



Waterbird communities along the estuarine salinity gradient of the Schelde estuary, NW-Europe

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Abstract. The zonation of non-breeding waterbirds along the Schelde estuary (The Netherlands–Belgium), one of the longest estuaries in NW-Europe with still a complete salinity gradient, including a large freshwater tidal area, was described. Numbers of birds were counted monthly over the period October 1991 to June 1997. Highest numbers of waterbirds were observed in late autumn and winter, with annual peak numbers ranging between 150,000 and 235,000 individuals for the whole estuary. Based on a multivariate analysis different waterbird communities were observed along the salinity gradient. The polyhaline areas of the estuary were numerically dominated by the waders Oystercatcher and Dunlin. Due to the presence of a large brackish marsh in the mesohaline zone, the waterbird community in this area was dominated by the herbivores Wigeon and Greylag Goose. In the oligohaline and freshwater tidal areas, the waterbird community was dominated by duck species, with Teal and Mallard being the most important. The international importance of the Schelde estuary for waterbirds was evidenced by the fact that for 21 waterbird species the 1% level criterion, according to the Ramsar convention, was exceeded. The relation of the observed diversity and community patterns with the functional and habitat diversity of the Schelde estuary as well as the effect of recent conservation measures to preserve this habitat were discussed.

Key words: communities, conservation, estuarine zonation, salinity gradient, Schelde estuary, waterbirds

Introduction

Estuaries are defined as inlets of the sea reaching into a river valley as far as the upper limit of tidal rise (Fairbridge 1980). Estuaries are cited among the most productive biomes of the world (Odum 1983; Day et al. 1989; Costanza et al. 1993) and support important biogeochemical processes that are central to the planet's functioning, e.g. nutrient cycling (Billen et al. 1991; Costanza et al. 1997). Birds benefit from this high level of productivity, and for many waterbird species estuaries are of vital importance for one or more stages of their life cycle (e.g. Pienkowski and Evans 1984; Smit and

Piersma 1989; Davidson et al. 1991; Ens et al. 1994). However, most of the threats to biodiversity are precisely in the estuarine zone and are a direct result of human population and demographic trends (Prater 1981; Smit et al. 1987; Davidson et al. 1991; Suchanek 1994; Gray 1997; McLusky 1999).

Because of their position at the top of the food web birds are good indicators of environmental changes (Furness and Greenwood 1993). Waterbirds are widely used in monitoring programmes as an indicator of the value of wetland habitats (Moser et al. 1993; Scott and Rose 1996). Within the Ramsar Convention (Convention of Wetlands of International Importance Especially as Waterfowl Habitat, Ramsar 1971, and 1982 Protocol) the 1% criterion states that a wetland should be considered internationally important if it regularly supports 1% of the individuals of a population of one species of waterfowl (Atkinson-Willes 1976; Boyd and Pirot 1989; Scott and Rose 1996). Several papers demonstrate the importance of coastal and estuarine areas for waterbirds (e.g. Meire et al. 1989; Davidson et al. 1991; Schekkerman et al. 1994; Meltofte et al. 1994). However, very few papers deal with the zonation of waterbird communities along a complete salinity gradient, including poly- and mesohaline as well as freshwater tidal areas. Especially freshwater tidal areas are nowadays very rare habitats, and knowledge on these areas is poor (Odum 1988).

The Schelde estuary is one of the longest estuaries in NW-Europe with still a complete salinity gradient according to the classification of estuarine divisions of McLusky (1993, 1999). In this paper the zonation of non-breeding waterbird communities along the salinity gradient of the Schelde estuary is described. Emphasis is given to the spatial and seasonal distribution. Annual trends will be discussed elsewhere. The importance of the Schelde estuary as a wetland for waterbirds according to the Ramsar convention is determined. The possible relation of the observed diversity and community patterns with the functional and habitat diversity of the Schelde estuary as well as the effect of recent conservation measures to preserve this habitat are discussed.

