Determinants of bird habitat use in TIDE estuaries

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SUMMARY

The distribution of waterbirds in estuarine habitats and the identification of the main factors affecting bird habitat use have been investigated within the TIDE project. A methodological approach has been proposed for this type of study (see TIDE Tool “Guidelines on bird habitat analysis methodology”) combining high water bird count data with the characterization of environmental conditions (including natural habitat areas, water quality parameter and indicators of anthropogenic disturbance) in multivariate analysis (community distribution models) and species-habitat regression models in order to identify a series of habitat requirements for different bird species.

Three TIDE estuaries, the Elbe (D), Weser (D), and Humber (UK), were used as case studies as they share similar broad characteristics (e.g. they have a strong tidal influence, important port areas) but also present a different distribution of the pressures and habitats along the estuarine continuum which might affect the bird habitat use in different ways, leading to different potential outcomes.

The estuarine hydrogeomorphological characteristics indirectly affect the distributions of higher predators within estuarine areas as they determine the extent of intertidal mudflats and marsh habitats. In particular, intertidal mudflats are important for waders and marsh for wildfowl and as refuge areas for fishes. Although TIDE only quantified the value of habitats available within the estuary at a small spatial scale (i.e. within an average area of $6km^2$ around the roosting sites), the obtained results suggested that habitat availability on a wider spatial scale (i.e. around the estuary) can also increase the numbers of birds roosting in certain estuarine areas by providing additional feeding grounds that can be used by birds. This effect has been observed, for example, with waders in the polyhaline zones of the Elbe, due to the presence of extensive mudflats in adjacent marine areas, or with wildfowl in the oligohaline zone of the Humber, due to the presence of adjacent inland habitats.

Larger estuarine habitats appear to support greater bird densities compared to smaller habitats, especially for generalist feeders (i.e. species that are able to take advantage from a wider range of food prey, such as Dunlin and Redshank). This may be due to the higher diversity of resources associated to wider habitats benefiting the aggregation of these generalist feeders. In turn, this is less evident for specialist feeders, such as Bar-tailed Godwit, which are more likely to depend on the distribution of specific prey, a factor that might be more relevant at a smaller spatial scale (i.e. within a mudflat) hence resulting in a contrasting relationship with the total intertidal habitat area.

Lower bird abundances are generally observed in areas where natural estuarine habitats are smaller, this reduced habitat availability being the result of the natural variability in the estuarine morphology (e.g. narrower mudflats present in the freshwater zone compared to the estuarine meso- and polyhaline zones) or the presence of anthropogenic developments and land-claim (e.g. smaller mudflat areas in the mesohaline zone of the Humber or in the freshwater and oligohaline zone of the Elbe). Hence, the availability of natural estuarine habitats mainly determines the density of waders and wildfowl, especially in the Weser and Humber.

Water quality characteristics such as the salinity gradient, nutrient levels and organic enrichment are also important in affecting species distribution, a feature particularly evident in the Elbe. The effect of the salinity gradient was predominant in the Elbe, especially for bird densities as a whole, but particularly for Dunlin (both increasing with the increasing salinity), although this effect is more likely related to other factors that are correlated with the

salinity gradient in the estuary rather than to an effect of salinity itself. These factors include the distribution and availability along the estuarine gradient of feeding habitats (both within the estuary and in adjacent areas, e.g. extensive mudflats in the Wadden Sea) and food resources (as indicated by longitudinal changes in benthic invertebrate communities), as well as the lower degree of anthropogenic disturbance favouring bird use of the outer sands / remote islands located in the polyhaline zone of the Elbe.

It is acknowledged that the findings are based on limited data and require an assumption of an association to be made between high water distribution and usage (the data used in the analysis) and low water foraging distribution being in the same general area. However, if these assumptions are valid, then the findings have important implications for estuary managers, in that the data indicate that larger mudflat areas have a greater carrying capacity for waterbirds per ha than smaller mudflat areas.

This has implications for habitat loss and mitigation/compensation measures, in that a development within an extensive intertidal mudflat will not only have a direct impact through habitat loss, but a potential additive effect through fragmentation of mudflat area. Furthermore, in terms of compensation for such losses, the provision of new habitat, for instance through managed realignment, needs to positioned so that it is contiguous to adjacent habitat, otherwise again a fragmentation effect may occur. In both scenarios (e.g. potential fragmentation and reduced carrying capacity through habitat loss and compensation), it may be necessary to provide ‘over compensation’ in the form of a greater offset provision ratio.

TABLE OF CONTENTS

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1 Introduction

One of the fundamental paradoxes the management of estuaries has to cope with is the fact that most of the major estuaries in the world are to some degree modified by Man, yet, in many countries, these systems include more nature protected areas than any other habitat (McLusky & Elliott 2004). Estuaries supply mankind with extensive economic goods and services, by providing, for example, fish and shellfish, aggregates for building, and water for abstraction. As such, several anthropogenic pressures concentrate in these areas. Also, estuarine areas are often designated under a series of European directives and conventions for their international importance as habitats for waterbirds populations (e.g. European Habitat and Species Directive, Bird Directive, Ramsar convention) and several conflicts may arise between the use of estuarine areas (and the resulting impacts on the natural environment) and their conservation as bird habitats. The understanding of the critical determinants of bird usage of estuarine habitats is therefore an important element to inform the management of these areas towards a reduction (through mitigation or compensation) of these conflicts/impacts.

The distribution of waterbirds in estuarine habitats and the identification of the main factors affecting bird habitat use has been investigated within the TIDE project. This knowledge will provide broad guidance for the management of these complex systems, e.g. by directing mitigation programmes towards the provision of better habitats for bird species.

The study focussed on three of the four TIDE estuaries, the Elbe (D), Weser (D), and Humber (UK). These estuaries share similar broad characteristics (e.g. they have a strong tidal influence, important port areas) and most of their area is protected under a series of designations. The Humber Estuary has been designated under the Species and Habitats Directives and is a Natura 2000 site. Underpinning this European level designation is a UK legal framework based around Sites of Special Scientific Interest (SSSIs). The mouth of the Weser and Elbe rivers is part of the International Wadden Sea system, the world’s largest intertidal wetland, designated as a UNESCO World Heritage site, Natura 2000 site and a site of national importance under the Ramsar convention. In particular, Special Protected Areas contributing to the Natura 2000 network in the Elbe estuary cover about 90% of the estuary’s water and foreshore surface areas, with more than 90% of the tidal Weser surface area and floodplains also belonging to the EU‘s Natura 2000 network of protected areas. The mosaics of tidal habitats present in these systems (e.g. mudflats, salt marshes, shallow water areas), in fact, provide important roosting and feeding habitats for several migratory waterbird species. Besides these common broad characteristics, the three estuaries present a different distribution of the pressures and habitats along the estuarine continuum which might affect the bird habitat use in different ways, leading to different results obtained for the different estuaries.

2 Structure of the report

This report synthesizes the results of the study on the distribution of waterbirds in estuarine habitats and the identification the main factors affecting bird habitat use.

Chapter 3 provides an overview of the type of data that were used in this study, including their availability (in terms of spatial and temporal coverage) and limitations. The obtained results, in fact, highly depend on the data analysed, therefore this knowledge provides the boundaries of applicability of the resulting models. Further details and examples on how the data were derived are provided in **Appendix 1**. Additional information on the methods applied to this study is provided in the Tool "Guidelines on bird habitat analysis methodology".

Chapter 4 describes the general characteristics of bird assemblages in TIDE estuaries, including information on the dominant species, total abundance and densities in the estuaries and their distribution across the salinity zones. Additional information is reported in **Appendix 2**.

Chapter 5 reports on the distribution of bird assemblages within each of the studied estuaries and its relationship with environmental variables, resulting from multivariate analysis and regression models. These results allow identification of the main environmental gradients affecting the distribution of waders and wildfowl communities across the estuarine areas. Additional detailed methods for this analysis and results are provided in **Appendix 3**.

Chapter 6 provides the results of species distribution models applied to selected wader and wildfowl species in the studied estuaries. Such results highlight the importance of different environmental variables (including habitat areas and characteristics and relevant water quality parameters) in affecting the distribution of species in the estuary, also providing the ranges of environmental conditions where higher species densities (or probability of occurrence) could be expected. Additional details on the analytical methods applied are provided in **Appendix 4**.

Chapter 7 provides an integrative discussion of the results reported in the previous chapters. A summary of the main findings of the study is reported as **Conclusions** in **Chapter 8** (although brief summaries of the main results are also reported as text boxes at the end of each of previous chapters).

3 Data used

Bird data were analysed for the three estuaries in combination with data on environmental characteristics (habitat area and quality, water quality parameters, disturbance indicator) in order to describe the species distribution within the estuarine areas and to identify the main environmental determinants of their habitat use. Multivariate regression models were applied to investigate the whole bird assemblage distribution (distinguishing between waders and wildfowl), whereas univariate regression models were calibrated to identify the main predictors of single species distribution within the estuary. Similar analyses were carried out in the three estuaries, in order to identify common patterns and elements of differentiations due to the local conditions.

This chapter provides an overview of the type of data that were used in this study, with further details and examples on how the data were derived being provided in Appendix 1.

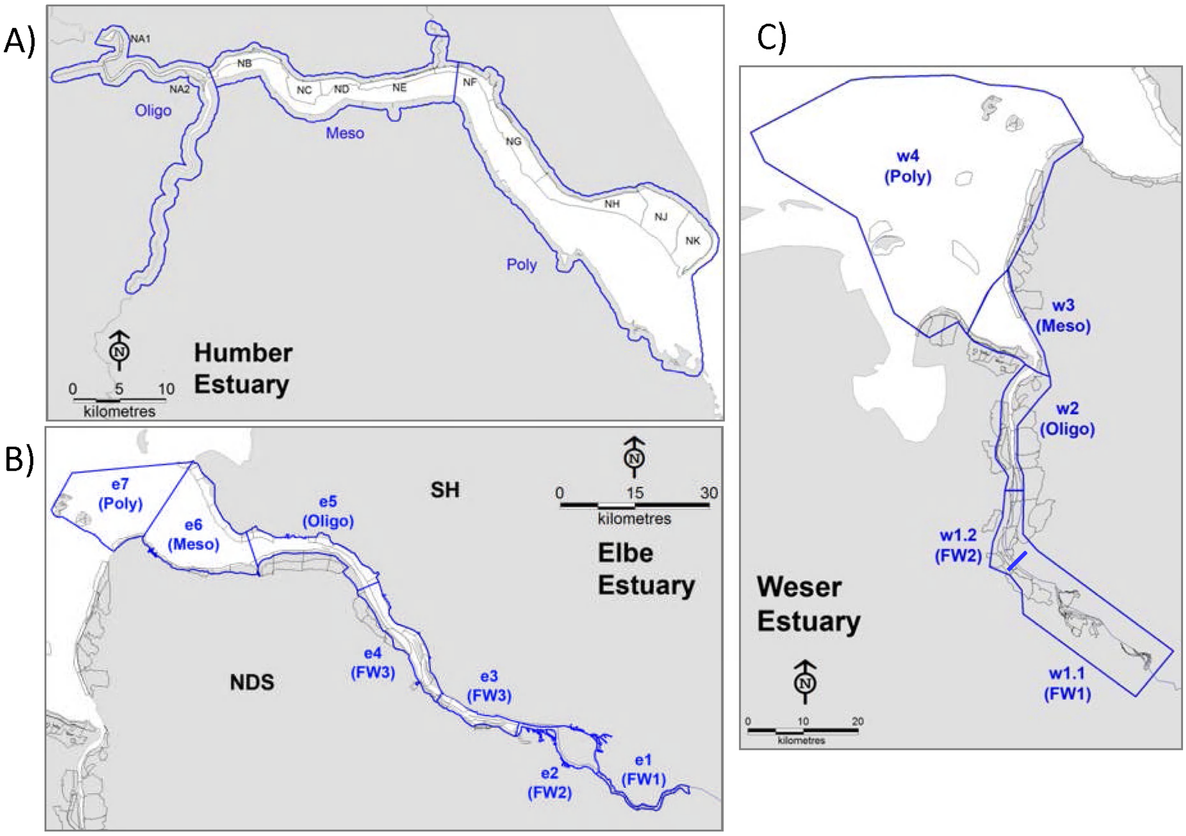


Figure 1. Counting units/sectors in the Humber (A), Elbe (B) and Weser (C) estuaries (in grey). Estuarine zones, as per TIDE zonation and salinity zonation (as derived from the Zonation of the TIDE estuaries) are indicated in blue (sector names are also indicated for the Humber Estuary; freshwater zones in this estuary are not shown as no bird data were available in them).

The annual maximum counts for wader and wildfowl species in estuarine spatial units at high-tide were analysed. The main focus of the analysis was on the spatial distribution of bird species, but also temporal variability was accounted for by including data collected in different years.

In the Humber, data for 11 units (WeBS sectors) covering the North bank of the estuary (Figure 1A) were available between 1991 and 2011 for waders and between 1975 and 2011 for wildfowl (WeBS national survey). In the Elbe, data for 59 units along the southern bank (Niedersachsen jurisdiction, NDS) and 19 units along the northern bank (Schleswig-Holstein jurisdiction, SH) (Figure 1B) were available between 1984 and 2011 for both waders and wildfowl (Joint Monitoring of Migratory Birds, JMMB). In the Weser, data for 82 units along the estuary (both banks) (Figure 1C) were available between 1984 and 2009 (Joint Monitoring of Migratory Birds, JMMB). In order to allow comparison between units of different size, count data were standardised to densities (ind/km^2) before any analysis, based on the area of each unit.

The spatial-temporal distribution of bird assemblages and species was related to a set of environmental variables describing the habitat characteristics, water quality and anthropogenic disturbance in each counting unit, sector or estuarine zone in different years. The environmental variables included in the analyses as possible predictors of bird habitat use are listed in Table 1.

Habitat coverage data in each unit/sector were calculated from historical maps available for the studied estuaries (details on the method used and an example of this calculation are reported in Appendix 1a). As a result, annual habitat coverage data for each unit/sectors were obtained from 1975 to 2011 in the Humber, 1984 to 1998 in the Elbe, and 1984 to 2003 in the Weser. For the Humber only, the intertidal habitat in the studied units was characterised also in a qualitative way through the identification of the **dominant intertidal habitat type** and the **coverage of hard substrata** (either pebbles or man-made vertical substratum) present within each sector (see Appendix 1b and 1c for details).

As regards **water quality data**, the average **salinity** in each sector in the Humber Estuary was calculated based on different sources (Gameson 1982, Falconer & Lin 1997, Humber salinity zonation 2000-2010; spatial variability was only considered, with the same salinity allocated to each sector in different years). For the Elbe and Weser, **chlorinity** was considered as an indicator of the salinity gradient and the data were obtained from the dataset used for the report on an inter-estuarine comparison for ecology in TIDE. Additional water quality data were derived for the Elbe and Weser from this dataset, based on their suitability as possible predictors of bird habitat use, their level of inter-correlation and in order to maximise the coverage in the selected dataset. In particular, eutrophication (in terms of changing nutrient inputs) is considered one of the main processes influencing the quality and the stocks of benthic prey for birds in the Wadden Sea, and **total phosphate (PO4)**, **summer chlorophyll** and **autumn NH4 and NO2** have been regarded as good indicators of the eutrophication status in this area (Ens et al. 2009). Also **Biochemical Oxygen Demand (BOD)**, an indicator of organic and nutrient loading influences, and **dissolved oxygen saturation (DOsat)** have been used as predictors of bird distribution in estuarine and coastal areas (Burton et al. 2002). It is of note that, in the available dataset for the Weser and the Elbe, summer chlorophyll data were sparse therefore they were not included in the analysis. In addition, this variable was highly correlated (Spearman correlation coefficient r_S>0.8) to BOD (positive correlation) and to chlorinity (negative correlation) in the Elbe estuary. In this estuary, autumn NH4 only was considered, being highly positively correlated (r_S>0.9) with autumn NH4 + NO2 values. As regards the Weser, DOsat was not considered, due to the limited availability for this variable in the dataset and its negative correlation (r_S>0.6) with chlorinity. In the water quality dataset, data were available seasonally from 2004 to 2009 in the Elbe, and 1992 to 2009 in the Weser and by wider estuarine zones (see report on Zonation of the TIDE estuaries), therefore units located within the same zone were given the same value (annual average values were calculated when seasonal values were not explicitly required). It is of note that, in the Weser, no water quality data were available for the mesohaline and polyhaline zones.

The quality of the intertidal habitat, in terms of provision of food resources to bird species, was also measured for each sector in the Humber Estuary based on the information provided in Allen (2006). In particular, the **total benthic invertebrate abundance** was considered as an estimate of the total amount of food potentially available to wading birds within each sector. Also the **type of benthic community** (based on its species composition and density) characterising the intertidal habitat in each sector was considered as a possible relevant factor in affecting bird use by accounting for the quality of the food resource potentially available together with its quantity. Further details on these aspects are reported in Appendix 1d.

For the Humber Estuary, an index of the frequency of potentially disturbing activities in the sectors was also calculated based on data provided in Cruickshanks et al. (2010). This variable was called **Disturbance** (see details in Appendix 1e). No such detailed data were available for the different spatial units in the Weser and Elbe. However, it is of note that a differentiation between the northern and southern bank occur within the same estuarine zone in the Elbe estuary, due to the different distribution of natural areas and areas of anthropogenic influence (e.g. industrial estates, infrastructures) in the two banks subject to different jurisdictions (Niedersachsen (NDS) for the southern bank, Schleswig-Holstein (SH) for the northern bank). Therefore, the two different **jurisdictions** were included in the analysis for the Elbe estuary as a factor that might possibly have an effect on bird use of estuarine habitats.

Although the main focus of the study was on the spatial distribution and habitat use, temporal variables were also included in the analysis in order to take account of this source of variability in the data. **Year** was considered in the species distribution models, as well as the **wider species population trend**. For the Humber estuary, data on annual total maximum counts for Great Britain (1975 to 2011) were collected for selected species from WeBS books[1] (details on this type of data are provided in Appendix 1f). For the Elbe and Weser Estuary, estimates of the population size in the Niedersachsen area only (for the Weser) and also in the Schleswig-Holstein area (for the Elbe) were derived from the population trends (between 1987 and 2008) analysed in Laursen et al. 2011 (detailed methods can be found also in Blew et al. 2005, 2007).

[1] Waterbirds in the UK Series – The Wetland Bird Survey. Published by the British Trust for Ornithology (BTO), the Royal Society for the Protection of Birds (RSPB) and the Joint Nature Conservation Committee (JNCC) in association with the Wildfowl & Wetlands Trust (WWT).

Table 1. Environmental variables included in the analysis.

	Humber	Elbe	Weser
Habitat	Intertidal (area, km2) - Int	Intertidal (area, km2) - Int	Intertidal (area, km2) - Int
	Eunis intertidal habitat type - Eun(1)		
	Subtidal (area, km2) - Sub	Subtidal, shallow (area, km2) - Subs	Subtidal, shallow (area, km2) - Subs
		Subtidal, deep (area, km2) - Subd	Subtidal, slope + deep (area, km2) - Sub
	Marsh (area, km2) - Mar	Foreland (area, km2) - For	Marsh (area, km2) - Mar
	Supralittoral, no-flooded zone (area, km2) - Sup		
	Hard substr., pebble (% coverage)(2)		
	Hard substr., man made (% coverage)(2)		
Water Quality	Salinity - Sal	Chlorinity (mmol/l) - Cl	Chlorinity (mmol/l) - Cl
		BOD5 (mmolO2/l) - BOD	BOD5 (mmolO2/l) - BOD
		DOsat (%) - DO	
		PO4 (mmol/l) - P	PO4 (mmol/l) - P
		NH4(autumn) (mmol/l) - N	NH4+NO2(autumn) (mmol/l) - N
Other	Intertidal benthic abundance (indiv./0.0079 m^2) - BAb		
	Intertidal benthic community type - Btype(1)		
	Disturbance - Dist	Jurisdiction (NDS, SH) - jurisd	
	Year - Y(1)	Year - Y(1)	Year - Y(1)
	Bird population trend - SP.GB (SP=species code)(1)	Bird population trend - SPpop (SP=species code)(1)	Bird population trend - SPpop (SP=species code)(1)

(1) variable used in the univariate models only (species distribution models)

(2) variable used in the multivariate models only (community distribution models)

4 General characteristics of bird assemblages in TIDE estuaries

In total, forty species (19 waders and 21 wildfowl) were included in the analysed datasets, although the number of species varied between estuaries (

Table 2). Species were allocated to functional groups (guilds) in order to highlight general patterns in the functioning of wader and wildfowl community. In particular, wader species were allocated to the following 4 guild categories:

- Generalist feeder species predominantly feeding on mudflat (*Mud F*);
- Specialist feeder species predominantly feeding on mudflat, preying on larger/specific prey (*F specialist*);
- Species predominantly roosting on mudflat (*Mud R*);
- Species showing a loose association with mudflat (*Mud*).

The guild categories identified for wildfowl species, in turn, are as follows:

- Estuarine feeder species, spending most of their life in estuaries (*Est F*);
- Species showing a loose association with marsh (*Marsh*); (in the Humber, these are usually feral expanding geese populations, mostly breeding in the upper estuarine zone);
- Species grazing on mudflats on *Zostera/Enteromorpha* (*Mud Grazer*);
- Species roosting on mudflats but feeding mostly inland (*Mud R/ F inland*);
- Fish eating duck/diver (*Subtidal*);
- Freshwater duck (FW duck);
- Sea duck (mostly marine) (*Sea duck*).

Overall, the Elbe estuary shows a high importance (in terms of average annual number of birds), with higher counts generally observed along the north bank (SH) of the estuary, particularly for waders (

Table 2, Appendix 1). The Humber estuary also proves to be an important site (in relative quantitative terms) particularly for waders.

Dunlin, a small wader commonly feeding on benthic prey in the estuarine mudflats, dominates the wader assemblages in the Weser and Elbe estuaries (where it accounts for 24% to 50% of the total average maximum annual count), this species being abundant and frequent also in the Humber (accounting for 20% of the total count) (

Table 2, Appendix 2). Other abundant wader species relying on estuarine mudflats for feeding are the Oystercatcher, Curlew, Bar-tailed Godwit, Knot and Grey Plover. Also Lapwing and Golden Plover, two wader species using estuarine mudflats mostly for roosting, are highly abundant, particularly in the Humber estuary (where Golden Plover dominates the wader assemblage in quantitative terms overall) but also in the Elbe (particularly in the southern bank, NDS) (

Table 2, Appendix 2).

