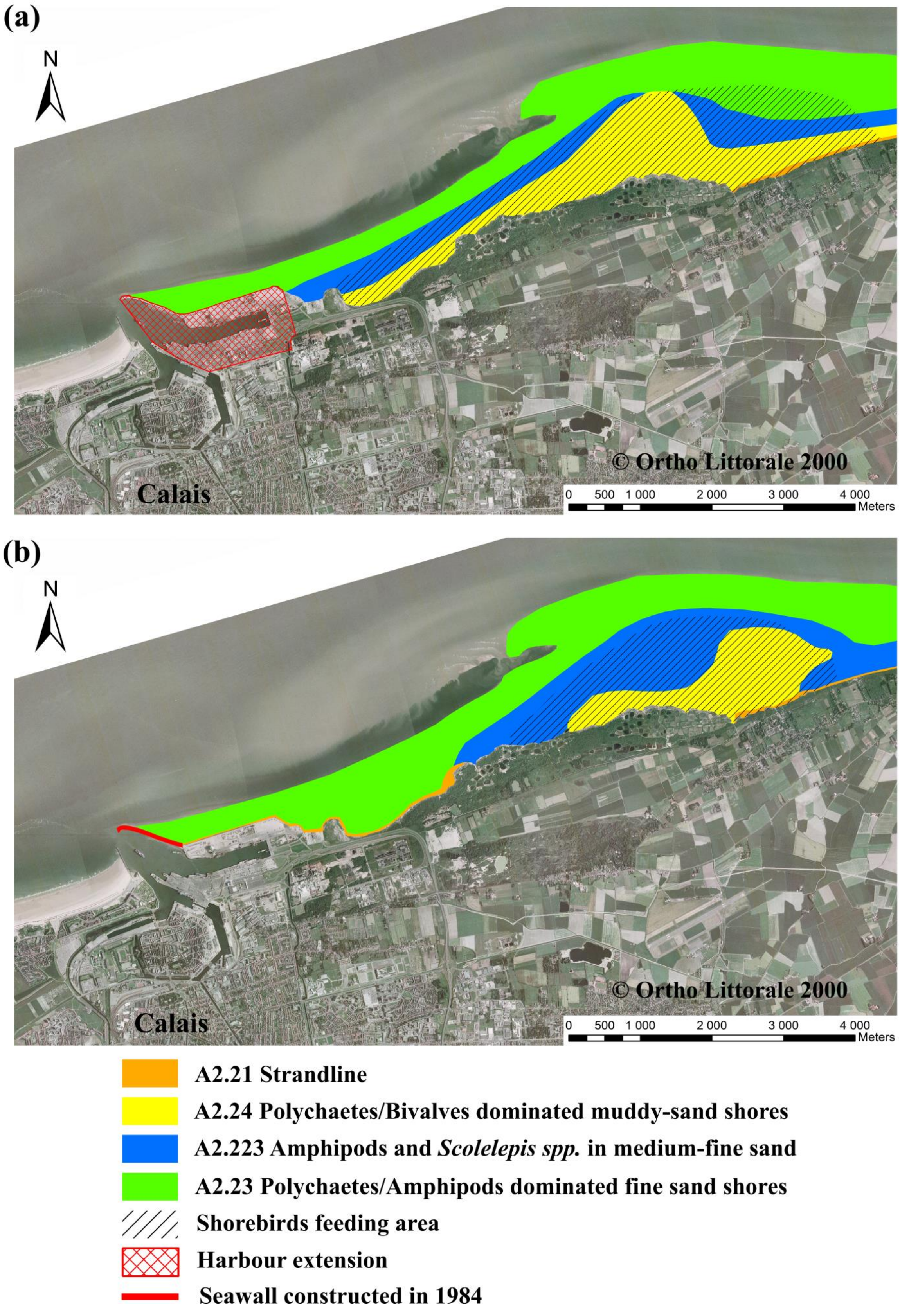
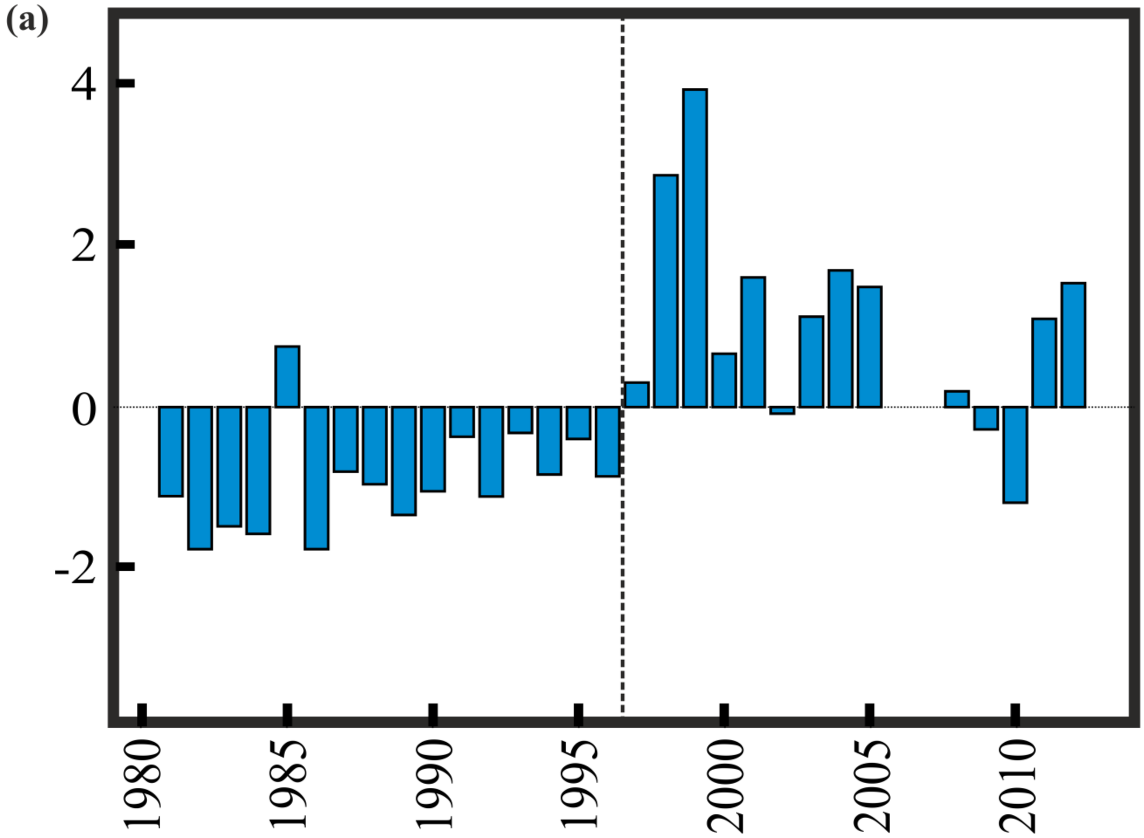