Materials and methods

Study area

The Schelde estuary measures 160 km from Vlissingen (The Netherlands) upstream to Gent (Belgium) (Figure 1). The width is about 100 m at Dendermonde, 500 m at Antwerpen, 1500 m near the Dutch–Belgian border, and 4500 m at Vlissingen with a maximum of 7800 m. The mean tidal range increases from 3.8 m at Vlissingen to 5.3 m at Antwerpen. At Gent the tidal range is still 2 m. The Westerschelde (55 km) represents the downstream Dutch part of the estuary. It is a well mixed region, characterized by a complex morphology with flood and ebb channels surrounding several large intertidal flats. The surface of the Westerschelde amounts to 310 km²,

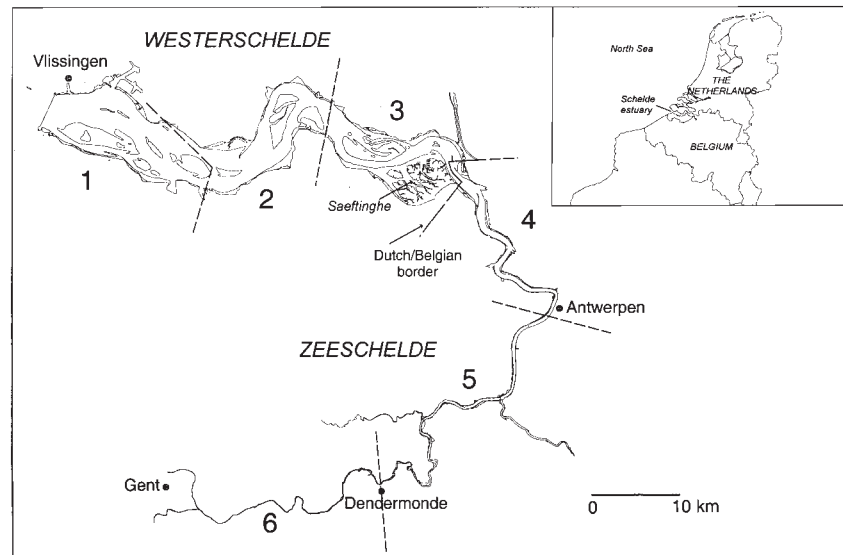


Figure 1. Map of the Schelde estuary situated between Vlissingen (The Netherlands) and Gent (Belgium), with its division in Westerschelde (areas 1–3), and Zeeschelde (areas 4–6).

with the intertidal area covering 35%. The Zeeschelde (105 km), the Belgian part of the estuary, is characterized by a single channel, bordered by relatively small mudflats and marshes (28% of total surface). The surface of the Zeeschelde amounts to only 44 km². Human activities are mainly concentrated in the Zeeschelde, where agglomerations and industries are located close to the river banks. The intertidal zone is often absent (e.g. quays, wharfs) or very narrow, consisting only of dikes with a steep hard substrate of rubble. Upstream of Dendermonde, the estuary is almost completely canalized.

Bird counts

In the Westerschelde, waterbird censuses were organised by the National Institute for Coastal and Marine Management (RIKZ) (e.g. Meininger et al. 1997, 1998). Every month counts were performed during high tide, when birds concentrated on roosts. In the Zeeschelde, a waterbird monitoring programme was carried out by the Institute of Nature Conservation (e.g. Ysebaert et al. 1998b, 1999). Here, monthly censuses were done at low tide from boats, when birds were present in the intertidal zone. In both Westerschelde and Zeeschelde count dates were set close to mid-month.

Neighbouring areas, between which bird movements were frequent, were counted on the same day. For the Westerschelde missing counts were covered by the method of imputing (Underhill and Prÿs-Jones 1994). The results presented in this study deal with counts over the period October 1991 to June 1997, representing 69 observation

months. For the Zeeschelde no counts were available for the period May–August 1992. During the 6-year observation period, only two winters (1995/96 and 1996/97) were really cold with respectively 14 and 18 days showing freezing temperatures all day. The other winters ranged from mild to normal with on average 4 days with freezing temperatures all day.