As regards wildfowl, estuarine feeder species such as Shelduck, Wigeon and Mallard show the highest abundance overall, particularly in the Humber (accounting for 75% of the total counts on average), Weser (48%) and in the northern bank of the Elbe (57%), with Shelduck being particularly important in this latter area in terms of both relative and absolute abundance (

Table 2, Appendix 2). Teal is also relatively abundant in particular in the Humber estuary, with 12% of the wildfowl total count accounted for by this species. Goose species commonly associated to marsh habitats are also abundant in these assemblages, with Barnacle Goose particularly represented in the Elbe estuary (where it accounts for between 36% and 54% of the wildfowl total counts) and European White-fronted Goose in the Weser (17% of the wildfowl total count) (

Table 2, Appendix 2).

When considering the broad scale spatial distribution of bird assemblages within the estuaries (in terms of differences between the estuarine salinity zones), an increase in the total density of waders and wildfowl is observed generally towards the outer estuary (Figure 2). The species most represented in these outer zones are Dunlin, Oystercatcher, Curlew and Knot among the waders, and Shelduck, Mallard, Wigeon and Barnacle Goose for the wildfowl. Particularly high densities are observed in the polyhaline zone of the southern bank of the Elbe estuary (Niedersachsen area), where bird data regard mainly the outer sands / remote islands. However, it should be noted that counting units in this zone are generally of very small area (max. 0.2 km^2) compared to those in the other zones of the same estuary (with a minimum area between 2 and 8 km^2) and that very high counts have been recorded in these areas, thus leading to the very high species density observed, particularly around the island of Scharhöm compared to the other areas.

The oligohaline zone in the Humber estuary also seems to support dense wader and wildfowl assemblages. Wader total density in particular shows higher values in this zone compared to similar zones in the other estuaries, with the abundance of the roosting species Golden Plover and Lapwing being mainly responsible for this result (Figure 2). It is of note that the Humber estuary is also the only site where a decrease in the total wildfowl density is observed towards the outer areas, mainly due to the higher density of Teal, Mallard and Wigeon in the oligohaline and mesohaline zones. A relatively low total density of wildfowl can be observed in the Weser in the polyhaline zone compared to the other salinity zones in the same estuary (despite the increase of Shelduck density with the salinity gradient) and to what is observed in the same zone in the Elbe (Figure 2).

General characteristics of bird assemblages in TIDE estuaries

The wader and wildfowl assemblages in the studied TIDE estuaries included a total of 19and 21 species respectively. Wader assemblages are numerically dominated by species using estuarine mudflats for feeding, like Dunlin, Oystercatcher, Curlew and Knot, but also species roosting on mudflats, like Lapwing and Golden Plover, are locally abundant. Wildfowl assemblages are dominated by duck species (Shelduck, Wigeon, Mallard and Teal being the most numerous), with also goose species being locally highly abundant (e.g. Barnacle Goose in the Elbe). In general, higher densities of wader and wildfowl species feeding on mudflats are found in the outer part of the studied estuaries (polyhaline zone), this pattern being particularly marked when considering the southern bank of the Elbe. However, in the Weser and especially in the Humber, the oligohaline zone appears to be important as well in supporting dense populations of waders roosting on mudflats (Lapwing and Golden Plover) as well as high wildfowl numbers, including Teal, Wigeon and Mallard.

Table 2. Bird species included in the analysed datasets from the Humber, Weser and Elbe (NDS=southern bank, SH=northern bank). Max annual count (per counting unit/sector) in each estuarine dataset is reported (empty cells indicate species not included in the analysed dataset). Species allocation to guilds is also indicated.

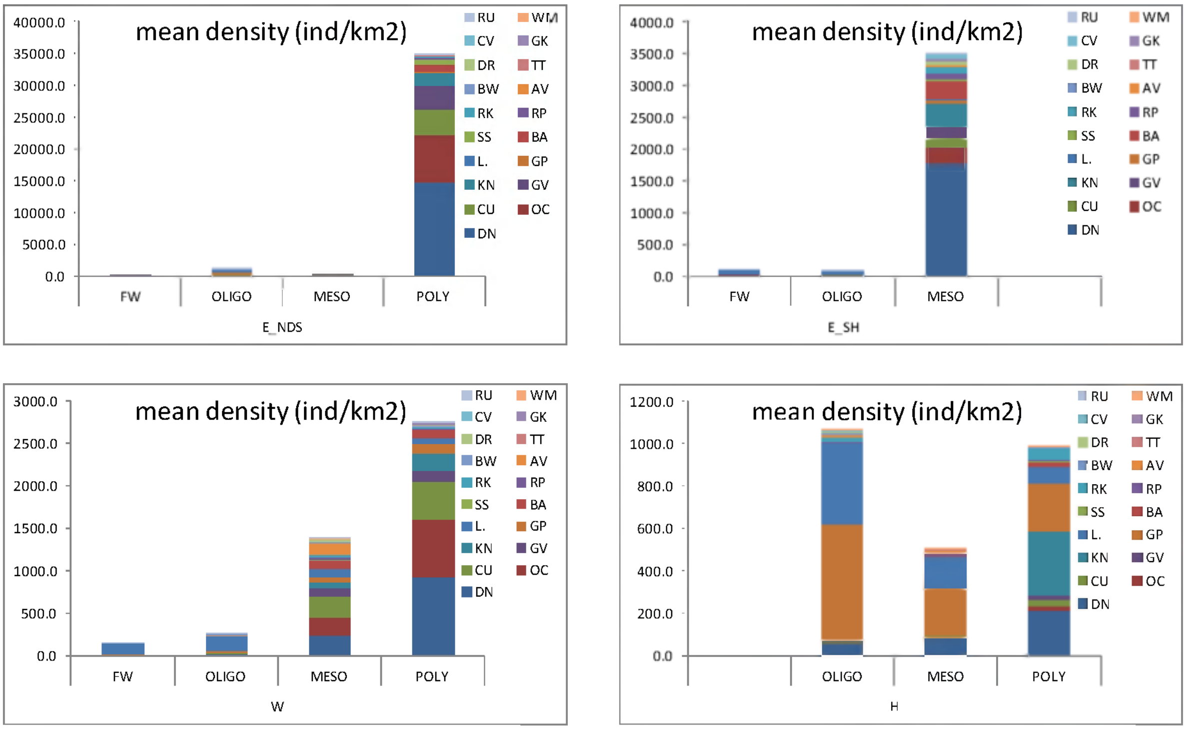
BTO Species code	Species (EN)	Species (scientific)	Group	Guild	Max count in the dataset Humber	Elbe (NDS)	Elbe (SH)	Weser
WADERS:								
DN	Dunlin	*Calidris alpina*	Sandpipers and allies	Mud F	25000	85000	144442	55000
KN	Knot	*Calidris canutus*	Sandpipers and allies	Mud F	35004	20000	32180	42000
GV	Grey Plover	*Pluvialis squatarola*	Plovers and lapwings	Mud F	5000	25000	8735	11050
RK	Redshank	*Tringa totanus*	Sandpipers and allies	Mud F [(1)]	7500	1580	11778	1000
CV	Curlew Sandpiper	*Calidris ferruginea*	Sandpipers and allies	Mud F		45	10805	500
DR	Spotted Redshank	*Tringa erythropus*	Sandpipers and allies	Mud F		3850	5412	810
RP	Ringed Plover	*Charadrius hiaticula*	Plovers and lapwings	Mud F	1410	1530	7742	1323
TT	Turnstone	*Arenaria interpres*	Sandpipers and allies	Mud F [(2)]	480	2630	437	500
WM	Whimbrel	*Numenius phaeopus*	Sandpipers and allies	F specialist	150	831	87	580
OC	Oystercatcher	*Haematopus ostralegus*	Oystercatchers	F specialist	4000	26604	15990	40000
CU	Curlew	*Numenius arquata*	Sandpipers and allies	F specialist	3000	42000	8398	23000
BA	Bar-tailed Godwit	*Limosa lapponica*	Sandpipers and allies	F specialist	5900	12000	16700	8000
BW	Black-tailed Godwit	*Limosa limosa*	Sandpipers and allies	F specialist	696	3500	13	2000
GP	Golden Plover	*Pluvialis apricaria*	Plovers and lapwings	Mud R	26260	18000	5100	5842
L.	Lapwing	*Vanellus vanellus*	Plovers and lapwings	Mud R	14488	23000	3084	8000
SS	Sanderling	*Calidris alba*	Sandpipers and allies	Mud	701	2400	7105	2394
AV	Avocet	*Recurvirostra avosetta*	Stilts and avocets	Mud	270	2400	3234	5000
GK	Greenshank	*Tringa nebularia*	Sandpipers and allies	Mud		1050	3711	2370
RU	Ruff	*Philomachus pugnax*	Sandpipers and allies	Mud		872	360	
WILDFOWL:								
SU	Shelduck	*Tadorna tadorna*	Ducks (Swans, ducks and geese)	Est F	4111	31100	45000	10300
WN	Wigeon	*Anas penelope*	Ducks (Swans, ducks and geese)	Est F [(3)]	8000	9700	11930	15000
MA	Mallard	*Anas platyrhynchos*	Ducks (Swans, ducks and geese)	Est F	5000	9700	8950	8427
T.	Teal	*Anas crecca*	Ducks (Swans, ducks and geese)	Est F	3163	7640	5018	11323
BY	Barnacle Goose	*Branta leucopsis*	Geese (Swans, ducks and geese)	Marsh	348	40000	27500	6000
WG	White-fronted Goose (European)	*Anser albifrons albifrons*	Geese (Swans, ducks and geese)	Marsh	96	9400	421	10160
GJ	Greylag Goose	*Anser anser*	Geese (Swans, ducks and geese)	Marsh	901	6760	1703	5000
CG	Canada Goose	*Branta canadensis*	Geese (Swans, ducks and geese)	Marsh	420			
BG	Brent Goose	*Branta bernicla*	Geese (Swans, ducks and geese)	Mud Grazer	813	4686	2770	7052
PG	Pink-footed Goose	*Anser brachyrhynchus*	Geese (Swans, ducks and geese)	Mud R / F inland	1500			
BE	Bean Goose	*Anser fabalis*	Geese (Swans, ducks and geese)	Mud R / F inland		970	0	1600
BS	Bewick's Swan	*Cygnus columbianus*	Swans (Swans, ducks and geese)	Mud R / F inland		1742	1	624
WS	Whooper Swan	*Cygnus cygnus*	Swans (Swans, ducks and geese)	Mud R / F inland		580	54	167
PT	Pintail	*Anas acuta*	Ducks (Swans, ducks and geese)	FW duck	550	1047	3561	2210
SV	Shoveler	*Anas clypeata*	Ducks (Swans, ducks and geese)	FW duck		1998	216	400
TU	Tufted Duck	*Aythya fuligula*	Ducks (Swans, ducks and geese)	FW duck		1490	32	719
PO	Pochard	*Aythya ferina*	Ducks (Swans, ducks and geese)	FW duck	400			
GA	Gadwall	*Anas strepera*	Ducks (Swans, ducks and geese)	FW duck		217	54	137
SP	Scaup	*Aythya marila*	Ducks (Swans, ducks and geese)	Sea duck	550			
CX	Common Scoter	*Melanitta nigra*	Ducks (Swans, ducks and geese)	Sea duck	200			
EE	Eider	*Somateria mollissima*	Ducks (Swans, ducks and geese)	Sea duck	200			

[(1)] Generalist feeder on mudflat but likes *Corophium*, between generalist and specialist feeding

[(2)] Generalist feeder on mudflat but also feeds on hard substratum cobbles and weed on estuaries

[(3)] Estuarine feeder, mostly grazing on marsh/grass in the estuary (and roosting on mudflats)

WADERS



WILDFOWL

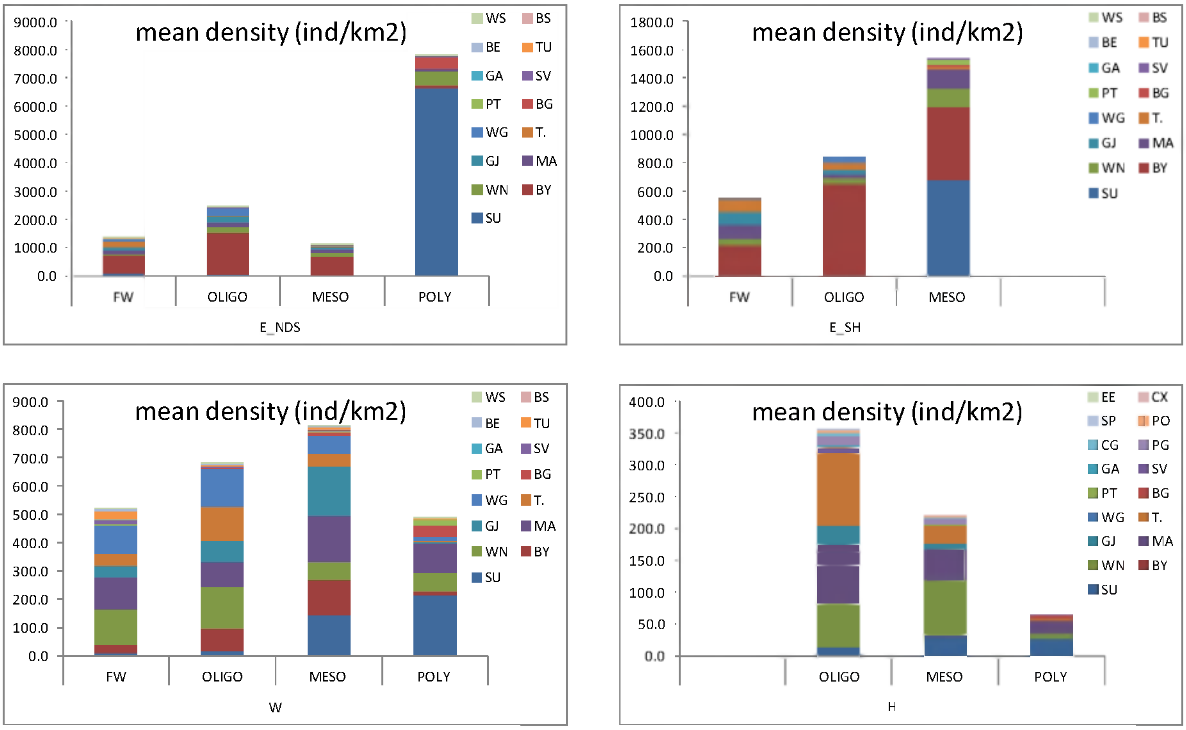


Figure 2. Mean density (ind.km^{-2}) of waders and wildfowl in the salinity zones within the Elbe (E; NDS=southern bank, SH=northern bank), Weser (W) and Humber (H, northern bank) estuaries. Species codes are as in

Table 2.

5 Bird assemblages distribution and relationship with environmental variables

The distribution of bird assemblages within the studied TIDE estuaries and its relationship with the environmental variables described in Chapter 3 was investigated by applying multivariate analysis to the data. This analysis allowed the identification of the main environmental gradients affecting the distribution of waders and wildfowl communities across the estuarine areas (units or sectors). A temporal component was also included in the analysis in order to account for possible changes in the spatial distribution of species over different periods of time (measured as 5-year periods) as a response to possible changes in the habitat availability and quality over the periods. Further information on the data treatment, the analysis and its limitations (due to data availability), and detailed results are provided in Appendix 3.

A high similarity was observed between bird species within the wader and wildfowl groups in their distribution within the three studied estuaries, particularly when considering the most abundant species (Dunlin, Golden Plover, Lapwing, Oystercatcher, Curlew for waders; Shelduck, Wigeon, Mallard, Teal for wildfowl) (Appendix 3). For wildfowl in particular, species having similar modes in the use of the estuarine habitat (as indicated by the functional groups described in Chapter 4) showed similar distribution in each of the studied estuaries, although some differences were observed between estuaries. For example, the estuarine feeder species are widely distributed across all the estuarine zones in the Elbe, whereas they show high densities in the polyhaline and mesohaline areas of the Weser and in the oligohaline and mesohaline areas of the Humber. A lower similarity in the spatial distribution within each estuarine system was observed between the wader species sharing similar habitat use (Appendix 3), although this is likely dependent on how functional groups were defined for waders. In contrast to wildfowl, for which functional groups allowed clear discrimination of different habitat preferences (e.g. freshwater and sea ducks) at the estuarine scale, a higher overlapping of the broad habitat preferences occurred between the functional groups defined for waders (e.g. specialist or generalist feeders, both of them feeding on mudflats; or species feeding or roosting on mudflats), thus leading to a lower agreement between the species distribution at the estuary scale and their allocation to the same functional group.

The multivariate analysis applied to the bird data (separately for waders and wildfowl and for each estuary) also highlighted a general predominance of the spatial variability in bird density distribution in the studied areas. Although certain variability in the species density occurred across the different periods covered by the data, the differences in the species distribution were higher among the different sectors/units located along the banks of each estuary (Appendix 3). Below, the results on the species distribution within the estuarine areas and their relationships with the environmental gradients in them are provided by estuary.

5.1 Humber

In the Humber estuary, most of the spatial variability in the distribution of wader and wildfowl assemblages is ascribed to the differentiation of assemblages among the sectors within the mesohaline zone (Appendix 3). This is due to the presence of distinct assemblages in the sectors ND and NE, generally characterised by low densities of almost all the wader and wildfowl species (with the exception of Turnstone). When considering the other sectors, it is evident how the spatial variability of waders and wildfowl assemblages broadly matches with the salinity gradient in the estuary (Appendix 3). For waders, this is mainly due to the higher density of Avocet, Lapwing, Golden Plover and Black-tailed Godwit in oligohaline sectors and the higher density of all the other species (in particular Dunlin and Knot, and with the exception of Turnstone) in the polyhaline sectors. For wildfowl, this is mainly due to the higher density of Teal, Mallard, Pink-footed Goose, Canada Goose and Pintail in oligohaline sectors and the higher density of Brent Goose as well as of sea ducks (e.g. Eider, Common Scoter) in the polyhaline sectors.

The application of multivariate multiple regression models shows that a high proportion (>80%) of this observed spatial variability in the distribution of species densities in the Humber estuary can be explained by the environmental variables included in the model (Table 3). The combination of habitats coverage in the different estuarine sectors, in particular, accounts for the larger portion of this variability compared to the other types of environmental variables (including salinity, food availability (as intertidal benthic abundance) and anthropogenic disturbance)[2]. The model selection process highlighted that the combination of almost all the considered variables is relevant in determining the distribution of waders and wildfowl species in the Humber, with the exception of marsh area for waders and intertidal benthic abundance for wildfowl.

When looking in detail at the importance of each environmental variable in affecting the density distribution of wader and wildfowl assemblages in the Humber estuary (as shown in Table 3[3] and by the graphic representation (through dbRDA[4] plots) of the multivariate regression models in Figure 3), the intertidal area in the estuarine sectors results to be the predictor that can best explain the density distribution of waders (with 40% of the wader species variability explained by this variable alone). In particular, the wader assemblage differentiation that has been observed between sectors in the mesohaline zone can be mainly associated to a low availability (in terms of area) of the intertidal habitat in sectors ND and NE, leading to the scarce presence of most waders in these areas. This is associated with a higher occurrence of hard substrata (pebbly areas and man-made structures), a likely responsible for the higher density of Turnstone in these sectors, due to its habit of feeding on hard substratum cobbles and weed. In turn, the area of the intertidal habitat in the sectors is positively correlated with the distribution of most of the species occurring with higher density in the outer estuary (e.g. Knot, Dunlin, Bar-tailed Godwit) (Table 4). Supralittoral area is the

2 Although this result might be influenced also by the higher number of habitat variables included in the analysis compared to the number of the other variables.

3 In particular, single predictor models (i.e., regression models relating the distribution of the species densities to one variable at a time) can be used to rank the importance of each environmental variable in affecting the bird assemblage distribution.

4 Distance-based Redundancy Analysis (Legendre and Anderson 1999)

weakest predictor of waders density distribution among those included in the model (Table 3).

When considering the wildfowl assemblage, the best predictor of its distribution in the Humber is the marsh area, this variable alone accounting for 26% of the species density variability. In general, higher density of most wildfowl species (in all sectors except for ND and NE) are associated to a higher availability of marsh habitat (in terms of coverage area) in the sector (Table 4, Figure 3). In turn, anthropogenic disturbance and subtidal area are the weakest predictors of wildfowl density distribution among those included in the model for the Humber (Table 3).

5.2 Weser

In the Weser estuary, most of the spatial variability in the distribution of wader assemblages is observed along the salinity gradient, with generally higher density of most of the species in the mesohaline and polyhaline zones (Appendix 3). It is of note that certain variability occurs among the units within each salinity zone, this being particularly evident in the freshwater and oligohaline areas. This is mainly due to a temporal variability of wader assemblages ascribed to general low densities of Black-tailed Godwit, Golden Plover and Lapwing recorded in the periods 1980-1984 and 2005-2009 compared to the other periods. The matching of the assemblage distribution with the salinity gradient in the Weser estuary is also evident for wildfowl, with higher densities of species feeding or grazing on mudflats like Shelduck and Brent Goose characterising the assemblages in the polyhaline areas (although also the freshwater duck Pintail shows higher density in this zone[5]). Mallard, Greylag Goose, Bean Goose and Barnacle Goose show higher density in the mesohaline areas, Teal and Wigeon in the oligohaline areas, and freshwater ducks like Shoveler, Gadwall and Tufted Duck showing higher densities in the freshwater areas. A relevant temporal variability of bird assemblages is observed also for wildfowl, particularly in the freshwater and oligohaline zones, and this can be mainly ascribed to general lower densities of species like for example Mallard, Wigeon, Barnacle Goose and Bean Goose recorded in these areas in the period 1980-1984 compared to following periods.

As there is only a very limited temporal overlapping between the habitat and the water quality datasets in the Weser, multivariate multiple regression models were applied separately to these datasets. As also observed in the Humber, a higher portion of the observed variability in the bird data in the Weser estuary is explained by habitat data alone (42% and 36% for waders and wildfowl assemblages, respectively) compared to the water quality variables (<20% of variance explained) (Table 3), although this might be influenced also by the fact that different datasets were analysed (e.g. water quality data are available for the freshwater and oligohaline zones only in this estuary), hence limiting the comparability of these results. The model selection process highlighted that the combination of all the habitat variables is relevant in determining the distribution of waders and wildfowl species in the Weser, whereas, for the water quality data, autumn NH4 and NO2 (for both

[5] It is of note that the allocation of species to guilds was based on the detailed knowledge of bird use in the Humber estuary. However, as the habitat use depends not only on the ecology of the species but also on the availability and distribution of resources within the estuaries, local adaptations might occur leading to possible discrepancies with the above guild allocation in other estuaries. In the specific case of Pintail, it is acknowledged that a classification as estuarine species might be more appropriate.

waders and wildfowl) and BOD (for wildfowl) were excluded from the best model explaining the species distribution in the estuary.