**Figure 2**
**Rolet et al.**



**(b)**

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

**Figure 3**
**Rolet et al.**

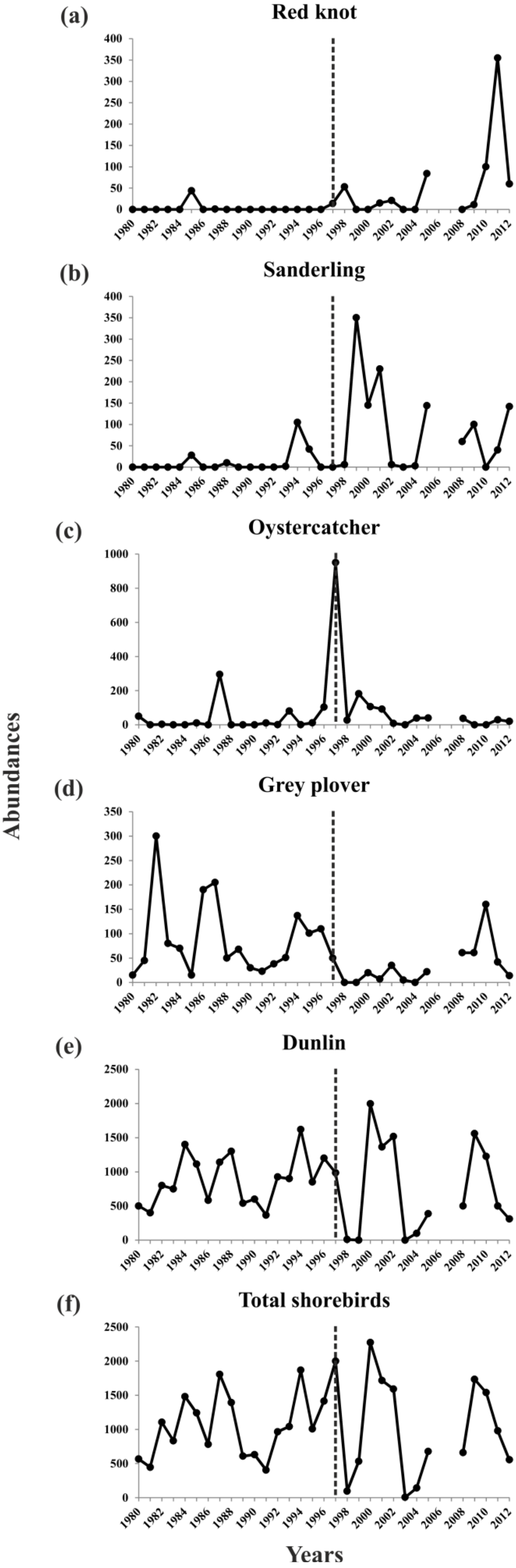


**Figure 4**
**Rolet et al.**

# 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 km$^2$) 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 *Scolelepis spp.* 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**
**Rolet et al.**