Data analysis

Numbers of divers, grebes, cormorants, herons, geese, swans, ducks, coots, and waders were dealt with. Exotic waterbird species (8 species) and species which were only observed once (9 species) were excluded from all further analyses. Gulls and terns were not considered.

Based on the classification of McLusky (1993, 1999) six areas were recognized along the estuarine salinity gradient (Figure 1, Table 1). In the Westerschelde, the boundaries of the areas were defined so that birds roosted and feeded in the same area (Mostert et al. 1990). Surfaces of the intertidal (tidal flats and marshes) and of the subtidal zone were obtained from non-published reports (Table 1). Area 3 was characterized by the presence of the marsh of Saeftinghe, one of the largest brackish marshes in NW-Europe. For the Zeeschelde the long stretches of only hard substrate with rubble (human-made constructions) were also considered as part of the intertidal surface. The surface of these constructions was estimated from aerial photographs, being 26, 54 and 52 ha, respectively for area 4, 5 and 6.

Vegetation structure of the marshes changed along the salinity gradient, from a relatively low vegetation in the saltmarshes of areas 1–2 to a more pronounced vertical structure with reed beds and willow scrubs in the freshwater tidal marshes of areas 5–6.

Monthly mean numbers of waterbirds for the whole study period were calculated for each waterbird species and for each area over the six observation years. Also means were calculated for four periods, that were distinguished by season-related functions of the estuary for waterbirds: (1) summer (moulting and breeding): June, July; (2) autumn (staging): August, September, October, November; (3) winter (wintering): December, January, February; (4) spring (staging): March, April, May.

Table 1. Surface area (ha) of the intertidal zone (tidal flats and marshes) and subtidal zone in the different areas along the Schelde estuary. Areas 1–3: Westerschelde. Areas 4–6: Zeeschelde.

Area	Classification	Tidal flats	Marsh	Subtidal	Total
1	Lower/middle (polyhaline)	2898	51	10195	13144
2	Middle/inner (poly/mesohaline)	2456	76	6564	9069
3	Inner (α -mesohaline)	3020	2383	3342	8745
4	Inner/upper (β -meso/oligohaline)	514	181	2005	2700
5	Upper/tidal fresh (oligohaline/limnetic)	196	297	948	1441
6	Tidal fresh (limnetic)	9.5	30.5	250	290
Total	Whole estuary	9093.5	3018.5	23304	35389

Year-to-year fluctuations in waterbird numbers were not considered, only the impact of severe versus mild winters on the estuarine zonation of waterbirds.

Waterbird species were divided into functional (trophic) guilds based on feeding type. All waders and the Shelduck were considered as carnivores, here called benthivores as they feed on benthos on the tidal flats, diving ducks and scoters as diving benthivores, grebes, divers, cormorants, herons and sawbills as piscivores. Several duck species (Teal, Mallard, Pintail) mainly foraged on the mudflats along the low water edge, probably feeding on small macrofauna (e.g. Oligochaeta) and organic material (pers. observ.), and were considered as omnivores. The remaining duck species (mainly Wigeon), geese, swans and coots were considered as herbivores.

As a measure of species diversity, the dominance pattern (numerical diversity) within areas and seasons was determined from *k*-dominance curves, that plot cumulative ranked abundances against (log) species rank (Lambshead et al. 1983). The zonation of waterbird communities along the salinity gradient was analysed by multivariate statistics based on annual means per season. The methods of classification and ordination (Gauch 1982) were used to indicate the degree of (dis)similarity in waterbird species composition (community structure) among areas for each season. The agglomerative clustering method (Group Average Sorting GAS of Bray–Curtis dissimilarities) (Clifford and Stephenson 1975) and ordination by non-metric multi-dimensional scaling (MDS) (Kruskal and Wish 1978) were applied. Data were fourth root transformed prior to analysis. The results for the winter season were representative for the other seasons, so only these results are discussed in detail. Dominance curves, GAS and MDS were performed with the statistical package PRIMER (Carr et al. 1993; Clarke 1993).