The habitat predictor that can best explain both waders and wildfowl density distribution is the intertidal area, with 19% and 12% respectively of the species density variability explained by this variable alone (Table 3). Larger intertidal areas are present in the mesohaline and polyhaline zones in the estuary and these conditions are associated to wader assemblages with higher density of species feeding on mudflats like Oystercatcher, Dunlin, Curlew and lower density of species like Lapwing and Black-tailed Godwit, and to wildfowl assemblages with higher density of species like Shelduck and Pintail and lower density of Teal and Greylag Goose (Figure 4, Table 4).

When considering water quality variables only as possible predictors, BOD is the best predictor of the distribution of wader species in the oligohaline and freshwater areas of the Weser estuary, although this variable alone explains only 6% of the variance in the data (Table 3). Lower BOD values (indicative of a lower organic and nutrient enrichment) are associated to oligohaline areas of the estuary, where a higher density of most of wader species is observed (compared to the freshwater zone), thus leading to negative correlations between these species densities and BOD (Figure 4, Table 4).

As regards wildfowl, the best water quality predictor of the assemblage distribution in the oligohaline and freshwater areas of the Weser estuary is PO4, this variable affecting mainly the temporal variability of the wildfowl assemblage, with a decrease of PO4 over the periods considered in the analysis (between 1990-1994 and 2005-2009) associated to higher density of most of species in later periods, in particular goose species like Barnacle Goose, Greylag Goose and European White-fronted Goose (Figure 4, Table 4).

5.3 Elbe

In the Elbe estuary, most of the spatial variability in the distribution of wader assemblages can be observed along the salinity gradient, with a generally higher density of most of the species in the mesohaline and polyhaline zones (Appendix 3). However, a marked differentiation is observed between the northern and southern banks of the estuary, particularly in the middle estuary (oligohaline and mesohaline zones). In the mesohaline zone, the north bank (e6SH) shows higher density of most wader species (e.g. Dunlin, Oystercatchers, Curlew, Ringed Plover, Greenshank) than the south bank (e6NDS). This difference is possibly related to the higher level of industrialisation of the south bank in this area compared to the north bank, where a more natural habitat is present, similar to the Wadden Sea habitat, leading to a higher similarity of its wader assemblage with that one observed in the polyhaline zone along the south bank (e7NDS). Similarly, the different degree of anthropogenic disturbance in the north and south bank is likely to affect also the differentiation of wader assemblages in the oligohaline zone, with higher species densities observed in the more natural area along the south bank (e5NDS) compared to the more disturbed area along the north bank (e5SH), the assemblages in this latter area being more similar to those in adjacent disturbed areas along the north bank in the freshwater zone of the estuary (e4SH and e3SH). It is of note that a wide variability in wader assemblages is present also in the inner estuary (freshwater zone), mainly due to the lowest density of all the species in the most inner part of the estuary (data from the southern bank only are available for this zone, e1NDS), upstream of the Hamburg inner harbour area. Similar differentiations between the north and south bank of the Elbe estuary are found when considering wildfowl assemblages, although, in this case, the temporal variability within the freshwater zone, with lower density of species in the inner areas, is predominant over the spatial variability along the whole estuarine gradient (Appendix 3). This latter variability is mainly related to the higher density of species such as Shelduck, Mallard, Brent Goose, Pintail and Wigeon in the natural areas in the polyhaline (south bank) and mesohaline (north bank) zone, and, in turn, to the higher density of swans, most of geese and freshwater ducks in oligohaline and freshwater areas of the estuary (including also the mesohaline portion of the southern bank).

There is no temporal overlapping between the habitat and the water quality datasets in the Elbe, therefore multivariate multiple regression models had to be applied separately to these datasets. In contrast to what observed for the Humber and the Weser, a high portion of the observed variability in the bird data in the Elbe estuary is explained by water quality variables alone (41% and 37% for waders and wildfowl assemblages, respectively) compared to the habitat areas (27% and 20% of variance explained, respectively) (Table 3), although this might be partly influenced by the different analysed datasets as well as by the slightly higher number of explanatory variables included in the water quality models (5 variables) compared to the habitat ones (4 variables). The model selection process highlighted that the combination of all the habitat and water quality variables considered is relevant in determining the distribution of waders and wildfowl species in the Weser.

The habitat predictor that can best explain both waders and wildfowl density distribution is the deep subtidal area, with 13% and 9% of the species variability explained by this variable alone respectively (Table 3). Wider deep subtidal areas occur mostly in the freshwater zones of the estuary (e3NDS and e4NDS), as well as in the south shore of the mesohaline zone of the estuary (e6NDS), with the associated assemblages usually showing lower densities of all the species (except for Tufted Duck), in contrast with the abundant assemblages observed in the northern bank in the mesohaline zone (Figure 5, Table 4).

When considering water quality variables only as possible predictors, the salinity gradient (as measured by water chlorinity) is the best predictor of the distribution of both wader and wildfowl assemblages in the Elbe, with 24% and 18% of the species variability explained by this variable alone respectively (Table 3). Almost all wader species (except for Lapwing and Ruff) are present with higher densities in polyhaline and mesohaline areas, and similar positive relationship with chlorinity is observed for several wildfowl species, for example Shelduck and Brent Goose, Wigeon, although there are some wildfowl species showing a negative correlation with the salinity gradient in the estuary (e.g. Teal, Greylag Goose) (Figure 5, Table 4). It is also of note that PO_4, as in the Weser, is a good predictor of wildfowl distribution in the Elbe estuary (with 16% of the species variability explained by this variable alone), this variable showing a different spatial pattern compared to the salinity one in the Elbe (in particular with higher values in the oligohaline and mesohaline zones compared to the polyhaline and freshwater areas).

Table 3. Results of the multivariate multiple regression models. The percentage of variance in the wader and wildfowl density explained by the environmental variables included in the models (as combination of all variables, habitats or water quality (WQ) variables only, or as single variables) is reported, as well as the number of observations included in the full model. The variables included in the best model (after backward selection using AIC criterion) are indicated with Y.

HUMBER:	Waders (18 species)			Wildfowl (22 species)		
Type (and no.) of environmental variables	% expl. Variance	no. obs modelled	Variables included in the Best model	% expl. Variance	no. obs modelled	Variables included in the Best model
Single regression models:						
1- Intertidal area	40%	27	Y	24%	28	Y
2- Subtidal area	12%	27	Y	9%	28	Y
3- Marsh area	30%	27	N	26%	28	Y
4- Supralittoral area	6%	27	Y	13%	28	Y
5- % Hard - pebble	30%	27	Y	22%	28	Y
6- % Hard - man made	12%	27	Y	23%	28	Y
7- Salinity	30%	27	Y	18%	28	Y
8- Intert Benth Abundance	22%	27	Y	10%	28	N
9- Disturbance	12%	27	Y	9%	28	Y
Multiple regression models:						
All variables (1-9)	87%	27		83%	28	
Habitat (1-6)	72%	27		71%	28	
Habitat areas only (1-4)	57%	27		51%	28	
WQ and others (7-9)	45%	27		29%	28	
ELBE:	**Waders (19 species)**			**Wildfowl (15 species)**		
Type (and no.) of environmental variables	**% expl. Variance**	**no. obs modelled**	**Variables included in the Best model**	**% expl. Variance**	**no. obs modelled**	**Variables included in the Best model**
Single regression models:						
1- Intertidal area	7%	61	Y	3%	67	Y
2- Subt_shallow area	9%	61	Y	5%	67	Y
3- Subt_deep area	13%	61	Y	9%	67	Y
4- Foreland area	7%	61	Y	6%	67	Y
5- Chlorinity	24%	90	Y	18%	91	Y
6- BOD5	5%	90	Y	9%	91	Y
7- %DOsat	9%	90	Y	6%	91	Y
8- PO4	10%	90	Y	16%	91	Y
9- NH4(aut)	6%	90	Y	4%	91	Y
Multiple regression models:						
Habitat (1-4)	27%	61		20%	67	
WQ (5-9)	41%	90		37%	91	
WESER:	**Waders (19 species)**			**Wildfowl (15 species)**		
Type (and no.) of environmental variables	**% expl. Variance**	**no. obs modelled**	**Variables included in the Best model**	**% expl. Variance**	**no. obs modelled**	**Variables included in the Best model**
Single regression models:						
1- Intertidal area	19%	42	Y	12%	42	Y
2- Subt_shallow area	4%	42	Y	6%	42	Y
3- Subtidal area	14%	42	Y	11%	42	Y
4- Marsh area	4%	42	Y	6%	42	Y
5- Chlorinity*	4%	66	Y	3%	72	Y
6- BOD5*	6%	66	Y	2%	72	N
7- PO4*	3%	66	Y	13%	72	Y
8- NH4+NO2(aut)*	3%	66	N	2%	72	N
Multiple regression models:						
Habitat (1-4)	46%	42		32%	42	
WQ (5-8)*	14%	66		18%	72	
*this dataset covers only the freshwater and oligohaline zones of the Weser estuary						

WADERS WILDFOWL

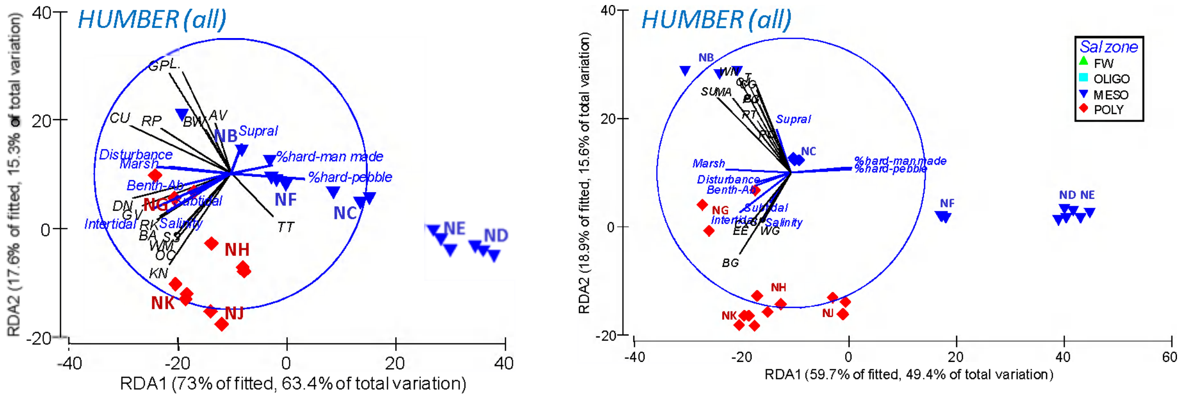


Figure 3. Multivariate multiple regression (dbRDA) performed on bird assemblage distribution and all environmental variables (full model) in the Humber Estuary. Vectors indicate the direction of increase in the species density (in black) and the environmental gradients (in blue). The points in the graph represent the data observations in each sector (shown as coloured labels in the graph) during different 5-year periods, with different symbols indicating salinity zones. A reduced dataset was used for this analysis (e.g. not including sectors in the oligohaline zone) due to limitations in the availability of environmental data (see Appendix 3 for details).

WADERS WILDFOWL

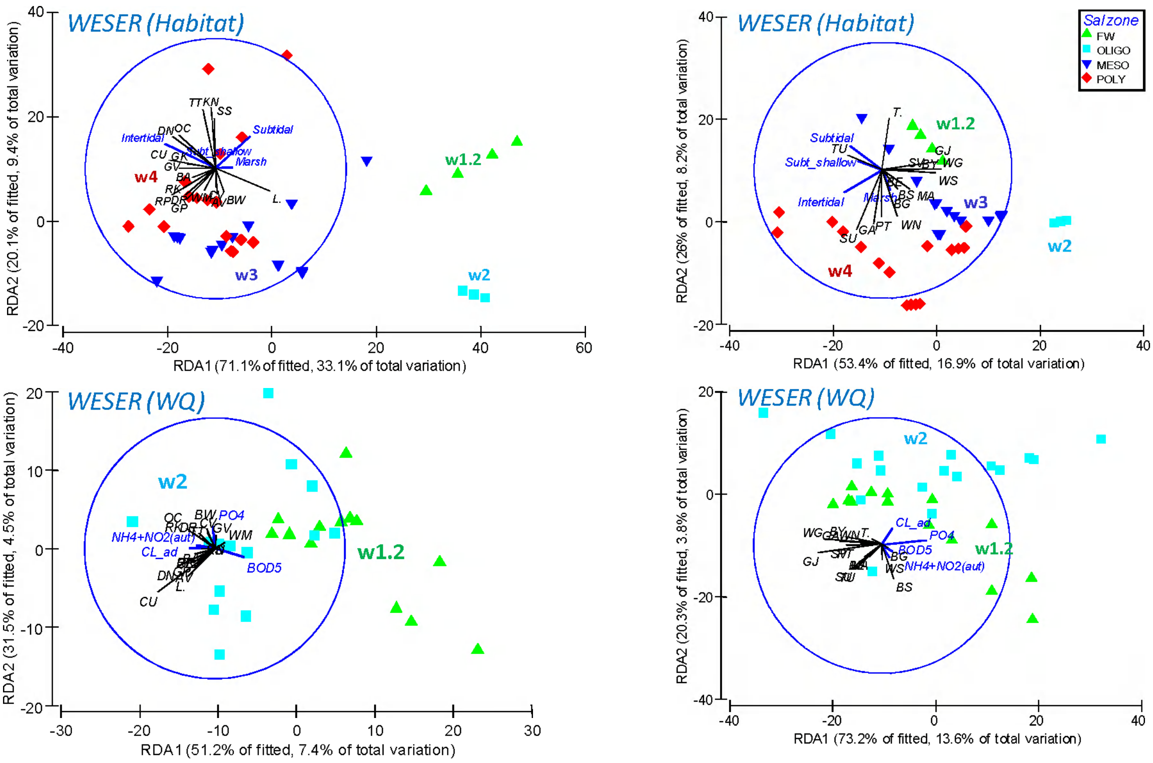


Figure 4. Multivariate multiple regression (dbRDA) performed on bird assemblage distribution and all environmental variables (full model) in the Weser Estuary. Vectors indicate the direction of increase in the species density (in black) and the environmental gradients (in blue) and symbols indicate salinity zones. Sectors are shown as coloured labels in the graph. A reduced dataset was used for this analysis (e.g. not including sectors in the oligohaline zone) due to limitations in the availability of environmental data.

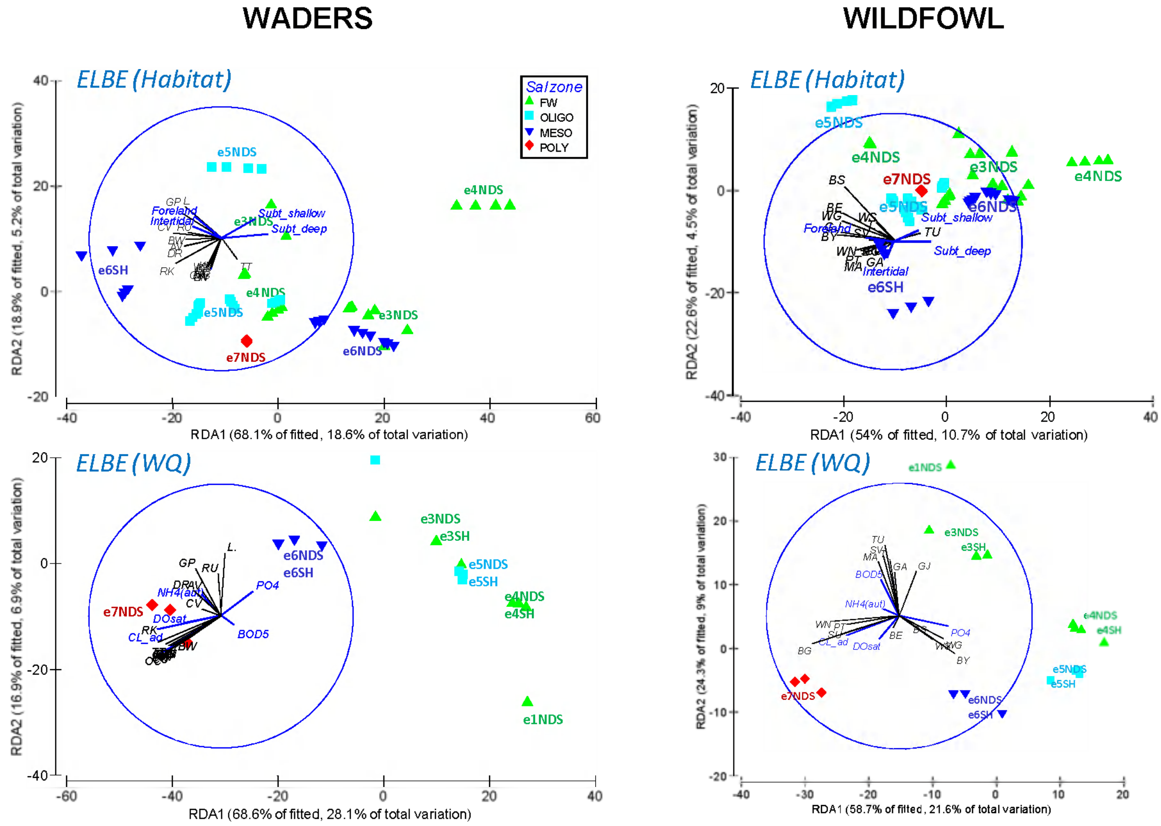


Figure 5. Multivariate multiple regression (dbRDA) performed on bird assemblage distribution and all environmental variables (full model) in the Elbe Estuary. Vectors indicate the direction of increase in the species density (in black) and the environmental gradients (in blue) and symbols indicate salinity zones. Sectors are shown as coloured labels in the graph. A reduced dataset was used for this analysis (e.g. not including sectors in the oligohaline zone) due to limitations in the availability of environmental data.

Table 4. Spearman's correlation coefficients between species density and environmental variables in the studied estuaries (H, Humber; W, Weser; E, Elbe). Significant correlations (p<0.05) are in black bold text.

		Habitat area														Water quality										Other parameters	
		Intertidal			Marsh/Foreland/Supralitto				Subtidal area					Hard habitat		Salinity			Oxygen parameters			Eutrophication					
	Estuary	H	W	E	H	W	E	H	H	W	E	W	E	H	H	H	E	W	E	E	W	W	E	W	E	H	H
BTO Species code	Guild	Intertidal	Intertidal	Intertidal	Marsh	Marsh	Foreland	Supralittoral	Subtidal area	Subt_shallow	Subt_shallow	Subtidal_slope+deep	Subt_deep	%hard - pebble	%hard - man made	Average Salinity	CL_ad	CL_ad	DOsat	BOD5	BOD5	PO4	PO4	NH4+NO2(aut)	NH4(aut)	Intert Benth Abundance	Disturbance
WADERS																											
OC	F specialist	**0.6**	**0.4**	0.1	-0.1	0.1	**0.3**	-0.3	0.0	0.2	**-0.6**	-0.1	**-0.6**	-0.2	-0.2	**0.5**	**0.5**	-0.2	**0.5**	0.0	-0.2	-0.1	**-0.3**	0.2	**0.3**	0.0	**0.5**
CU	F specialist	0.3	**0.4**	0.2	**0.7**	0.2	**0.4**	0.1	0.2	-0.2	**-0.5**	**-0.5**	**-0.6**	**-0.5**	-0.3	0.2	**0.7**	0.0	**0.5**	-0.2	-0.1	**-0.3**	-0.2	0.2	**0.2**	**0.5**	**0.4**
BA	F specialist	**0.7**	**0.3**	0.2	**0.4**	0.0	**0.3**	-0.3	0.2	**-0.4**	**-0.5**	**-0.5**	**-0.5**	-0.3	-0.3	**0.6**	**0.5**	-0.1	**0.4**	-0.1	-0.2	-0.1	**-0.3**	-0.1	0.2	**0.5**	0.4
BW	F specialist	-0.1	**-0.5**	**0.3**	0.1	-0.1	**0.4**	-0.2	0.1	0.1	0.0	0.1	-0.2	-0.1	0.3	0.1	0.1	0.0	0.1	0.0	-0.1	**0.2**	0.2	**0.3**	**0.3**	0.2	0.4
WM	F specialist	**0.6**	0.1	0.2	0.0	-0.2	**0.3**	-0.2	0.0	**-0.4**	**-0.3**	**-0.4**	-0.2	-0.2	-0.3	**0.5**	**0.3**	-0.1	**0.4**	-0.2	-0.1	0.0	0.1	-0.1	**0.3**	0.0	**0.4**
DN	Mud F	**0.6**	**0.4**	0.2	0.2	0.1	0.2	-0.2	0.0	-0.1	**-0.5**	**-0.3**	**-0.5**	**-0.4**	-0.1	**0.6**	**0.4**	0.1	**0.4**	0.0	-0.2	-0.1	**-0.3**	0.2	**0.3**	0.2	**0.7**
KN	Mud F	**0.8**	**0.4**	0.1	0.1	0.1	0.1	-0.3	0.2	-0.1	**-0.5**	-0.3	**-0.4**	-0.2	-0.3	**0.7**	**0.5**		**0.4**	0.0			**-0.4**		0.1	0.2	0.3
GV	Mud F	**0.7**	**0.4**	0.2	**0.5**	0.0	0.2	-0.3	0.3	-0.2	**-0.5**	**-0.4**	**-0.5**	-0.3	-0.4	**0.6**	**0.5**	0.1	**0.4**	-0.1	0.0	0.1	**-0.3**	0.0	**0.2**	**0.6**	**0.4**
RK	Mud F*	**0.5**	0.0	0.1	0.1	-0.2	0.2	-0.3	0.0	-0.2	**-0.6**	**-0.5**	**-0.5**	-0.3	-0.2	0.5	**0.5**	-0.1	**0.4**	-0.2	-0.1	0.1	0.0	0.2	**0.3**	0.2	**0.7**
RP	Mud F	0.1	0.0	0.2	0.2	-0.3	0.2	0.1	-0.2	-0.1	**-0.5**	**-0.4**	**-0.4**	-0.3	0.0	0.1	**0.3**	0.0	**0.3**	-0.1	-0.1	0.0	0.0	0.1	**0.3**	0.0	**0.7**
TT	Mud F*	-0.1	0.3	0.0	-0.4	0.1	0.1	-0.1	0.0	0.1	**-0.5**	-0.1	**-0.3**	0.0	**0.5**	0.1	**0.6**	0.1	**0.5**	-0.1	0.0	0.1	**-0.3**	0.1	0.1	-0.1	0.0
DR	Mud F		0.1	**0.4**		-0.1	**0.5**			-0.3	**-0.4**	**-0.5**	**-0.4**				**0.3**	0.1	**0.3**	-0.2	**-0.3**	-0.1	0.1	0.0	**0.2**		
CV	Mud F		0.1	**0.3**		0.2	**0.3**			-0.2	**-0.5**	-0.2	**-0.3**				**0.3**	0.1	**0.3**	-0.2	-0.1	0.1	-0.1	0.1	0.1		
L.	Mud R	-0.2	-0.3	**0.3**	**0.4**	0.2	**0.5**	**0.6**	-0.2	**-0.3**	0.0	-0.1	-0.2	-0.2	-0.1	**-0.4**	**-0.3**	0.0	**-0.3**	**-0.2**	0.0	-0.2	**0.5**	**0.3**	**0.3**	-0.1	0.2
GP	Mud R	-0.2	-0.1	**0.3**	**0.5**	0.0	**0.6**	0.4	-0.1	-0.3	**-0.3**	**-0.4**	**-0.5**	-0.3	0.0	-0.2	**0.5**	0.1	**0.5**	**-0.5**	-0.1	0.1	**0.4**	**0.2**	**0.2**	0.2	**0.5**
AV	Mud	-0.1	-0.1	**0.6**	**0.4**	-0.2	**0.6**	**0.6**	-0.2	-0.1	-0.2	-0.3	**-0.4**	-0.1	-0.1	-0.3	0.0	0.0	0.0	-0.1	-0.1	-0.2	0.1	0.1	**0.3**	0.1	0.1
SS	Mud	**0.5**	0.0	0.0	-0.1	**-0.3**	0.1	-0.2	0.0	**0.4**	**-0.5**	**0.3**	**-0.4**	-0.2	-0.2	**0.5**	**0.6**		**0.5**	-0.2			**-0.2**		0.1	0.0	**0.5**
GK	Mud		**0.4**	0.2		**0.3**	**0.3**			**-0.3**	**-0.5**	**-0.5**	**-0.5**				**0.3**	0.0	**0.3**	0.0	-0.1	-0.1	-0.1	0.1	**0.4**		
RU	Mud			**0.5**			**0.5**				-0.1		**-0.3**				-0.1		0.0	-0.1			**0.4**		**0.4**		
WILDFOWL																											
SU	Est F	**0.6**	**0.3**	0.2	**0.8**	0.2	0.1	-0.1	0.1	-0.1	**-0.4**	**-0.3**	**-0.5**	**-0.7**	**-0.5**	**0.4**	**0.3**	**-0.3**	**0.2**	0.2	-0.1	-0.2	**-0.4**	0.1	**0.4**	0.3	0.2
WN	Est F*	**0.4**	-0.1	**0.3**	**0.9**	**0.3**	**0.4**	0.1	0.0	0.0	**-0.3**	-0.3	**-0.3**	**-0.8**	**-0.6**	0.2	**0.3**	-0.1	**0.3**	-0.1	0.0	-0.2	0.0	0.0	**0.2**	0.4	-0.1
MA	Est F	0.2	0.0	0.2	**0.6**	-0.1	0.2	0.1	-0.1	**-0.4**	**-0.3**	**-0.5**	**-0.3**	**-0.4**	**-0.4**	0.3	-0.1	-0.2	0.0	0.2	0.0	-0.1	-0.2	0.0	**0.3**	0.2	-0.2
T.	Est F	0.1	**-0.5**	**0.2**	0.3	0.1	**0.3**	0.0	-0.3	-0.2	0.0	-0.1	-0.2	-0.3	-0.1	**0.4**	**-0.3**	**-0.3**	**-0.3**	**0.3**	0.0	-0.2	-0.2	0.0	**0.3**	-0.2	-0.3
BY	Marsh	0.1	0.0	**0.4**	**0.6**	0.2	**0.6**	0.2	-0.2	**-0.4**	-0.2	**-0.4**	**-0.4**	**-0.4**	-0.3	0.2	0.1	**-0.3**	0.0	**-0.6**	-0.2	**-0.7**	**0.7**	**-0.3**	-0.1	0.0	-0.3
GJ	Marsh	0.3	**-0.3**	0.2	**0.7**	0.0	**0.4**	0.3	-0.1	**-0.4**	0.0	**-0.3**	**-0.3**	**-0.7**	**-0.6**	-0.1	**-0.4**	**-0.3**	**-0.5**	0.1	-0.1	**-0.6**	**0.2**	-0.1	**0.2**	0.2	-0.2
WG	Marsh	0.3	-0.2	0.2	0.1	0.1	**0.4**	-0.2	0.1	**-0.5**	0.0	**-0.4**	**-0.3**	-0.2	-0.1	0.0	-0.2	**-0.3**	-0.2	**-0.3**	-0.1	**-0.6**	**0.5**	-0.2	0.1	0.1	0.3
CG	Marsh	-0.3			0.0			**0.6**	**-0.6**					0.0	-0.1	-0.1										-0.3	**-0.5**
BG	Mud Grazer	**0.8**	**0.4**	0.0	**0.5**	**0.4**	0.2	**-0.7**	**0.5**	-0.2	**-0.5**	**-0.3**	**-0.5**	**-0.6**	**-0.4**	**0.4**	**0.7**	0.0	**0.7**	**-0.3**	-0.1	0.0	-0.1	0.0	**0.3**	**0.5**	**0.8**
PT	FW duck	**0.6**	**0.4**	**0.4**	**0.7**	**0.4**	**0.5**	-0.2	0.2	**-0.4**	**-0.3**	**-0.5**	**-0.4**	**-0.7**	**-0.6**	0.4	0.2	-0.1	0.2	0.0	-0.1	**-0.4**	-0.1	0.0	**0.3**	**0.5**	0.2
PO	FW duck	0.1			0.1			0.3	**-0.6**					-0.4	-0.4	0.1										-0.1	-0.3
SV	FW duck		-0.1	**0.4**		0.2	**0.2**			-0.2	0.0	-0.1	-0.2				-0.1	-0.2	-0.1	0.1	0.0	-0.2	0.1	-0.1	**0.4**		
TU	FW duck		-0.1	-0.1		**0.4**	-0.2			0.2	**0.2**	0.3	**0.2**				**-0.2**	**-0.3**	-0.1	**0.3**	0.1	**-0.3**	-0.1	-0.1	**0.2**		
GA	FW duck		0.3	0.1		**0.3**	0.0			-0.1	-0.1	-0.2	0.0				**-0.5**	**-0.4**	**-0.4**	0.2	0.0	**-0.5**	0.2	-0.2	**0.3**		
SP	Sea duck	**0.5**			0.1			**-0.5**	0.0					-0.3	-0.2	**0.4**										0.1	**0.5**
CX	Sea duck	**0.5**			0.2			-0.3	0.0					**-0.4**	-0.3	**0.5**										0.2	**0.4**
EE	Sea duck	**0.5**			0.4			**-0.5**	0.3					**-0.4**	-0.3	0.2										0.3	**0.5**
PG	Mud R / F inland	0.3			**0.7**			0.1	-0.1					**-0.6**	**-0.4**	0.1										0.1	-0.2
BE	Mud R / F inland		0.1	**0.2**		0.0	**0.4**			-0.3	-0.1	-0.2	**-0.4**				0.0	-0.2	0.0	**-0.2**	0.1	**-0.2**	**0.4**	-0.1	0.2		
BS	Mud R / F inland		0.2	0.2		0.2	**0.5**			-0.3	0.0	**-0.3**	**-0.3**				-0.1	**-0.3**	0.0	**-0.3**	0.1	-0.1	**0.5**	0.1	0.2		
WS	Mud R / F inland		-0.1	0.1		0.3	0.2			-0.2	0.1	-0.2	-0.2				0.0	**-0.2**	0.0	**-0.4**	0.2	**-0.3**	**0.7**	-0.1	0.1		

Bird assemblages distribution and relationship with environmental variables

The spatial differentiation of wader and wildfowl assemblages (in terms of overall species density distribution) within the studied TIDE estuaries is predominant over temporal changes, although a higher importance of temporal effects have been observed in the Weser compared to the Elbe and Humber, mainly due to low species densities recorded during the period 1980-1984 in this estuary. The availability of estuarine habitats (in terms of habitat area) is relevant in driving the density distribution of waders and wildfowl, especially in the Weser and Humber. The intertidal area is the most important variable influencing wader density distribution, e.g. with higher densities of species such as Dunlin, Knot, Oystercatcher associated with larger intertidal areas, mostly in the outer parts of these estuaries. This variable is also related to wildfowl distribution in the Weser, whereas marsh area is more important to this bird group in the Humber. Water quality parameters are also relevant determinants of species distribution, their effect being particularly important in the Elbe, where the salinity gradient results as the first predictor of wader and wildfowl species density, due to the general higher densities observed in the polyhaline and mesohaline zones. It is of note that, in this estuary, a differentiation in the species density occurs between the north and south banks, particularly in the oligohaline and mesohaline zones, broadly matching with the distribution of human pressures in these areas showing a negative effect on birds abundance (possibly through direct disturbance or as an indirect effect on the natural habitat availability).

6 Species distribution models

Seven species have been selected based on their representativeness of different guilds, their distribution in the studied estuaries and local relevance, taking into account also their frequency of occurrence in the estuary: Dunlin, Golden Plover, Redshank, Bar-tailed Godwit for waders; Shelduck, Pochard and Brent Goose for wildfowl.

Multiple regression models were applied to each one of these species in order to identify the main environmental determinants of their habitat use within the studied TIDE estuaries. Details on the analysis are provided in Appendix 4. The main results of the habitat distribution models for the selected species are reported below.

6.1 Dunlin

Dunlin distribution was analysed in all the three estuaries and, in most of cases, the species mean density was modelled (Appendix 4). Only in the Elbe the density of the species could not be related to water quality variables, therefore the probability of occurrence was modelled instead. A summary of the resulting models obtained for Dunlin in the studied estuaries is reported in Table 5 and the shape of the effect of each selected continuous predictor variable on the model response is shown in Figure 6 and Figure 7.

The best models, as selected by the analysis, included 4 to 5 variables, which explained more than 75% of the total variability in the species density distribution in the estuaries (Table 5, Figure 6). All these models include intertidal and subtidal habitat (shallow subtidal in particular in the Weser and Elbe models) among the predictors, these two variables ranking between first and fourth in terms of their importance in affecting the species density distribution (as single predictor models). Marsh area is included as an additional habitat variable in the Weser model (scoring 2 in terms of ranked importance as a single predictor), although its effect on Dunlin density in the other estuaries cannot be ruled out, due to its positive correlation with the intertidal area in them. In both the Humber and the Weser, a general increase of mean density of Dunlin is predicted where larger habitat areas occur, although the range of variability of these covariates is markedly different between the two estuaries, due to the larger area of sectors in the Humber (between 6 and 42 km^2, 17 km^2 on average) compared to the area of the counting units in the Weser (between 0.4 and 21 km^2, 5 km^2 on average)[6] (Figure 6). Besides these differences, a general low density of Dunlin is expected when the intertidal area in the sector/unit is <1 km^2, whereas higher density is predicted to be found with intertidal areas >3 km^2 in the Weser and >16 km^2 in the Humber (although relative higher density is predicted also with intertidal area between 3 and 9 km^2 in this latter estuary). An increase in Dunlin density is also predicted with higher subtidal area (>0.9 km^2 in the Weser, and >20 km^2 in the Humber, with a maximum at around 25 km^2) and with increasing marsh area (in particular with values >2.5 km^2) in the Weser, although a similar relationship can be expected also in the Humber, given the positive correlation of marsh area with the intertidal area in the sectors. The results obtained for the Elbe estuary show an opposite relationship of Dunlin density with the habitat areas (in particular intertidal and shallow subtidal), with higher density values expected at smaller habitat areas (<0.8 km^2

[6] The habitat area in fact is calculated using single sectors/counting units as spatial units, therefore the maximum habitat area measured has the area of the sector/counting unit as upper limit.

intertidal, <0.7 km^2 shallow subtidal). It is of note also that, when the effect of habitat area is excluded, the relationship with the salinity gradient is still relevant to Dunlin density in the Elbe estuary (with salinity zone included in the final model) with higher Dunlin density expected in oligohaline and mesohaline zones.

Predictors such as year and population size are also selected as relevant to the species density distribution (these two variables being negatively correlated in the Humber), indicating that the density of Dunlin observed in the estuarine habitats may be significantly affected by inter-annual local fluctuations as well as by the temporal changes of the population size at a wider spatial (regional/national) scale. However, it is of note that this temporal variability is of lower importance compared to the effect of spatial (habitat) variables on Dunlin density, confirming the general results derived for the whole bird assemblage (as obtained from the multivariate analysis). The disturbance index was also identified as a relevant predictor of Dunlin density in the Humber Estuary. Contrary to what would be expected, higher density values were predicted in sectors with higher values of the disturbance index (NF, NG and NK, in particular; Appendix 1). This is likely to be an artefact of the analysis derived from the possible inadequacy of the measured index as a proxy for disturbance in the present analysis, rather than being a reflection of a real preference of the species for more disturbed areas (see Discussion for a detailed explanation).

Table 5. Summary of the habitat distribution models applied to Dunlin in the Humber, Weser and Elbe estuaries. Single predictor models are also reported as a means to rank the importance of the single variables in affecting the species distribution. The variables highlighted in grey are those variables that were excluded from the analysis because of collinearity (their relationship with the other variables included in the analysis is indicated in parenthesis). The variables in bold (and with the asterisk) are those variables that were selected as relevant predictors of the species distribution in the final (best) model.

	Humber (all)		Weser (habitat + Salz)		Elbe (habitat + Salz)		Elbe (habitat + Salz)		Elbe (water quality)	
Variable modelled	density (Sqrt2)		density (Sqrt2)		density (Log)		probab. of presence		probab. of presence	
Best model:										
n	146		140		169		171		247	
dev. expl.	85.5%		77.0%		79.2%		43.8%		32.6%	
no. covariates incl.(*)	4		5		5		5		5	
Covariates (single predictor models - % deviance explained and rank of predictor importance based on AIC)										
Habitat	**Int**	**56.1 (3)** *	**Int**	**48.8 (4)** *	**Int**	**65.5 (1)** *	Int (+For)	13.2 (4)		
	Eun	57.2 (2)								
	Sub	**77.7 (1)** *	**Subs**	**50.3 (3)** *	**Subs**	**34.9 (4)** *	**Subs**	**19.1 (3)** *		
			Sub (+Subs)	27.6 (5)	Subd (+Subs)	19.8 (5)	Subd (+Subs)	5.4 (6)		
	Mar (+Int)	45.9 (5)	**Mar**	**52.7 (2)** *	For (+Int)	46.7 (2)	**For**	**28.2 (1)** *		
	Sup (-Sub, -Sal)	53.0 (4)								
Water Quality	Sal (+Int, +Sub)	35.6 (7)	Salz	61.9 (1)	**Salz**	**45.4 (3)** *	**Salz**	**15.6 (2)** *	**Cl**	**20.9 (1)** *
									BOD (-P)	6.5 (6)
									DO (+Cl)	17.9 (2)
									P	**12.5 (3)** *
									N	**13.8 (3)** *
Other (temporal)	**Y**	**0.5 (8)** *	**Y**	**8.4 (6)** *	**Y**	**2.4 (7)** *	**Y**	**3.3 (7)** *	**Y**	**3.1 (5)** *
	DN.GB (-Y)	0.2 (9)	**DNpop**	**1.1 (7)** *	**DNpop**	**0.03 (8)** *	DNpop	0.3 (8)	DNpop	0.5 (8)
Other (spatial)	**Dis**	**38.9 (6)** *			jurisd	9.42 (6)	**jurisd**	**6.5 (5)** *	**jurisd**	**0.7 (7)** *

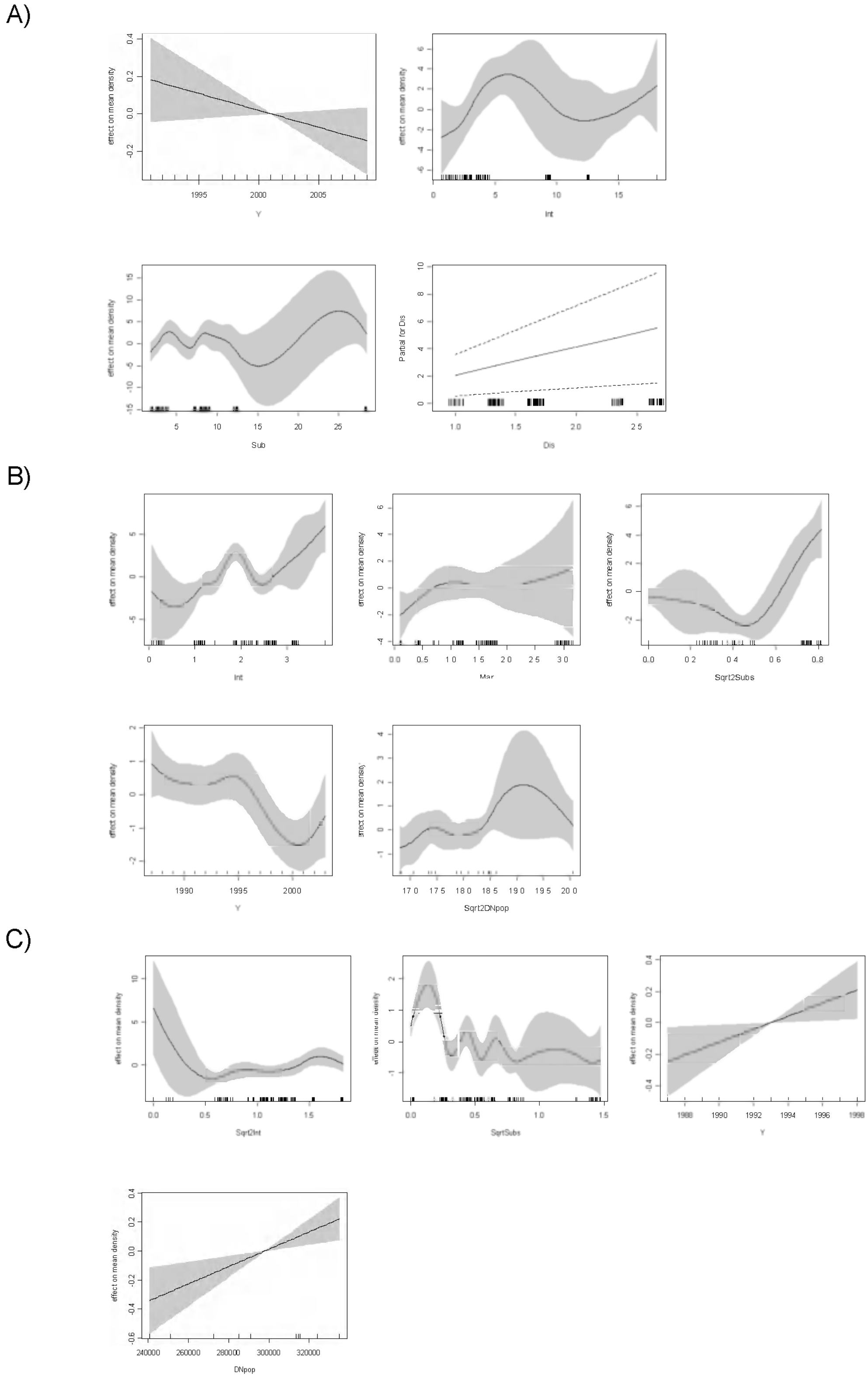


Figure 6. Effect of each explanatory continuous variable on the mean density of Dunlin, measured as contribution on the linear term of the best selected model for the Humber (all environmental covariates) (A), Weser (habitat + Salinity zone (Salz)) (B) and Elbe (habitat + Salz) (C). The fitted values are adjusted to average zero and the dotted bands indicate 95% pointwise confidence intervals. Tick marks along the x-axis show the location of observations along the variable range. The transformations of explanatory variables are abbreviated as follows: Sqrt, square root; Sqrt2, forth-root; Log, logarithmic transformation.

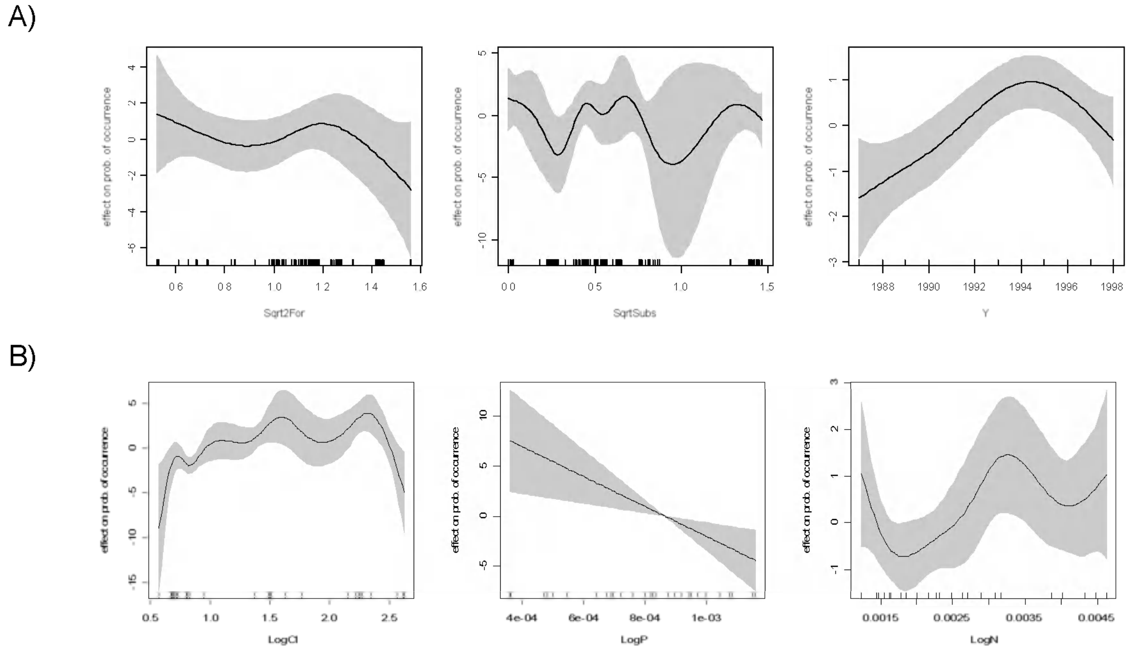


Figure 7. Effect of each explanatory continuous variable on the probability of occurrence of Dunlin, measured as contribution on the linear term of the best selected model for the Elbe (habitat + Salz) (A) and Elbe (water quality) (B). The fitted values are adjusted to average zero and the dotted bands indicate 95% pointwise confidence intervals. Tick marks along the x-axis show the location of observations along the variable range. The transformations of explanatory variables are abbreviated as follows: Sqrt, square root; Sqrt2, forth-root; Log, logarithmic transformation.