Finally, the mean of the annual peak numbers for the whole study period was determined for each waterbird species and compared with the 1% criterion of the Ramsar Convention to evaluate the international importance of each of the six areas and of the Schelde estuary as a whole (Perennou et al. 1994; Scott and Rose 1996). The population estimates were based on Meininger et al. (1995), Scott and Rose (1996) and Rose and Scott (1997).

Results

Species composition and total numbers of waterbirds

A total of 80 waterbird species were observed in the Schelde estuary, with respectively 69, 61 and 68 species in the Westerschelde areas 1, 2 and 3, and 56, 47 and 37 species in the Zeeschelde areas 4, 5 and 6. Scientific names for species mentioned in the text are given in Table 2.

The monthly mean numbers of waterbirds showed clear seasonality (Figure 2), with lowest numbers in the period April–July and a peak in the period November–January. Ducks and waders dominated throughout the year, whereas geese were only

Table 2. Species list of the 21 internationally important waterbirds observed in the Schelde estuary during the whole study period (1991/92–1996/1997). For each species the mean of the annual peak numbers per area and for the whole Schelde estuary, the absolute maximum number and the number of months the 1% level was exceeded (on a total of 69 observation months), as well as the number corresponding with the 1% criterion of the Ramsar Convention are given. Numbers exceeding the 1% level are in bold.

Species name	Area 1		Area 2		Area 3		Area 4		Area 5		Area 6		Schelde estuary (absolute max.)		Months	1% criterion
	(mean max.)		(mean max.)		(mean max.)		(mean max.)		(mean max.)		(mean max.)		(mean max.)			
Spoonbill – <i>Platalea leucorodia</i>	2	0	64	0	0	0	0	0	0	0	0	0	79	139	9	30
Greylag Goose – <i>Anser anser</i>	857	111	36657	1754	5	0	0	0	5	0	0	0	38833	51070	32	2000
Shelduck – <i>Tadorna tadorna</i>	3032	1215	3445	1335	1421	93	0	0	0	0	0	0	7811	10719	33	3000
Wigeon – <i>Anas penelope</i>	5412	3472	37435	1925	24	2	0	0	24	0	0	0	41117	67099	32	12500
Gadwall – <i>Anas strepera</i>	6	3	69	587	565	66	0	0	565	0	0	0	1160	1748	33	300
Teal – <i>Anas crecca</i>	130	52	1803	2410	10412	740	0	0	10412	0	0	0	13309	17938	34	4000
Mallard – <i>Anas platyrhynchos</i>	5359	2914	9717	1113	5843	1487	0	0	5843	0	0	0	22518	26437	11	20,000
Pintail – <i>Anas acuta</i>	71	136	2731	166	375	23	0	0	375	0	0	0	3056	4584	30	600
Pochard – <i>Aythya ferina</i>	46	5	11	316	3500	1272	0	0	3500	0	0	0	4418	11081	5	3500
Oystercatcher – <i>Haematopus ostralegus</i>	11317	7966	1694	165	5	1	0	0	5	0	0	0	18724	23762	45	9000
Avocet – <i>Recurvirostra avosetta</i>	570	205	654	447	2	1	0	0	2	0	0	0	1546	2133	16	700
Ringed plover – <i>Charadrius hiaticula</i>	1499	293	274	112	0	0	0	0	0	0	0	0	2452	3487	5	500/2000*
Kentish Plover – <i>Charadrius alexandrinus</i>	355	18	6	1	0	0	0	0	0	0	0	0	437	610	1	610
Grey plover – <i>Pluvialis squatarola</i>	4292	880	1351	105	0	0	0	0	0	0	0	0	5357	8388	47	1500
Knot – <i>Calidris canutus</i>	2607	463	240	0	14	0	0	0	14	0	0	0	2957	8749	2	3500
Sanderling – <i>Calidris alba</i>	788	554	48	0	0	0	0	0	0	0	0	0	1384	1840	5	1000
Dunlin – <i>Calidris alpina</i>	14385	13835	3378	747	672	0	0	0	672	0	0	0	29014	43957	25	14,000
Bar-tailed Godwit – <i>Limosa lapponica</i>	1565	1060	1434	43	0	0	0	0	0	0	0	0	4049	4837	21	1000/7000**
Curlew – <i>Numenius arquata</i>	2195	1176	1414	147	1	0	0	0	1	0	0	0	4225	5588	12	3500
Spotted Redshank – <i>Tringa erythropus</i>	262	37	798	1	0	0	0	0	0	0	0	0	1116	1307	3	1200
Redshank – <i>Tringa totanus</i>	819	733	550	102	3	0	0	0	3	0	0	0	1959	2822	8	1500