When the probability of occurrence of Dunlin is modelled in the Elbe estuary, in relation to either habitat data or water quality variables, it is evident that a lower proportion (<45%) of the data variability is explained by the selected models compared to the density models (>75%), with a higher percentage of deviance explained by the habitat dataset compared to the water quality one (Table 5).

Both models include salinity as a relevant predictor, this variable being among the first two variables in order of importance for their influence on the species distribution, with a higher probability of Dunlin occurrence at intermediate salinities (chlorinity values between 1 and 2.5 mmol/l), in oligohaline and mesohaline zones, when the effect of habitat area is excluded (Figure 7). In the habitat model, shallow subtidal area is again identified as a relevant predictor of Dunlin distribution, although a clear pattern is not evident from the shape of this effect (Figure 7). Also marsh area (Foreland) is included as a relevant predictor in the model, being the most important one among those considered. A higher probability of occurrence for the species is expected with lower marsh area (<0.9 km^2), a condition that is also usually associated with lower intertidal area (as these two variables are positively correlated in the Elbe). This negative relationship of Dunlin occurrence with the marsh and intertidal habitat area is likely to be an artefact of the analysis rather than reflecting a real preference of the species for smaller marsh and intertidal areas. In fact, the analysed dataset for the Elbe included very small counting units (hence leading to small habitat areas in them) where Dunlin was detected with very high frequency and numbers, an effect that is likely to be the consequence of the location of these units in undisturbed and remote zones within the extensive mudflat areas available in the Waddensea.

As regards the water quality model, both nutrients concentrations (as PO4 and autumn NH4) are included as relevant predictors of the species occurrence, with lower probability of presence in areas where PO4 is higher and NH4 is between 0.003 and 0.006 mmol/l (Figure 7). In both models, the location of the counting unit with respect to the north and south bank of the estuary (with higher probability of presence in the north bank than in the south bank) and the year are also selected as relevant to the species distribution, although these variables have a lower importance (scoring 5 to 7 in terms of ranked importance as a single predictor) compared to the others included in the models.

6.2 Redshank, Golden Plover and Bar-tailed Godwit

The density distribution of Redshank, Golden Plover and Bar-tailed Godwit was analysed in the Humber estuary. A summary of the resulting models obtained for these species is reported in Table 6 and the shape of the effect of each selected continuous predictor variable on the model response is shown in Figure 8.

REDSHANK is a wader species occurring in large flocks during winter in the Humber estuary. Seven environmental variables have been selected in the final model as best predictors of its density distribution in the estuary, explaining 82% of the density data variability. The most important predictor of the density of this species is the intertidal area available within the sector, with a linear increase of the species density with this habitat area. The intertidal habitat type is also important to this species, with higher densities expected where a component of littoral sand (LSa) is present (alone or mixed with littoral mud or mixed sediments), and a linear positive relationship is also observed with the total benthic abundance (density) in the intertidal habitat, although the importance of this factor is lower than the above ones. A certain amount of supralittoral habitat (between 0.1 and 0.3 km^2) in the sector is also a relevant predictor of higher densities of Redshank in the Humber, although this habitat is less important than the intertidal one. Similarly to what observed for Dunlin, an increase in Redshank density is expected in sectors where a higher disturbance index is measured. Also for this species, a relevant effect of temporal trends (measured by year) and of the wider population size on the local estuarine population is present, although these variables are the least important predictors of Redshank density among those considered in the analysis.

GOLDEN PLOVER is a species regularly occurring in the Humber estuary, using estuarine areas particularly for roosting. Six environmental variables have been selected in the final model as best predictors of its density distribution in the estuarine areas, explaining 96% of the density data variability. In terms of habitat availability (area), higher densities of the species are predicted where subtidal area in the sectors is <10 km^2 and marsh area is >0.6 km^2, with subtidal area being the most important predictor among those included in the model. Given the positive correlation of marsh area with intertidal area in the estuary, higher density of the species would also be expected where larger intertidal mudflats occur, with the type of substratum (in particular littoral sands) in this intertidal habitat being a relevant determinant of the species density. The characteristics of the benthic resources in the intertidal habitat have also been selected as relevant predictors of the species density, with higher density where community types g and h occur (with moderate numbers of species and largely characterised by oligochaetes including *Tubificoides benedii*, the bivalve *Macoma balthica* and polychaetes such as *Hediste diversicolor*, *Streblospio shrubsolii* and

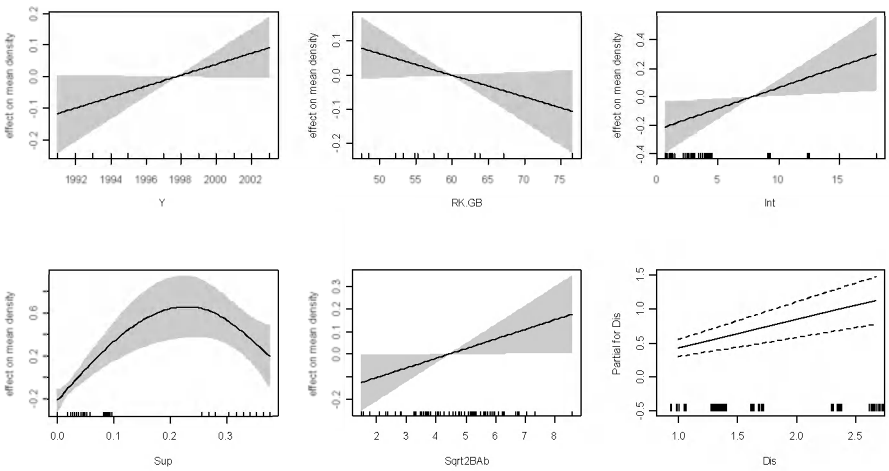
Pygospio elegans) but where total benthic abundance is lower, although these two variables, together with the temporal effect of year, are the least important in affecting the species density distribution in the estuary.

BAR-TAILED GODWIT is long billed wader occurring regularly in the Humber estuary. Six environmental variables have been selected in the final model as best predictors of its density distribution in the estuarine areas, explaining 85% of the density data variability. The most important predictor of the density of this species is the intertidal area available within the sector, with higher density expected where intertidal area is <5 km^2. The type of intertidal habitat is also important for this species, in particular where the substratum is dominated by littoral sands, whereas a negative relationship is observed with the total benthic abundance in this habitat. Also for this species, a relevant effect of temporal trends (measured by year) and of the wider population size on the local estuarine population is present, although these variables are the least important predictors of Bar-tailed Godwit density among those considered in the analysis.

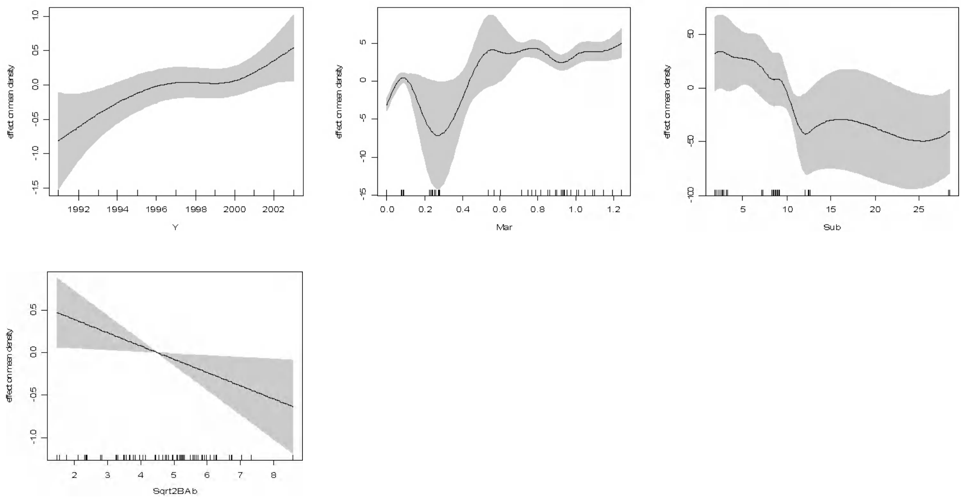
Table 6. Summary of the habitat distribution models applied to selected waders species in the Humber Estuary. Single predictor models are also reported as a means to rank the importance of the single variables in affecting the species distribution. The variables highlighted in grey are those variables that were excluded from the analysis because of collinearity (their relationship with the other variables included in the analysis is indicated in parenthesis). The variables in bold (and with the asterisk) are those variables that were selected as relevant predictors of the species distribution in the final (best) model.

	Waders					
	RK		GP		BA	
Variable modelled	density (Log)		density (Sqrt2)		density (Sqrt2)	
Best model:						
n	91		90		91	
dev. expl.	82.3%		95.8%		85.0%	
no. covariates incl.(*)	7		6		6	
Covariates (single predictor models - % deviance explained and rank of predictor importance based on AIC)						
Habitat	**Int**	**70.8 (1) ***	Int (+Mar)	75.4 (1)	**Int**	**71.3 (1) ***
	Eun	**58.0 (3) ***	**Eun**	**41.0 (4) ***	**Eun**	**58.1 (4) ***
	Sub (-Sup)	64.0 (2)	**Sub**	**71.9 (2) ***	Sub (-Sup)	61.9 (2)
	Mar (+Int)	55.8 (5)	**Mar**	**44.5 (5) ***	Mar	58.1 (3)
	Sup	**38.5 (6) ***	Sup (-Sub)	60.7 (3)	**Sup**	**46.4 (6) ***
Water Quality	Sal (+Int, +Sub, -Sup)	28.5 (8)	Sal (+Int, +Sub, -Sup)	0.4 (9)	Sal (+Int, +Sub, -Sup)	36.6 (7)
Other	**Y**	**0.05 (11) ***	**Y**	**0.01 (11) ***	**Y**	**0.1 (10) ***
	RK.GB	**2.3 (10) ***	GP.GB	0.1 (10)	**BA.GB**	**0.02 (11) ***
	Dis	**50.4 (4) ***	Dis	25.4 (6)	Dis	21.8 (8)
	BAb	**21.6 (9) ***	**BAb**	**30.6 (7) ***	**BAb**	**13.6 (9) ***
	BType	40.1 (7)	**BType**	**25.4 (8) ***	BType	54.0 (5)

A)



B)



C)

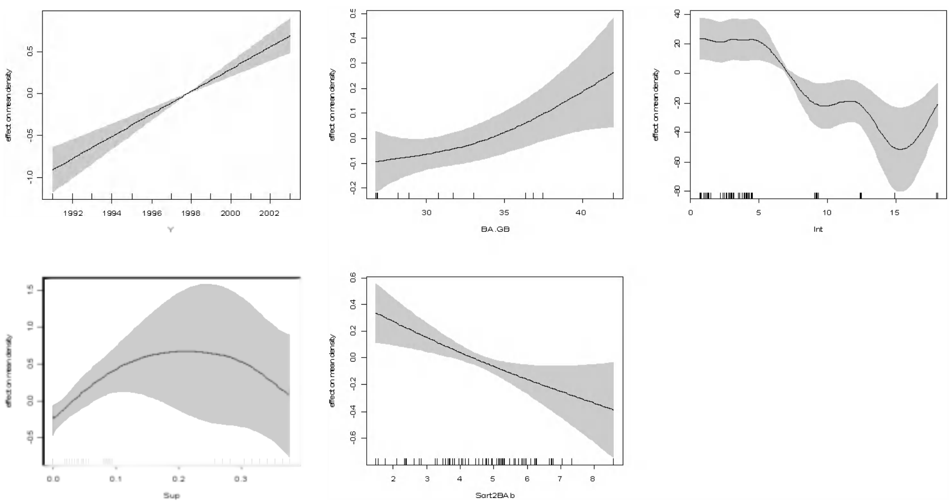


Figure 8. Effect of each explanatory continuous variable on the mean density of Redshank (A), Golden Plover (B) and Bar-tailed Godwit (C), measured as contribution on the linear term of the best selected species models for the Humber Estuary. The fitted values are adjusted to average zero and the dotted bands indicate 95% pointwise confidence intervals. Tick marks along the x-axis show the location of observations along the variable range. The transformations of explanatory variables are abbreviated as follows: Sqrt, square root; Sqrt2, forth-root; Log, logarithmic transformation.

6.3 Shelduck, Pochard and Brent Goose

The density distribution of Shelduck, Pochard and Brent Goose was analysed in the Humber estuary. A summary of the resulting models obtained for these species is reported in Table 7 and the shape of the effect of each selected continuous predictor variable on the model response is shown in Figure 9.

SHELDUCK is a large duck which is present throughout much of the Humber estuary, where it feeds on mudflats. Six environmental variables have been selected in the final model as best predictors of its density distribution in the estuarine areas, explaining 83% of the density data variability. The most important predictors of the density of this species are the subtidal and the intertidal area, both variables showing an almost linear positive relationship with this species. The species density is also expected to increase with the supratidal area in the estuarine sectors, particularly with areas >0.5 km^2. However, the type of intertidal habitat is also relevant in affecting the species distribution, with higher density expected where littoral mud substratum dominates. Similarly to that observed for other species, an increase in Shelduck density is predicted in sectors where a higher disturbance index is measured. However, it is emphasised that rather than this being a reflection of a real preference of the species for more disturbed areas, this result is likely to be an artefact of the analysis, due to the possible inadequacy of the measured index as a proxy for disturbance (see Discussion for a detailed explanation). A relevant effect of temporal trends (measured by year) on the local estuarine population is also present, although this variable, together with the disturbance index, are the least important predictors of Shelduck density among those considered in the analysis.

POCHARD is a largely freshwater duck that can be found in the estuary during winter, although its frequency of occurrence in the studied dataset is relatively low (23%), due to the distribution of the species mostly in the upper estuary sectors (oligohaline and upper mesohaline areas). The probability of occurrence was modelled for the species in the Humber and six environmental variables have been selected in the final model as best predictors of its distribution in the estuarine areas, explaining 74% of the data variability. Although most of the habitat areas (except for supralittoral area) are included as important predictors of the occurrence of the species in the estuary, it is the relationship with intertidal and marsh areas that show the most marked patterns, with a higher probability of finding Pochard in sectors where the intertidal area is <10 km^2, but there is a wider marsh area (>0.84 km^2) compared to other sectors. The type of intertidal habitat also seems to be a relevant predictor of the species occurrence, although the relationship with this factor is not clear, due to the similar contribution of the different types to the probability of presence but with a wider variability of the data where mixed substrata dominated by littoral mud occur. Also for this species, the potential degree of disturbance index (in this case showing a negative linear effect on the species, although the rate of decrease of the probability of occurrence is very low) and the effect of temporal trends (measured by year) on the local estuarine population is present, these variables being the least important predictors of the species presence among those considered in the analysis.

BRENT GOOSE is a migrating species found during winter months in estuaries and saltmarshes, grazing upon surface plants and green algae on mudflats. For this species, the probability of occurrence was modelled in the Humber due to the limited frequency of presence (44%). Six environmental variables have been selected in the final model as best predictors of its distribution in the estuarine areas, explaining 79% of the data variability. All the variables accounting for habitats area within the sectors are included as predictors of the occurrence of the species in the estuary, with intertidal area being the most important one. In particular, based on the obtained model, a higher probability of occurrence of the species is expected where the intertidal area is maximised in the sector (in particular when >10 km^2), in combination with small marsh area (<0.5 km^2), intermediate supralittoral area (between 0.1 and 0.6 km^2) and either smaller (<7 km^2) or larger (>27 km^2) subtidal area. An increase in Brent Goose occurrence is also predicted in sectors where a higher disturbance index is measured, but, as highlighted before, this is likely to be an artefact of the analysis rather than being a reflection of a real preference of the species for more disturbed areas (see Discussion for a detailed explanation). A relevant effect of temporal trends (measured by year) on the local estuarine population is also present, although, as observed for other species, this variable, together with the disturbance index, are the least important predictors of the species presence among those considered in the analysis.

Table 7. Summary of the habitat distribution models applied to selected wildfowl species in the Humber Estuary. Single predictor models are also reported as a means to rank the importance of the single variables in affecting the species distribution. The variables highlighted in grey are those variables that were excluded from the analysis because of collinearity (their relationship with the other variables included in the analysis is indicated in parenthesis). The variables in bold (and with the asterisk) are those variables that were selected as relevant predictors of the species distribution in the final (best) model.

	Wildfowl					
	SU		**PO**		**BG**	
Variable modelled	density (Sqrt2)		probab. of presence		probab. of presence	
Best model:						
n	254		250		254	
dev. expl.	83.5%		73.6%		78.8%	
no. covariates incl.(*)	6		6		6	
Covariates (single predictor models - % deviance explained and rank of predictor importance based on AIC)						
Habitat	**Int**	**71.6 (2) ***	**Int**	**26.5 (4) ***	**Int**	**58.2 (1) ***
	Eun	**17.5 (5) ***	Eun	32.3 (2)	Eun	51.1 (3)
	Sub	**72.1 (1) ***	**Sub**	**30.8 (1) ***	**Sub**	**55.8 (2) ***
	Mar	57.5 (3)	**Mar**	**27.0 (5) ***	**Mar**	**35.9 (5) ***
	Sup	**48.7 (4) ***	Sup	18.8 (6)	**Sup**	**27.1 (6) ***
Water Quality	Sal (+Int, +Sub)	0.6 (8)	Sal (+Int, +Sub)	22.4 (3)	Sal (+Int, +Sub)	42.4 (4)
Other	**Y**	**2.3 (7) ***	**Y**	**1.2 (8) ***	**Y**	**1.3 (9) ***
	SU.GB (+Y)	0.1 (9)	PO.GB (-Y)	0.1 (9)	BG.GB	0.5 (8)
	Dis	**11.8 (6) ***	**Dis**	**1.1 (7) ***	**Dis**	**6.5 (7) ***
	BAb	-	BAb	-	BAb	-
	BType	-	BType	-	BType	-

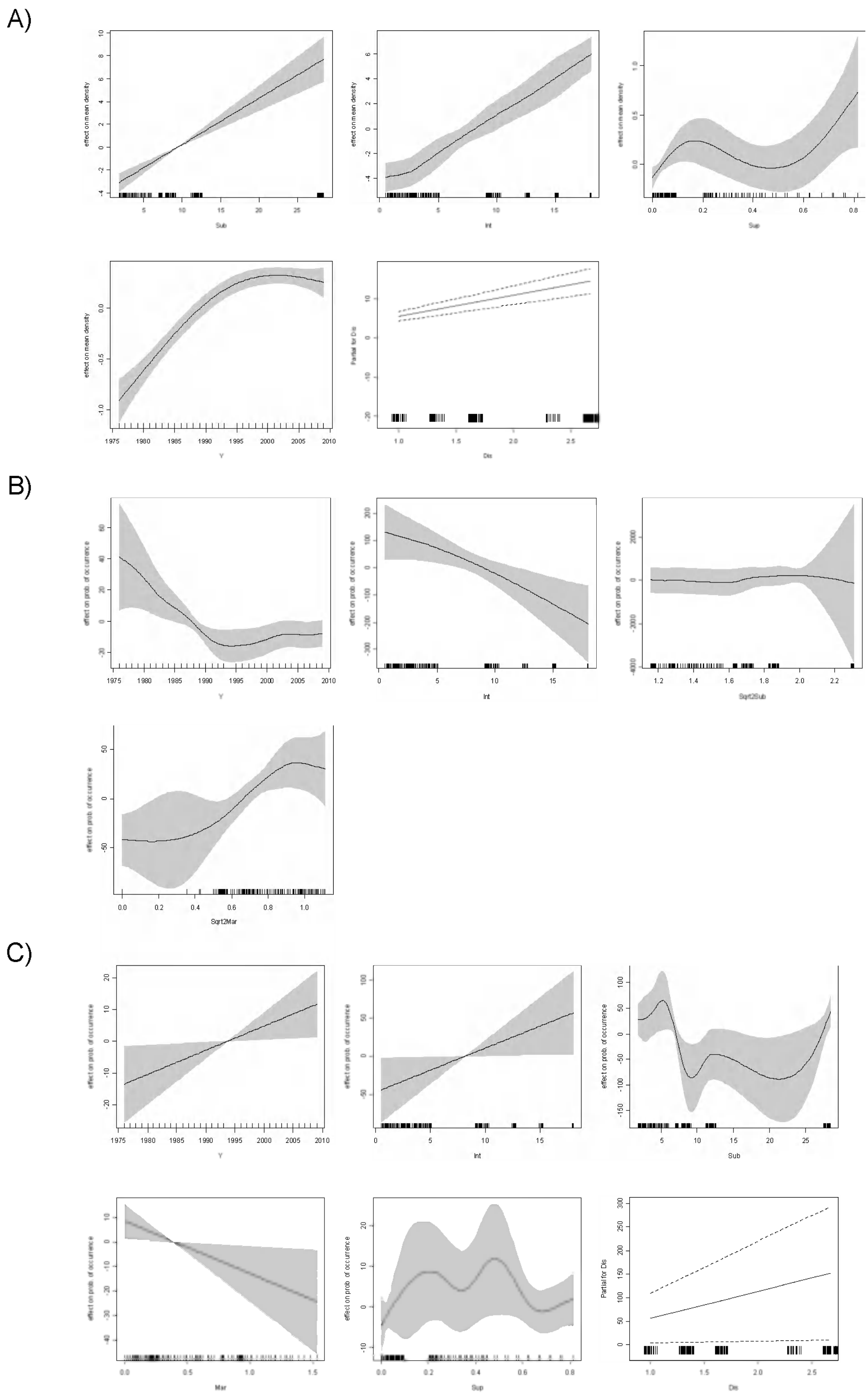


Figure 9. Effect of each explanatory continuous variable on the mean density of Shelduck (A), and on the probability of presence of Pochard (B) and Brent Goose (C), measured as contribution on the linear term of the best selected species models for the Humber Estuary. The fitted values are adjusted to average zero and the dotted bands indicate 95% pointwise confidence intervals. Tick marks along the x-axis show the location of observations along the variable range. The transformations of explanatory variables are abbreviated as follows: Sqrt, square root; Sqrt2, forth-root; Log, logarithmic transformation.

Species distribution models

Multiple regression models applied to Dunlin (in the three estuaries) and to Golden Plover, Redshank, Bar-Tailed Godwit, Shelduck, Pochard and Brent-Goose (in the Humber) allowed the identification of the main environmental determinants of their habitat use within the studied TIDE estuaries. In general, no single factor is responsible for the species distribution, although some factors may show a higher importance than others in affecting it. Overall, although relevant to some species, temporal changes have a secondary effect on the species distribution within the estuaries compared to spatial factors. The area of intertidal and shallow subtidal habitats (but also marshland) is particularly important in affecting Dunlin density distribution. In the Weser and Humber higher density of the species is predicted where wider more extensive habitats occur, whereas in the Elbe an opposite relationship is observed. In the Elbe, salinity is also a relevant factor in predicting the distribution of this species, with higher density and occurrence expected in oligohaline and mesohaline zones. In this estuary, the presence of the species is also affected by nutrients, with lower occurrence where high phosphate concentration and intermediate ammonium concentrations are present. In this estuary, wider and more extensive intertidal habitats are also the most important determinant of higher density of two other wader species feeding on mudflats, Redshank and Bar-tailed Godwit. For both species, this condition is usually also associated with the presence of littoral sands and to either higher (for Redshank) or lower (for Bar-tailed Godwit) density of benthic invertebrates in the intertidal. In turn, Golden Plover density in the Humber is increased by the presence of smaller subtidal areas but also of wider marsh (and also intertidal) areas, combined to sandy substrata in the intertidal. The extension of intertidal and marsh habitats are also generally important in affecting the distribution of the studied wildfowl species in the Humber, although different relationships have been observed. Higher density of Shelduck (a species feeding on mudflats) is predicted in larger sectors where wider subtidal, intertidal and supralittoral habitats occur, in combination with more muddy substrata in the intertidal and relatively higher disturbance. Brent Goose (a species grazing on mudflats) is also more likely to occur where wider intertidal habitats are present in the estuary, in association with smaller marsh areas and intermediate areas of the supralittoral habitat. In turn, Pochard (a freshwater duck) is more likely to occur where wider marsh areas are present together with smaller intertidal habitat.

7 Discussion

The Humber, Weser and Elbe estuaries are important sites for the conservation of bird populations. They are essential components in a network of wetland sites constituting the East Atlantic Flyway stretching from the Arctic Circle, to southern Europe, west Africa and sometimes as far as southern Africa, providing migratory birds with suitable feeding and resting habitats during the great migrations between northern breeding grounds and southern wintering sites (English Nature 2003, McLusky and Elliott 2004, van Roomen et al. 2012). As a result, these estuaries support internationally important populations (i.e. where there is a regular occurrence of at least 1% of their flyway or biogeographical population) of several species, for example Dark-bellied Brent Goose, Shelduck, Golden Plover, Lapwing and Knot in the case of the Humber (English Nature 2003), making this estuary one of the top five most important wetland sites in the UK, and the top ten in Europe, for the population of over-wintering and migratory birds which depend on it.

The importance of these estuarine areas for bird populations is mainly due to the availability of a mosaic of habitats (intertidal mudflats and sandflats, marshes, grasslands) for feeding and/or roosting, leading to the designation of substantial parts of these areas as Special Protection Areas, under the European Birds Directive, Special Conservation Areas, under the Habitats and Species Directive, as well as Ramsar sites because of their international importance as wetlands. However, these estuaries are also places of intense human activities (e.g. port activities, water abstraction, fishery, habitat claim) thus leading to the presence of several conflicts with the conservation of these sites as bird habitats (see TIDE report "Analysis of the TIDE estuarine conflict matrices"). A key element for the management of these conflicts (e.g. through provision of appropriate mitigation and compensation of the impacts arising from human activities) is the knowledge of the distribution of bird species within these sites and, in particular, the understanding of the critical determinants affecting their use of estuarine habitats. With this purpose, the influence of several environmental characteristics (covering aspects such as habitat availability and type, quality of the feeding area, level of anthropogenic disturbance) on the distribution of bird species within the Humber, Weser and Elbe estuaries has been investigated.

The studied estuaries are characterised by broadly similar conditions (e.g. strong tidal influence, transport of large quantities of sediment, presence of large port areas), and a broadly similar distribution of bird species within these areas has been observed, with higher bird abundance generally present in the outer parts of these estuaries, where large intertidal feeding areas are often present (this is particularly true in the Humber and Weser estuaries) and species using also other coastal habitats occur with higher frequency and abundance. Higher waterbird abundances in the polyhaline and mesohaline zones have also been reported in the Scheldt estuary (Ysebaert et al. 2000). However, a certain variability in the species-habitat association has been observed among the studied estuaries (e.g. with the oligohaline zone in the Humber showing a higher relevance, particularly to waders, compared to similar salinity zones in the other estuaries), highlighting the importance of local conditions in affecting habitat use by birds. The habitat tolerances of most wader species, in fact, may be fairly broad, and a certain degree of opportunism is present (Prater 1981, McLusky and Elliott 2004), thus leading to adaptations to local conditions due e.g. to the different distribution and availability of food resources in the estuary. In addition, as shown by the multivariate and univariate models applied in this study, it is usually the combination of several variables that affects the species distribution in an estuarine area rather than a single factor alone (although certain variables may have a higher relevance than others), thus highlighting the complexity of the species-habitat relationship.

In general, an overall positive relationship has been observed between bird species densities and the habitat area, in particular the intertidal area, suggesting that larger mudflats might have a greater carrying capacity per unit of area. The size of any productive area in an estuary is generally positively associated to its carrying capacity in supporting wading birds, in terms of maximum number of individuals (or biomass) that can be sustained (Meire 1993, Elliott et al. 1998). However, when the density of individuals in the estuarine area is considered (i.e., the number of individuals per unit area), a lower wader density has been reported in larger estuarine areas, this negative relationship possibly ascribed to the inclusion of many unsuitable feeding areas (e.g. deeper subtidal areas) in these cases (Prater 1981). Although this explanation may be valid at the larger inter-estuarine scale, a different one might support the opposite pattern at the smaller intra-estuarine scale as observed in the present study, particularly when considering the area of suitable feeding habitats such as intertidal mudflats. Given that food is considered to be the major determinant of shorebird distribution (Prater 1981, McLusky and Elliott 2004), the relationship with the intertidal habitat area may be linked to the availability of food resources in it. In particular, wider, more extensive habitat areas are likely to have a higher diversity of microhabitats (hence a possible higher diversity in the food resources) and this might lead to a higher probability for bird species of accessing different food resources, possibly resulting also in a reduction in the possible intra- and inter-specific competition, thus allowing a higher concentration of individuals in larger habitat areas. However, it is acknowledged that habitat size alone will not necessarily determine wader distribution, with other site specific factors also influencing this.

This relationship is likely to be particularly relevant to generalist mudflat feeders, as observed in the case of Dunlin, Redshank and Shelduck. However, these species showed a different preference for the type of intertidal habitat, with Shelduck density being associated mostly to substrata dominated by littoral mud, whereas Redshank occurring in greater densities where a littoral sand component is also present in the substratum. Dunlin and Redshank feed throughout the estuary on marine polychaete worms, crustaceans and molluscs, such as the Baltic Tellin *Macoma balthica*, tending to be near the water's edge (McLusky and Elliott 2004). A positive effect of intertidal habitat area on these species density has been observed in the Humber and Weser (for Dunlin) (particularly with intertidal area >3 km^2), with higher concentrations of the species in the outer estuarine areas, where larger counting units (hence larger habitat areas) are present. In addition the presence of wider suitable habitats is likely to provide unrestricted views (compared, for example, to narrower mudflats in the upper Humber estuary) for the early detection of predators. It is of note that although Redshank can be considered a generalist feeder, it also shows some preference for *Corophium* in many estuaries (including the Humber), this invertebrate occurring mainly on the upper and mid shore flats, where mostly Redshank feed (Prater 1981). Higher density of Redshank is also related in the Humber to muddy sand / sandy mud substrata with general high total benthic abundance.

It is of note that an opposite (negative) relationship of Dunlin density with the habitat area has been observed in the Elbe estuary, this result likely being an artefact of the analysis being influenced by the data obtained from the polyhaline zone of this estuary (e7NDS), regarding outer sands and remote islands in the Wadden Sea. In fact, in this zone there is the combination of very small counting units (max. 0.2 km^2, hence small area of the habitats therein) compared to those in the other zones of the estuary (with a minimum area between 2 and 8 km^2) and extremely high counts, hence very high density, of Dunlin, particularly around the island of Scharhöm compared to the other areas, thus driving the negative relationship of the species density with habitat areas for the whole estuary. It is of note also that when the effect of habitat area is excluded, the relationship with the salinity gradient is still relevant to Dunlin density in the Elbe estuary (with salinity zone included in the final model) with higher Dunlin density expected in oligohaline and mesohaline zones. This suggests that factors other than salinity and habitat availability within the single units are the likely determinants of the very high density values observed for Dunlin in the polyhaline zone of the Elbe, and it might be expected that there will be a positive relationship between the availability of foraging area and roost size in many instances, flocks tending to minimize flight distance between preferred foraging and roosting areas where possible.

In turn, the higher diversity of microhabitat (and the associated food resources) is likely not to have a positive effect on specialist feeders, the relationship between the habitat area and the bird density being dependent on the availability of specific prey/microhabitat. An example is Bar-tailed Godwit in the Humber, showing higher density in sectors with smaller intertidal area (<5 km^2). Although, like Dunlin and Redshank, this species feeds on benthic prey available on estuarine mudflats, it shows a higher degree of specialism, feeding on larger prey (e.g. large polychaetes and bivalves; Scheiffarth 2001). Due to their long bill, Bar-tailed Godwit can access to larger prey that usually bury themselves more deeply than do smaller individuals (as in the case of larger *Macoma balthica*) (Prater 1981). Different studies have highlighted the presence of larger *Macoma* individuals in the lower intertidal compared to the upper intertidal zone (Bouma et al. 2001, Hiddink et al. 2002), the former habitat likely being more readily accessible from the shore roosting sites where the mudflat is smaller (and possibly narrower) compared to wider mudflats. The negative relationship observed between Bar-tailed Godwit density and the total benthic abundance in the intertidal habitat is also likely to support the preference of the species for feeding habitats where benthic communities are dominated by larger prey (usually in lower densities compared to smaller invertebrates).

Higher density of Golden Plover is also predicted in the Humber where larger intertidal marsh habitats (>0.6 km^2) occur, in combination with smaller subtidal areas (<10 km^2). The association of higher densities of the species with a particular intertidal habitat type (littoral sand) and benthic community was also observed, but this cannot be explained by the feeding preferences of the species. Golden Plover, in fact, use estuarine habitat mainly for roosting, with feeding primarily on inland habitats (e.g. habitats with short vegetation, like bare peats, wet vegetation, pasture fields with short swards).

When investigating the occurrence of two wildfowl species, namely Pochard and Brent Goose in the Humber Estuary, different relationships with habitat areas are observed, as a result of the different feeding habitats of these two species. Pochard is a freshwater duck, with omnivorous feeding habits, the analysis identifying its most suitable habitat within the estuary to be where there is a higher ratio between marsh and intertidal area (i.e. marsh area >0.84 km^2 and intertidal area <10 km^2), the former habitat likely to be preferred by the species due to the diversity and abundance of feeding resources (including seeds, roots, rhizomes and the vegetative parts of grasses, sedges and aquatic plants, as well as aquatic insects and larvae, molluscs, crustaceans, worms, amphibians and small fish). In turn, the Brent Goose feeds almost exclusively on the *Zostera/Enteromorpha* beds, this food resource being likely more available where larger intertidal areas (>10 km^2) occur.

The distribution of anthropogenic activities along the estuarine banks proved to have a relevant effect on the distribution of bird species, generally resulting in a lower density of birds in areas where the estuarine bank has been modified through the creation of artificial hard substrata (e.g. docks and seawalls in sectors ND and NE in the Humber) or where industrial sites and other infrastructures are concentrated (like in the Elbe estuary, leading to differences between the north and south bank within similar salinity zones of the estuary). A specific index of anthropogenic disturbance has been included in the analysis for the Humber estuary. However, although a negative effect of anthropogenic disturbance would be expected on bird densities, a positive relationship between the bird density and the index used was often observed (e.g. for Dunlin, Redshank and Shelduck). Although Dunlin, Redshank and Shelduck may be fairly tolerant to disturbance from recreation (English Nature 2003), it is likely that the above result is an artefact of the analysis deriving from the inadequacy of the measured index as a proxy for disturbance given the spatial scale considered by the analysis.

In fact, although the index accounts for the frequency of potentially disturbing activities in the estuarine areas (including shore-based, water-based and airborne activities), this might not correspond to an actual disturbance to bird populations roosting within a sector. Indeed, it might be expected that roost sites are actively identified by birds in areas where disturbance is at a low level. Therefore, there could be a mismatch between the location of the disturbing activity and the location of roosting/compression sites within a sector, this mismatch not being captured by the analysis, as the sector as a whole was used as the minimum spatial unit. In addition, there might be other correlated factors, i.e. showing a similar distribution among sectors as disturbance, but not measured here, that might have contributed to this result. All these elements may have led to artefacts in the analysis resulting in the apparent positive effect of disturbance level on Dunlin, Redshank and Shelduck density.

The data availability for the water quality in the studied estuaries limits the interpretation of the obtained results to the Elbe estuary and to the freshwater and oligohaline zone of the Weser. Water quality characteristics (including indicators of the salinity gradient, nutrient levels, organic enrichment) resulted more important in affecting bird assemblages as a whole in the Elbe compared to the Weser, although this comparison must be taken with caution, due to the different datasets analysed and also the differences in their spatial coverage of the estuarine area. The effect of the salinity gradient was predominant in the Elbe (where data covered the whole salinity gradient) when considering the density of bird assemblages as a whole, as well as the occurrence of Dunlin. In this site, as in the rest of the Wadden Sea, other species show a strong association with salinity, as with the Brent

Goose, usually concentrating on the islands and the outer coast. The principal effect of the changes in the salinity regime is usually related to changes in communities of benthic invertebrates (Cole et al. 1999). However, the results for the Elbe might be influenced by an artefact of the analysis, due to the small size of counting units in the outer (polyhaline) estuary where high bird counts were recorded, leading to very high bird densities as described before. PO_4 also proved to be a relevant predictor of wader and wildfowl overall distribution in the Elbe, with higher densities of most of wader species (including Dunlin and Redshank) and of several wildfowl species (including Shelduck and Brent Goose) recorded in the outer estuary where PO_4 levels are lower. The probability of occurrence of Dunlin in the estuary was also higher at lower PO_4 concentration (<0.002 mmol/l). Nutrient and organic enrichment can lead to an increase in benthic populations such as opportunistic marine worms, whereas a decline in the input of nutrients may correlate with lower phytoplankton biomass, resulting in a decline of the stocks of filter feeding bivalves and a consequent decline in shellfish eaters, as observed in the western Dutch Wadden Sea (van Roomen et al. 2012). However, as regards the results obtained for the Elbe estuary, there might be a relevant effect of the very high bird densities resulting in the polyhaline zone of the Elbe estuary, as explained before, where the lowest PO_4 levels are lower, thus suggesting the influence of other factors not included in the analysis.

Finally, it should be noted that the interpretation of the results described above in terms of bird habitat use might be limited by the fact that high-tide counts were used to derive the analysed species densities in the estuary. These counts, are carried out when most of the preferred intertidal feeding habitats are temporarily unavailable to the species, with most either foraging on the upper shore in sub-optimal areas or roosting in the area while waiting for the tide to retreat. A certain site fidelity of the species was assumed, hence considering the obtained density data as representative of the bird use of the area, as most species tend to simply move up and/or along shore during tidal compression (and depending on tide), with roosts usually located as close to preferred foraging areas as possible. However, it must be acknowledged that the use of high-tide counts might lead to an underestimation of the birds using an area at low tide, particularly for those species (e.g. Redshank, Curlew and Oystercatcher) which can move inland in search of food when their estuarine food resources are not accessible (Prater 1981). Using low-tide counts is likely to allow better relationships of the actual density with the habitat availability and characteristics in the counting unit areas, although this type of data might present other limitations compared to the high-tide counts. For example, in the Humber, low-tide counts are carried out at a lower frequency (e.g. c. every 5 years) hence limiting the availability of data for the statistical analysis.

Table 8. Summary of the resulting relevant descriptors of habitat suitability for the different species in the studied estuaries.

		Species density							Occurrence			
		Dunlin	Dunlin	Dunlin	Redshank	Golden Plover	Bar-tailed Godwit	Shelduck	Dunlin	Dunlin	Pochard	Brent Goose
		Humber	Weser	Elbe	Humber	Humber	Humber	Humber	Elbe	Elbe	Humber	Humber
Habitat area	Intertidal	+ (3-9 km2, or >16 km2)	+ (>3 km2)	- (<0.8 km2)	+ (>9 km2)	(+)	- (<5 km2)	+ (>7.5 km2)	(-)		- (<10 km2)	+ (>10 km2)
	Marsh/Foreshore	(+)	+ (>2.5 km2)	(-)	(+)	+ (>0.6 km2)			- (<0.9 km2)		+ (>0.9 km2)	- (<0.5 km2)
	Subtidal	+ (>20 km2)	+ (>0.9 km2, shallow)	- (<0.7 km2, shallow)	(-/+)	- (<10 km2)	(-/+)	+ (>10 km2)	+/-		+/-	+/- (<7 km2, or >27 km2)
	Supralittoral	(-)			+/- (0.1-0.3 km2)	(+)	+/- (0.1-0.3 km2)	+ (>0.6 km2)				+/- (0.1-0.6 km2)
Habitat quality	Substratum type (Eunis)				littoral sand component	littoral sand	littoral sand dominant	littoral mud dominant				
	Total benthic abundance				+ (>1.45 ind/0.0079 m2)	- (<1.45 ind/0.0079 m2)	- (<1.45 ind/0.0079 m2)					
	Benthic community type					types g-h						
Anthropogenic influence	Activity level (potential disturbance)	+			+			+			-	+
	Jurisdiction								SH > NDS	SH > NDS		
Water Quality	Salinity gradient	(+)		+ (except for polyhaline)	(+)	(+)	(-/+)	(+)	+/- oligo-mesohaline	+/- oligo-mesohaline	(+/-)	(+/-)
	Eutrophication (PO4)									- <0.002 mmol/l		
	Eutrophication (autumn NH4)									+/- <0.003 mmol/l or >0.006 mmol/l		
	Organic enrichment (BOD)									(+)		
	Water oxygenation									(+/-)		
Temporal aspects	Year	-	-	+	+	+	+	+	+/-	-	-	+
	Wider population	(-)	+	+	-		+	(+)			(+)	

Symbols + and – indicate a general positive or negative relationship with the relevant environmental descriptor (thresholds and ranges identifying optimal conditions for the species occurrence/density are provided in brackets). +/- indicates a fluctuating relationship (when no clear increase or decrease pattern can be identified; the shape of these relationships being shown in Chapter 6). When symbols are within brackets, these indicate predictors that have not been included in the models because of their correlation with other variables included, but, due to their collinearity with the relevant descriptors, their influence cannot be excluded.

8. CONCLUSIONS

8.1 Analysis Conclusions

In order to effectively manage estuarine environments under the complex system of conservation priorities and provision of goods and services (and the consequent possible conflicts) which are usually in place on these areas, managers should be clearly informed about the relationships occurring between the species and the environment (natural and anthropogenic), in order to properly address possible changes in the latter.

This study investigated these relationships in three TIDE estuaries (Weser, Elbe and Humber), by focusing on bird use of estuarine habitats. The results highlighted that it is usually a combination of different factors that determines bird use, with the spatial factors (i.e. those affecting the distribution among different areas within an estuary) showing an overall higher influence compared to temporal ones (i.e. those factors accounting for inter-annual changes in bird abundances).

In general, the outer zones of estuaries are likely to support more diverse and dense bird assemblages, as a result of the higher availability of suitable estuarine habitats (e.g. in the Humber wider, more extensive, intertidal mudflats and marsh areas are available in the polyhaline sectors) as well as the proximity of other suitable habitats along the adjacent coastal area. However, locally, inner (oligohaline) areas may also be relevant in supporting abundant bird populations of some species, for instance Lapwing, Golden Plover Teal, Wigeon and Mallard in the Humber.

The analysis described in this report identified the extent of habitats (in particular intertidal mudflats) to be highly important in affecting bird distribution within estuarine areas. This strong association between bird distribution and habitat areas is likely mediated by the food availability (in quantitative and qualitative terms), a factor that is usually considered as the major determinant of bird distribution within estuaries. Although a higher carrying capacity is usually associated with wider, more extensive estuarine habitats, the positive relationship with density of several bird species observed here suggests that the possible higher diversity of resources associated with more extensive habitats allows higher concentrations of species that are able to take advantage of a wider range of food prey, as in the case of Dunlin and Redshank. In turn, specialist feeders (such as Bar-tailed Godwit) are more likely to depend on the distribution of specific prey, a factor that might be more relevant at a smaller spatial scale (i.e., within a mudflat) hence resulting in contrasting relationship with the total intertidal habitat area. Water quality characteristics (e.g. nutrients, water oxygenation) also showed a relative importance in affecting species distribution, although this effect was only particularly evident in the Elbe.

The application of habitat distribution models has allowed the identification of a series of habitat requirements for several waterbird species, resulting in the potential for the derivation of guidelines on the provision of important environmental characteristics of a habitat in terms of combinations allowing the maximisation of occurrence and abundance of a species. A summary of these characteristics is reported for each of the species investigated in Table 8.

Except for the Elbe, where the results are likely to be driven by the very high density of species observed in the outer estuary, where small counting units were present around some islands in the Wadden Sea, Dunlin showed a general preference for wider, more extensive intertidal areas, where larger mudflats, but also marshes and shallow subtidal areas occur.

These conditions are usually associated with the outer parts of the estuary and the analysis identified the most suitable habitats for Redshank and Shelduck in the Humber also to be associated with the wider, more extensive intertidal areas (>7 km^2), although higher densities of additional species are expected where littoral sands are present. Intertidal areas dominated by littoral sand adjacent to intermediate supralittoral areas and with higher total densities of benthic invertebrates are likely to support higher densities of Redshank. Intertidal areas dominated by littoral mud and adjacent to extensive shallow subtidal zones and relatively wide supralittoral areas (>0.6 km^2) were identified as being preferred by Shelduck.

Golden Plover density distribution in the Humber was mostly associated with sectors where the area is dominated by wider marsh and intertidal habitats with subtidal area being smaller. The presence of sandy substrata in the littoral zone was also characteristic, but with lower intertidal benthic densities present. In contrast, higher densities of Bar-tailed Godwit can be expected on the Humber in areas featuring smaller intertidal mudflats (<5 km^2), where lower total densities of benthic invertebrates occur, as well as intermediate supralittoral areas, these characteristics being possibly related to the higher selectivity of this species towards specific prey, as explained above.

8.2 Management Recommendations

Based on the analysis, and other broader information, the following management recommendations are therefore made:

- The positive relationship between intertidal habitat area and waterbird density is a potentially important conclusion for estuarine management, as it suggests that the fragmentation of intertidal habitat from a range of anthropogenic activities, as well as the effective reduction in the width of mudflat from coastal squeeze may result in a reduction of waterbird usage density.

- Based on the above, compensatory measures such as managed realignment resulting from intertidal development offsetting may need to consider the delivery of sufficient (additional) habitat area to accommodate fragmentation effects of the land-claim in addition to direct losses e.g. an increase in the offset area compensation ratio.

- Habitat recreation in estuaries is not always successful, and carrying capacity can be lower than more natural areas. As such, the management priority should be to minimise habitat loss from development (ideally avoid loss), and in particular, avoid fragmentation with an ‘over compensation’ principle applied in offsetting areas.

- Although not identified as a key determinant from this analysis (probably due to the nature of the data used), disturbance has been identified as a significant influence on habitat utilisation by waterfowl species, and as such, management needs to ensure disturbance stimuli are restricted and where possible provide refugia where disturbance is at a low/background level.

- In particular the provision of undisturbed high tide roost areas, both on the upper shore of the estuary and the immediate hinterland is considered very important, these should be located in close proximity to preferred foraging areas and where possible integrated under the Natura 2000 designation, and, in the case of agricultural land, managed in conjunction with the land owner to maximise the conservation potential (e.g. crop types, fallow periods, cropping timing etc)

8.3 Recommendations for Future Studies

- Due to the high variability in bird counts in the freshwater estuarine zone, a higher degree of uncertainty is likely to be associated with the results, hence higher caution should be used when interpreting the results for this zone.
- The analysis could be improved by taking into account not only the habitat availability in the immediate vicinity of the high water compression and roosting sites, but also the availability within a wider area, the size of this being determined based on the knowledge of the movements of the species between high water and low water sites.
- The species-habitat distribution modelling should be extended to all the key species occurring in an estuary in order to identify their environmental needs in the local area. This will allow better prediction of the effects on estuarine use should the environmental conditions change (e.g. reduction in habitat availability, changes in water quality). It is of note that the validity of the model's results is limited by the dataset used to create the model itself. Therefore a model developed based on data on a given estuary (or part of it, e.g. mesohaline and polyhaline zone only) could provide useful guidance for the management of the species in that estuary (or part of it) alone and should not be used as guidelines for other areas.
- When using the results of species-habitat distribution models for management purposes (e.g. creation of suitable habitat for a species), attention should be given to the combinations of environmental conditions that are defined by the model as important in determining bird habitat use rather than in managing a single environmental factor alone. However, it is of note that environmental factors can be ranked based on their importance in affecting the species habitat use, hence priorities can be identified in the habitat management.
- More comprehensive low water usage data sets would be of particular value in further defining key relationships between environmental variables and habitat utilisation.

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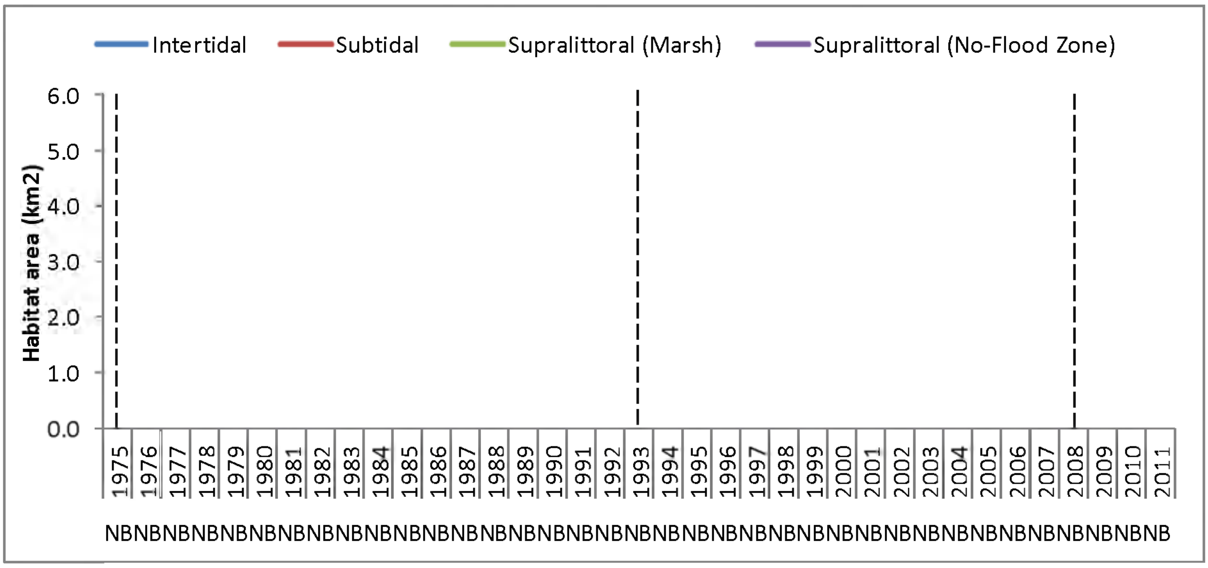
Appendix 1

Environmental data used for the Humber Estuary - additional details

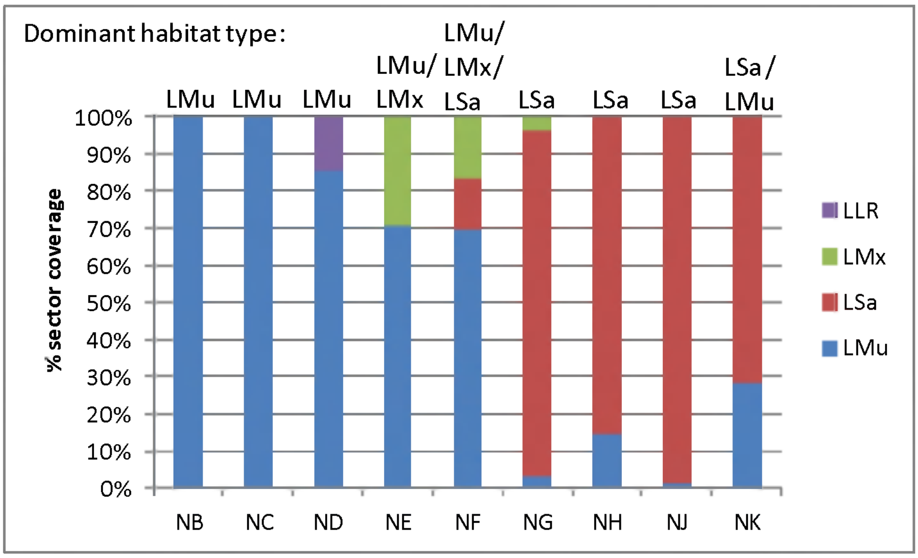
a) Calculation of habitat areas (km^2) in counting units over time based on historical habitat maps.

Habitat areas were measured in each estuary in selected years based on available historical habitat maps. Habitat maps for the years 1975, 1993 and 2008 were obtained for the Humber through the digitisation of Admiralty Charts, using bathymetry levels to distinguish subtidal, intertidal and supratidal habitats (in this case habitat maps did not cover the two upper sectors, NA1 and NA2). Maps for 1950 and 1995 were used for the Elbe and 1950 and 2000 maps were obtained for the Weser. A monotonous linear decrease/increase of the area of each habitat between these years was considered and the habitat area was calculated accordingly for the missing years, extending the calculation to a maximum of 3 years after the year of the last available habitat map.
An example of this calculation for sector NB in the Humber Estuary is reported below. Dashed black lines indicate the habitat data derived with direct measure from historical habitat maps (in this case, available for the years 1975, 1993 and 2008).



b) Dominant intertidal habitat type

The dominant intertidal habitat type present within WeBS sectors was identified based on the EUNIS 3 habitat map given in Hemingway et al. (2008) and on the % coverage of these habitats in each sector. EUNIS 3 habitats included Littoral mud (LMu), Littoral sand (LSa), Littoral mixed sediments (LMx), Low energy infralittoral rock (LLR) and dominant habitats were identified with a coverage >15% in each sector (see figure below). Spatial variability was only considered (same value allocated to each sector in different years) and no data were available for the two upper sectors in the estuary (NA1 and NA2).



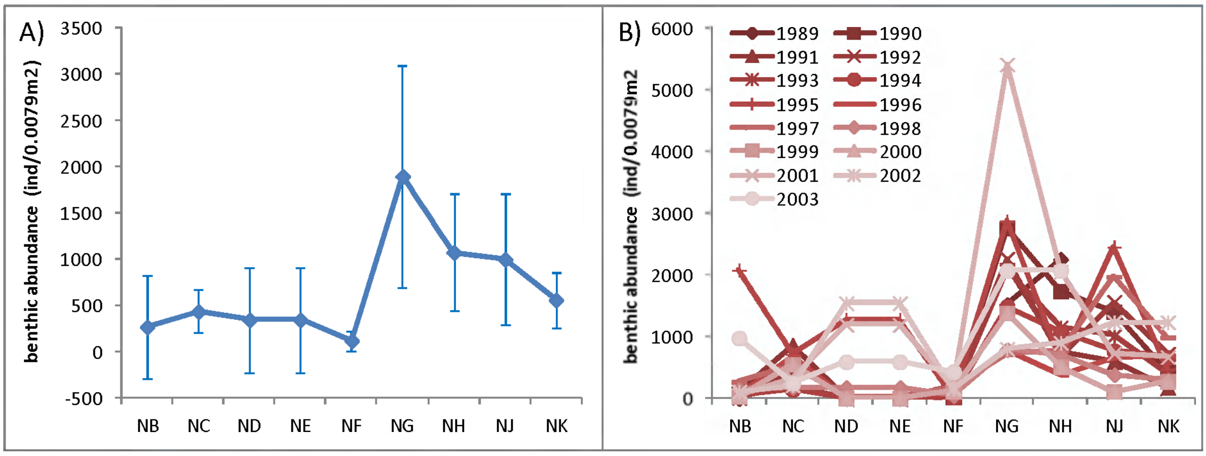
c) Hard substrata in sectors of the Humber Estuary

The occurrence of hard substrata (either pebbles or man-made vertical substratum) in the intertidal zone within each sector in the Humber Estuary was measured as % of sector length covered by such substrata. Measurements were made based on the visual inspection of aerial maps obtained from Bing, Google Map and Google Earth. Spatial variability was only considered (same value allocated to each sector in different years). Hard substrata were recognized only in sectors ND (70% hard-pebbly), NE (5% hard-pebbly, 60% hard-man made) and NF (9% hard-pebbly, 50% hard-man made).

d) Intertidal benthic invertebrate communities (total abundance and type)

The average abundance of benthic invertebrates in the intertidal habitat within each sector in the Humber Estuary was calculated based on the data reported in Allen (2006), as an indicator of the amount of potential food resources available in the intertidal area. Total benthic abundance (indiv/0.0079 m^2) was given in different mid shore stations distributed across the sectors annually, from 1989 to 2003 (=13 to 15 observations per sector, as some data are missing for certain sectors in certain years). Both spatial and temporal variability was taken into account. No data were available for sectors NA1 and NA2.

The figure below reports the resulting abundance (ind./0.0079m^2) of intertidal benthic invertebrates in the WeBS sectors of the Humber Estuary calculated as average per sector (± SD) (A), or provided as annual values between 1989 and 2003 in each sector (B).



The intertidal benthic invertebrate community type within each sector in different years was also identified based on the cluster analysis given in Allen (2006), as an indicator of the variability of the type of food resources available in the intertidal area. The analysis was carried out on average density data at different stations located at mid and low shore in the northern bank of the estuary, and only stations at mid shore (giving the widest spatial and temporal coverage) were taken into account. Eight main community types (a to h) were distinguished (with a maximum similarity <40%) roughly corresponding to a gradient from inner to outer estuary and to an increase in species richness and abundance. Both spatial and temporal variability was taken into account and no data were available for sectors NA1 and NA2. The resulting characteristics species within intertidal north bank site groups derived from the cluster analysis in Allen (2006) are reported below. The main community types (considering only mid shore samples) are indicated by red boxes.

1	Mean A	% occ
Streblospio shrubsolii	1.00	100.00
Heterochaeta costata	0.50	50.00
Lumbricillus	0.50	50.00
Mean No. of Species	2.00	
Mean Abundance	2.00	

Type f

2.1	Mean A	% occ	2.2	Mean A	% occ
Tubificoides benedii	48.43	100.00	Corophium volutator	141.23	84.62
Macoma balthica	25.43	100.00	Tubificoides benedii	33.85	92.31
Streblospio shrubsolii	9.43	64.29	Macoma balthica	22.15	84.62
Corophium volutator	5.43	57.14	Hediste diversicolor	12.08	100.00
Nephtys hombergii	3.29	71.43	Eteone	1.23	46.15
Pygospio elegans	2.57	57.14	Streblospio shrubsolii	1.00	38.46
Nephtys	2.14	28.57	Heterochaeta costata	1.00	15.38
Hydrobia ulvae	2.07	35.71	Pygospio elegans	0.77	30.77
Eteone	1.36	50.00	Paranais litoralis	0.54	30.77
Hediste diversicolor	1.21	57.14	OLIGOCHAETA	0.54	7.69
Mean No. of Species	7.57		Mean No. of Species	5.46	
Mean Abundance	103.86		Mean Abundance	[illegible]	

Type h

3.1	Mean A	% occ	3.2	Mean A	% occ
Tubificoides benedii	758.04	96.43	Macoma balthica	160.92	100.00
Macoma balthica	280.18	100.00	NEMATODA	124.31	38.46
Pygospio elegans	131.00	100.00	Pygospio elegans	114.54	96.15
Hydrobia ulvae	78.71	96.43	Streblospio shrubsolii	93.92	76.92
Eteone	31.32	100.00	Tubificoides benedii	74.81	69.23
Hediste diversicolor	29.96	100.00	Cerastoderma edule	51.19	92.31
Manayunkia aestuarina	28.04	42.86	Hydrobia ulvae	36.58	88.46
Enchytraeidae	18.57	25.00	Nephtys	30.50	57.69
Nephtys	11.71	35.71	Nephtys hombergii	23.65	96.15
PELECYPODA	10.29	10.71	Retusa obtusa	16.23	84.62
Mean No. of Species	12.11		Mean No. of Species	12.39	
Mean Abundance	1424.29		Mean Abundance	777.15	

Type g

4	Mean A	% occ
Enchytraeidae	527.86	95.45
NEMATODA	365.64	77.27
Tubificoides benedii	318.77	100.00
Macoma balthica	78.14	100.00
Hediste diversicolor	65.68	100.00
Manayunkia aestuarina	23.86	77.27
Abra tenuis	13.00	36.36
Eteone	4.77	63.64
Hydrobia ulvae	4.45	54.55
Pygospio elegans	2.23	40.91
Mean No. of Species	10.41	
Mean Abundance	1409.73	

5	Mean A	% occ	6	Mean A	% occ
Hydrobia ulvae	181.36	100.00	Corophium volutator	1.71	100.00
Streptosyllis websteri	33.55	54.55	Hediste diversicolor	0.71	28.57
Psammodrilus balanoglossoides	18.82	54.55	OLIGOCHAETA	0.71	28.57
POLYCHAETA	16.64	36.36	Streblospio shrubsolii	0.71	28.57
Opheliidae	12.73	36.36	Macoma balthica	0.43	14.29
Paraonis fulgens	12.18	63.64	POLYCHAETA	0.14	14.29
Syllidae	9.36	27.27	Tubificoides benedii	0.14	14.29
NEMERTEA	6.55	45.45			
Enchytraeidae	7.73	45.45			
Microphthalmus	4.91	18.18			
Mean No. of Species	15.36		Mean No. of Species	2.29	
Mean Abundance	345.27		Mean Abundance	4.57	

Type d

7	Mean A	% occ
Hediste diversicolor	2.63	100.00
Heterochaeta costata	0.63	50.00
Corophium volutator	0.25	25.00
Paranais litoralis	0.25	25.00
POLYCHAETA	0.25	25.00
Tubificoides benedii	0.25	25.00
Enchytraeidae	0.13	12.50
Pygospio elegans	0.13	12.50
Mean No. of Species	2.75	
Mean Abundance	4.50	

Type b

8	Mean A	% occ
OLIGOCHAETA	560.50	100.00
Paranais litoralis	517.75	75.00
Corophium volutator	93.50	75.00
Hediste diversicolor	19.50	50.00
Lembos longipes	0.25	25.00
Mean No. of Species	3.25	
Mean Abundance	[illegible]	

Type c

9	Mean A	% occ
Heterochaeta costata	4.62	100.00
Streblospio shrubsolii	1.23	23.08
Corophium volutator	0.46	30.77
NEMATODA	0.46	15.38
Pygospio elegans	0.15	15.38
Polydora	0.08	7.69
Scolelepis squamata	0.08	7.69
Tubificoides benedii	0.08	7.69
Mean No. of Species	2.08	
Mean Abundance	7.15	

Type e

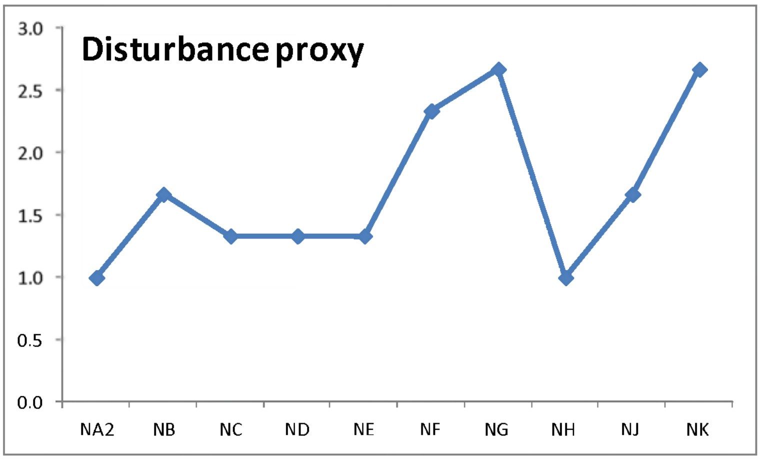
10	Mean A	% occ
Heterochaeta costata	210.42	96.49
Paranais litoralis	59.25	45.61
Enchytraeidae	58.63	89.47
Corophium volutator	54.81	80.70
Hediste diversicolor	41.09	87.72
NEMATODA	10.49	50.88
Streblospio shrubsolii	5.68	38.60
COLLEMBOLA	3.49	10.53
ACARIFORMES	2.39	19.30
Manayunkia aestuarina	2.07	28.07
Mean No. of Species	6.72	
Mean Abundance	452.23	

Type a

11.1	Mean A	% occ	11.2	Mean A	% occ	11.3	Mean A	% occ
Paranais litoralis	7.46	100.00	Heterochaeta costata	134.82	100.00	Paranais litoralis	226.15	100.00
Heterochaeta costata	2.08	61.54	Paranais litoralis	1.36	63.64	Heterochaeta costata	182.45	95.00
Corophium volutator	1.00	53.85	Hediste diversicolor	1.27	63.64	Enchytraeidae	3.80	40.00
Tubificoides benedii	0.38	15.38	Corophium volutator	0.82	45.45	Corophium volutator	3.30	80.00
Enchytraeidae	0.31	23.08	Tipulidae	0.64	27.27	Lumbricillus	0.75	15.00
Hediste diversicolor	0.23	23.08	Macoma balthica	0.09	9.09	Streblospio shrubsolii	0.35	15.00
Lumbricillus	0.23	7.69	NEMATODA	0.09	9.09	Amphichaeta sannio	0.35	10.00
Amphichaeta sannio	0.15	7.69	Streblospio shrubsolii	0.09	9.09	Hediste diversicolor	0.30	20.00
Macoma balthica	0.09	7.69				Tipulidae	0.25	15.00
Streblospio shrubsolii	0.08	7.69				Tubificidae	0.25	15.00
Mean No. of Species	3.08		Mean No. of Species	3.27		Mean No. of Species	4.80	
Mean Abundance	12.00		Mean Abundance	139.18		Mean Abundance	418.65	

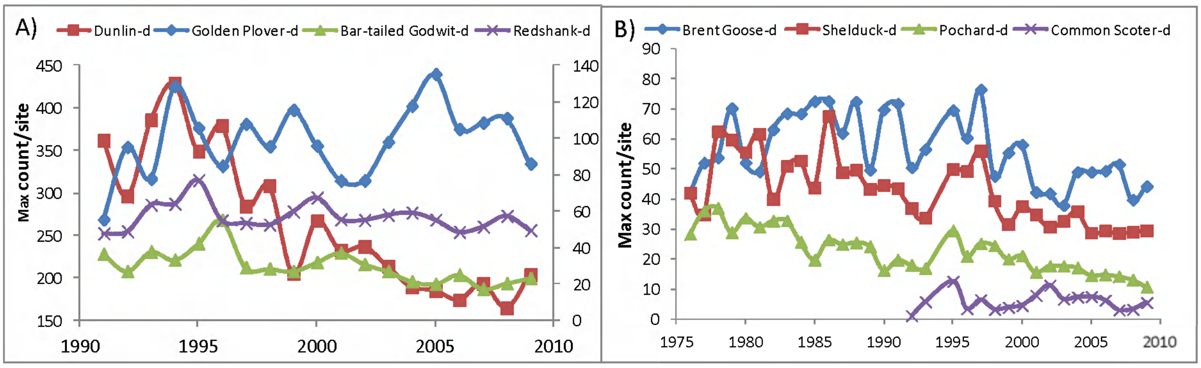
e) Disturbance

An index of the frequency of potentially disturbing activities in the sectors was calculated. Scores were given in Cruickshanks et al. (2010) to shore-based, water-based and airborne activities (overall) in each sector, ranging from 1 (Rare) to 5 (Very frequent), with also 0 values possibly allocated (Unknown occurrence/does not occur). The index of (potential) disturbance was calculated by averaging the score values in each sector. Spatial variability was only considered (same value allocated to each sector in different years). No data were available for sector NA1. The resulting average values of the Disturbance index in the WeBS sectors are shown in the figure below.



f) Wider bird population trends

An example of the data used to characterise the wider bird population trends for the Humber estuary is reported below. For this estuary, data on annual total maximum counts for Great Britain (between 1975 and 2011) were collected for selected species from WeBS books (Waterbirds in the UK Series – The Wetland Bird Survey. Published by the British Trust for Ornithology (BTO), the Royal Society for the Protection of Birds (RSPB) and the Joint Nature Conservation Committee (JNCC) in association with the Wildfowl & Wetlands Trust (WWT)). Count data were standardised by number of sites counted in the months when the maxima were recorded. The figure below reports an example of the resulting GB population trend (max annual count/site) of selected wader species (A) and wildfowl species (B). The Left vertical axis in (A) shows Dunlin data, whereas the other species are shown in the right vertical axis.

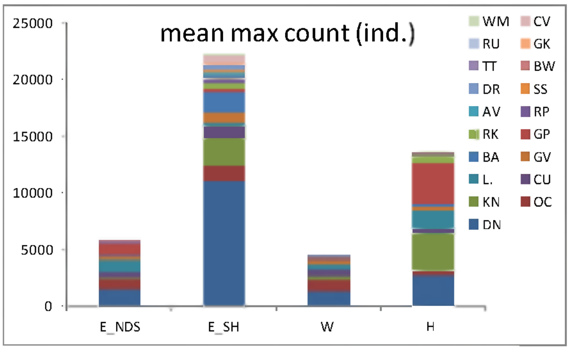


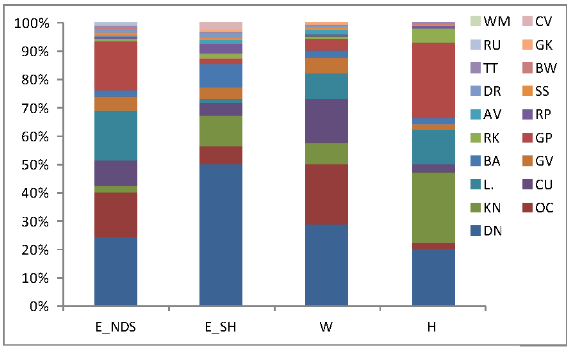
Appendix 2

Annual maximum count of wildfowl and waders in the Elbe, Weser and Humber

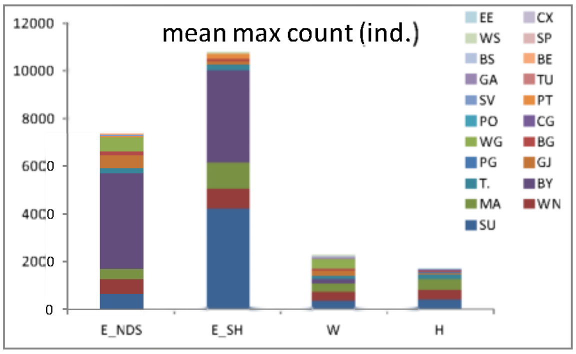
Mean values (left graph) and percentage contribution of the different species (right graph) are reported for each estuary (E_NDS = Elbe, southern bank; E_SH = Elbe, northern bank; W = Weser; H = Humber). Species codes are as in Table 2 (in Chapter 4).

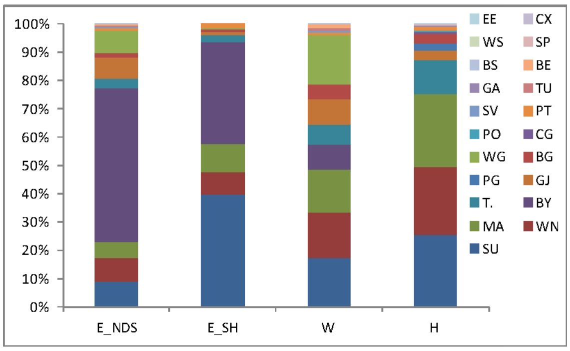
WADERS





WILDFOWL





Appendix 3

Details on the analysis and results on bird assemblages distribution and its relationship with environmental variables in TIDE estuaries

Methods

Multivariate analysis was applied to bird data in order to explore the main patterns of spatial variation in wader and wildfowl community. In the Humber, bird species density was averaged over 5-year periods per sector (period 1=1975-1979, 2=1980-1984, 3=1985-1989, 4=1990-1995, etc) in order to account also for the general temporal variability (but reducing inter-annual fluctuations). For the Weser and Elbe, the analysis was performed on bird data averaged over a combination of estuarine zone, jurisdiction (north/south bank, Weser only) and 5-year period. Bird densities were forth root transformed and the Bray-Curtis similarity matrices were calculated before applying cluster analysis to highlight similarities in spatial-temporal distribution of different species in the studied estuaries. The general pattern in species distribution across estuarine zones was also investigated by using ordination analysis (Principal Coordinate analysis, PCO). Analysis of similarity (ANOSIM) between guilds and between sectors (in the Humber) and estuarine zones (in the Elbe and Weser) was carried out to test for statistical significance in the observed patterns.

Multivariate multiple linear regression analysis was performed on bird species data and on continuous explanatory variables in order to identify the main factors affecting the overall bird assemblage spatial-temporal distribution. The multivariate multiple regression full model (including all explanatory variables) was investigated by using distance-based redundancy analysis (dbRDA). DISTLM routine was also applied to identify the best subset of variables explaining wader data variability (best reduced model, selected by backward selection method using AIC criterion). Correlation analysis (Spearman's) was carried out to identify the main relationships between species densities and environmental variables.

It should be noted that the datasets analysed (including data averages by sector/zone and 5-year period) have variable spatial and temporal coverage which might affect the analysis results. The dataset for the Humber (bird species densities and all the environmental variables) covers only sectors in the mesohalyne and polyhaline zones and includes 27 observations for waders (between 1990 and 2005) and 28 observations for wildfowl (between 1985 and 2005). The datasets for the Elbe cover all the salinity zones (from freshwater to polyhaline), including 68 observations for which both bird densities and habitat areas are available (between 1984 and 1998) and 92 observations for which both bird densities and water quality parameters are available (between 2004 and 2009). As the datasets on habitats and water quality parameters are not temporally overlapping, the analysis has been carried out separately for the two types of abiotic characteristics in this estuary. The dataset for the Weser for which both bird densities and habitat areas are available covers all the salinity zones (from freshwater to polyhaline), including 43 observations (between 1984 and 2003). In turn the dataset for which both bird densities and water quality parameters are available includes 92 observations (between 2004 and 2009) covering only the freshwater and oligohaline zone. As the datasets on habitats and water quality parameters are only marginally overlapping (between 1992 and 2003, with a total of 6 observations), the analysis has been carried out separately for the two types of abiotic characteristics also in this estuary.

Results

The cluster analysis distinguishes groups of species within wader and wildfowl assemblages mainly on the basis of their overall abundance, with the clusters shown in the upper part of the dendrograms

(Figure 3.1) usually including the most abundant species found in the estuaries (e.g. Dunlin, Golden Plover, Lapwing, Oystercatcher, Curlew for waders; Shelduck, Wigeon, Mallard, Teal for wildfowl). There is a general agreement between the cluster analysis and the guilds classification for wildfowl only, as confirmed by the presence of a significant difference between wildfowl guilds in all the estuaries (Table 3.1). However, this is likely ascribed to the general higher abundances observed for all the species within the estuarine feeder and marsh associated guilds rather than to a common spatial distribution within the different estuaries. For example, the estuarine feeder species are widely distributed across the estuarine zones in the Elbe, whereas they show high densities in the polyhaline and mesohaline areas of the Weser and in the oligohaline and mesohaline areas of the Humber. In turn, the groupings of wader species identified by the cluster analysis seem not to agree with the guilds distinction, as confirmed by the absence of a significant difference between wader guilds in all the estuaries (Table 3.1). This might be ascribed to the fact that the considered guilds basically account for species depending on mud for feeding or roosting, hence these might not distinguish different uses at the spatial scale considered (among sectors) (e.g. different guilds distribution of birds feeding on mud might occur within a sector, along the shore height gradient, based on the prey availability and preferences, but this might not be evident when considering the sector as a whole and when comparing different sectors).

The ordination analysis applied to bird data in the different sectors/units (Figure 3.2) shows the main spatial-temporal differentiation in the wader and wildfowl assemblage distribution within each estuary. Data points in the ordination plots (i.e., observations by unit/sector by 5-year period) have been classified according to the salinity zone in order to obtain preliminary information on the degree of agreement of the species distribution with the salinity zonation of the estuaries. ANOSIM test has been carried out also between salinity zones in each estuary with this purpose (Table 3.2).
It's clear from the analysis how spatial patterns dominate over temporal ones, resulting in clusters of samples from different periods within each sector/estuarine zone, and in higher distances between sector/zones samples than between temporal samples within each sector/zone in the ordination plot (Figure 3.2).

Table 3.1. ANOSIM results (R value and significance p-level) of comparisons between guilds distribution for waders and wildfowl in the Humber, Weser and Elbe estuaries (ns=not significant).

	Humber	**Weser**	**Elbe**
Waders	R=0.107 (ns)	R=0.050 (ns)	R=0.092 (ns)
Wildfowl	R=0.579 (p<0.001)	R=0.773 (p<0.001)	R=0.801 (p<0.001)

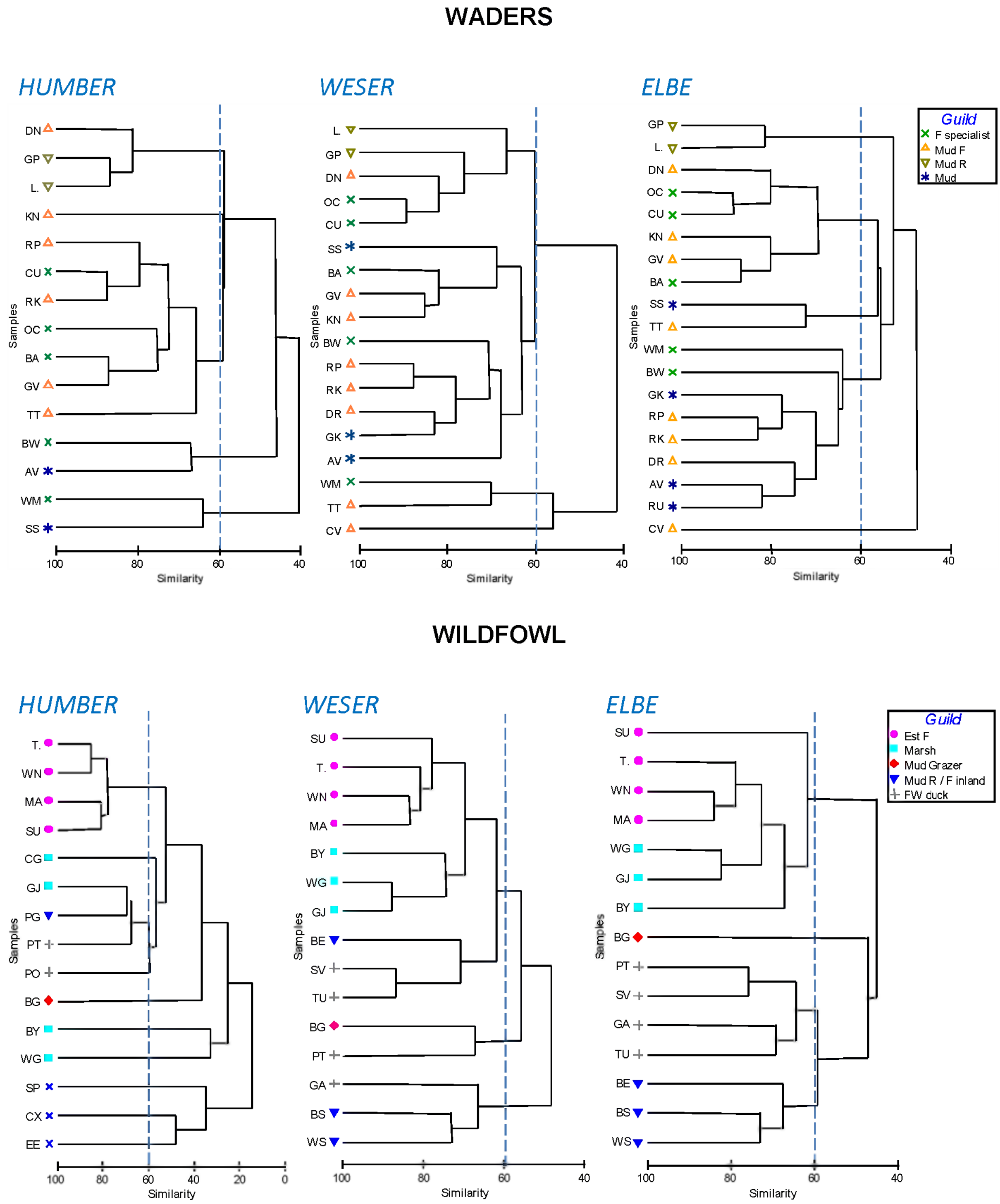


Figure 3.1. Custer analysis of wader and wildfowl species in the Humber, Weser and Elbe estuaries, based on Bray-Curtis similarity calculated on average species density (ind.km^{-2}) across estuarine zones, periods and estuarine bank (Elbe only). Symbols indicate species guilds.

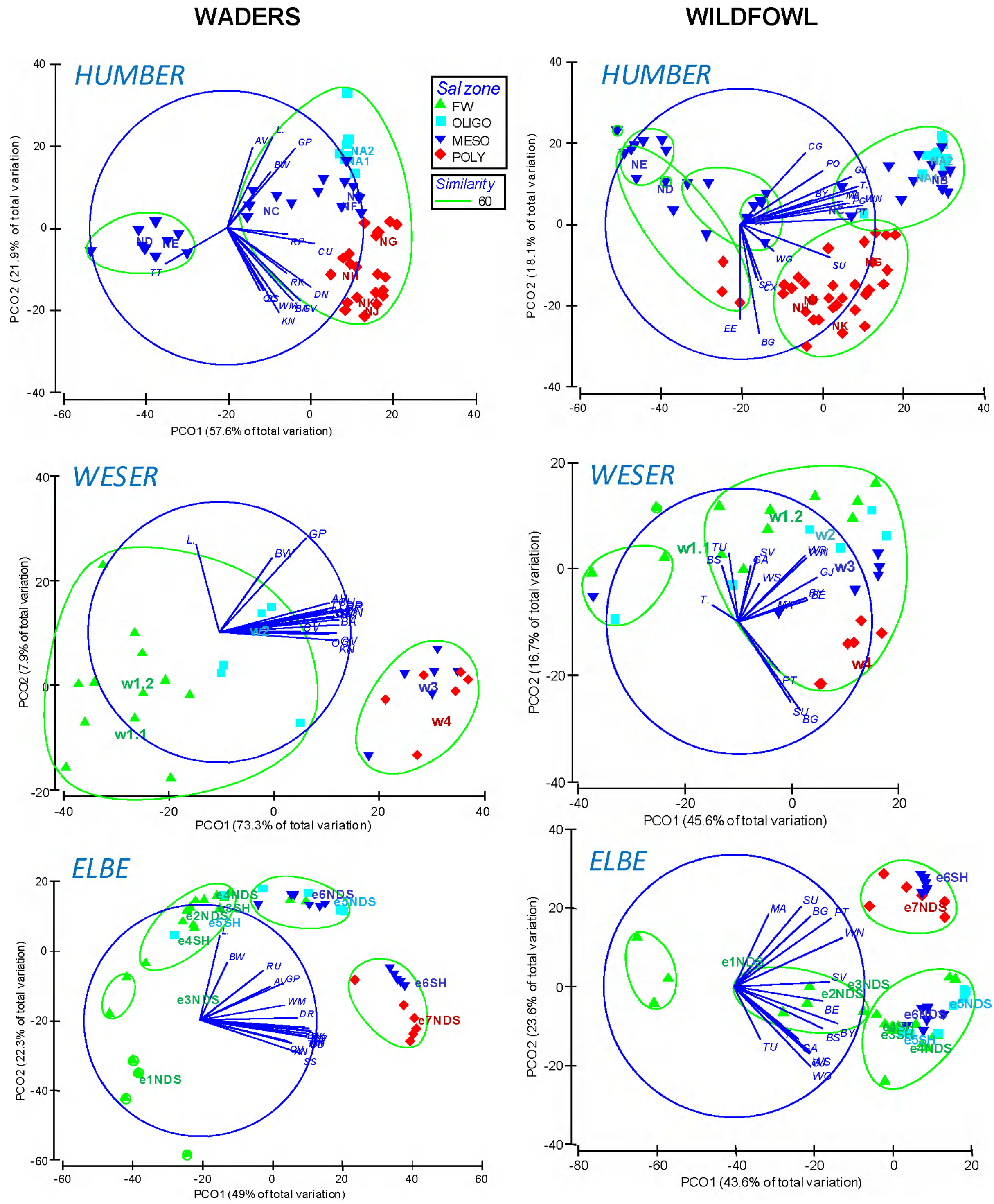


Figure 3.2. Ordination (principal coordinates) analysis of wader and wildfowl assemblages in the Humber, Weser and Elbe estuaries, based on Bray-Curtis similarity calculated on the average species density (ind.km-2) by estuarine zone (sectors NA1 to NK in the Humber, zone w1.1 to w4 in the Weser, zone e1 to e7 in the Elbe), period (1=1975-79, 2=1980-84, etc.) and estuarine bank (for Elbe only: NDS=southern bank, SH=northern bank). Vectors indicate the direction of increase in the species density and symbols indicate salinity zones. The centroids of each estuarine zone (with also distinction by estuarine bank in the Elbe) are shown as coloured labels in the graph. Samples showing a similarity in their bird assemblage ≥60% (as obtained from cluster analysis – not shown) are grouped by green circles.

Table 3.2. ANOSIM results (R value and significance p-level) of comparisons of wader and wildfowl assemblage structure between salinity zones in the Humber, Weser and Elbe estuaries (ns=not significant).

	Humber	Weser	Elbe*
Waders	R=0.390 (p<0.001)	R=0.725 (p<0.001)	R=0.184 (p<0.05)
Wildfowl	R=0.280 (p<0.001)	R=0.163 (p<0.05)	R=0.116 (ns)

*The estuarine bank (northern, SH or southern, NDS) was included in the analysis for the Elbe as a crossed factor in the analysis.

Appendix 4

Details on the analysis on wader and wildfowl species distribution models in TIDE estuaries

Regression models were applied to single species (Dunlin, Golden Plover, Redshank, Bar-Tailed Godwit, Shelduck, Pochard and Brent-Goose) data and environmental variables within each estuary.

The species density by sector/counting unit by year was used as response variable. Only when the frequency of occurrence of the species in the dataset was <75% (mainly due to a more heterogeneous distribution of the species, with association to certain sectors/units and absence from others), the probability of presence was modelled as response variable (based on presence-absence data) by using a logistic regression. A summary of the models calibrated for the species in the three TIDE estuaries (including information on the size of datasets (n) analysed) is reported in the table below.

		Estuary (environmental dataset)				
Species	response variable analysed	Humber (all env.)	Elbe (habitat + Salinity)	Elbe (water quality)	Weser (habitat + Salinity)	Weser (water quality)
Dunlin	density	model calibrated, n=146	model calibrated, n=169	NA (50% of density data are zeros - model on density was not calibrated (zero inflation))	model calibrated, n=140	NA (data available for freshwater and oligohaline zones only, and 92% of data are zeros - model was not calibrated (zero inflation))
	probability of presence	NA (no absence - model on presence absence could not be calibrated)	model calibrated, n=171	model calibrated, n=247	NA	
Redshank	density	model calibrated, n=91	NA	NA	NA	NA
Golden Plover	density	model calibrated, n=90	NA	NA	NA	NA
Bar-tailed Godwit	density	model calibrated, n=91	NA	NA	NA	NA
Shelduck	density	model calibrated, n=254	NA	NA	NA	NA
Pochard	density	NA (77% of density data are zeros - model on density was not calibrated (zero inflation))	NA	NA	NA	NA
	probability of presence	model calibrated, n=250	NA	NA	NA	NA
Brent Goose	density	NA (56% of density data are zeros - model on density was not calibrated (zero inflation))	NA	NA	NA	NA
	probability of presence	model calibrated, n=254	NA	NA	NA	NA

The environmental variables reported in

Table 2 (in Chapter 4) were used as explanatory variables (covariates) and no interaction terms were considered between the predictors, in order to allow a simpler interpretation of model results. As for the multivariate analysis and due to data availability limitations (see also Appendices 1 and 3), separate models relating the species density distribution with either habitat areas or water quality variables were employed in the Weser and the Elbe, whereas the effects of all environmental variables were analysed simultaneously in a single model for the species in the Humber. However, salinity zone (Salz) was included as a factor in the analyses of habitat datasets in the Weser and Elbe in order to take account of the possible combined effect of habitat area and salinity gradient on the species distribution within these estuaries.

When necessary, data were transformed (square root, forth root or log transformation, whichever the most appropriate) in order to remove the possible effect of outliers, normalise the data distributions and to increase homogeneity of variance.

The number of candidate explanatory variables (or predictors) to be included in the model was firstly reduced by removing highly correlated variables. Following Fielding and Haworth (1995), a Spearman correlation analysis was conducted and variables with high correlation coefficient ($|r_S|>0.7$) were not considered for model calibration, in order to avoid multicollinearity. In addition, given that even a moderate collinearity might be problematic, particularly if the ecological signal is weak (Zuur et al. 2009), variables with $|r_S|>0.6$ were also considered and were excluded from the analysis whenever their relationship with the response variable was weak ($|r_S|<0.5$).

Relationships between the species mean distribution and environmental variables were studied by means of generalized additive models (GAM) (Zuur et al. 2007). GAMs allow to model some predictors non-parametrically in addition to linear and polynomial terms (Guisan et al. 2002), allowing the decision of the response shapes to be fully determined by data. This is achieved by introducing a smoothing function for the continuous predictors. GAMs were fitted by using the 'mgcv' library (Wood 2000) for R software packages (R Development Core Team 2008). This type of model is represented in 'mgcv' as penalized GLM, each smooth term of a GAM being represented using an appropriate set of basic functions (Wood and Augustin 2002). The GAM model-building procedures followed the guidelines of Wood (2000), using penalized regression splines. This allows the degrees of freedom for each smooth term in the model to be chosen simultaneously as part of model fitting by minimizing the Generalized Cross Validation (GCV) score of the whole model (Wood, 2006). Density data were fitted using a Gaussian family with the canonical identity link, whereas presence–absence data were fitted using a binomial family with the canonical logit link, optimizing the GCV score. Model selection was carried out by means of backward selection using AIC as selection criterion. The resulting best model was validated graphically by examination of possible patterns in the residuals, in order to check that assumptions (homogeneity, independence, normality) were fulfilled. Single predictor models were also considered and their AIC value was used to rank the importance of each environmental variable in affecting the species distribution.