* 2000 for the months May, August and September, 500 in the other months (Meininger et al. 1995).

** 7000 for the months May, July and August, 1000 in the other months (Meininger et al. 1995).

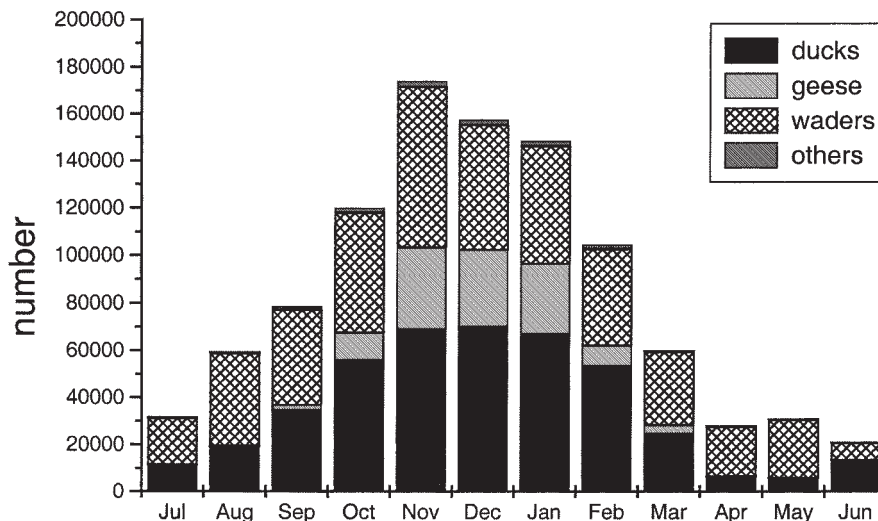


Figure 2. Monthly mean numbers of ducks, geese, waders and other waterbirds counted in the Schelde estuary during the whole study period (1991/92–1996/97).

abundant during late autumn and winter. The annual peak numbers for the whole study period ranged between 150,000 and 235,000 individuals.

When considering the occurrence of waterbirds along the estuarine salinity gradient, it appeared that in all seasons more than 75% of all waterbirds occurred in the Westerschelde (areas 1–3), with respectively 40% in area 3 in autumn and winter and 40% in area 1 in spring and summer (Figure 3). In the Zeeschelde highest numbers were observed in area 5, especially in autumn and winter. Relative to the available intertidal surface in each area, numbers ha^{-1} (diving benthivores and piscivores excluded) were especially high in the freshwater tidal areas 5–6.

Only 3–5 species accounted for more than 75% of the total number observed in each area and in each season, as demonstrated by the k -dominance curves based on the autumn average (Figure 4). Numerical diversity was lowest in area 6 where two species accounted for 83% of the total number of waterbirds observed. In area 4 dominance was lowest and hence numerical diversity greatest.

Zonation of waterbird communities along the estuarine salinity gradient

The GAS-classification for the winter period resulted in a clear separation of the six areas along the salinity gradient (Figure 5). This was confirmed by the MDS ordination diagramme. Area 6 was clearly separated from the other areas, with the exception of the two more severe winters 1995/96 and 1996/97, which were found both in the cluster dendrogram as in the ordination diagramme close to the area 5 cluster. This could be explained by a change in the occurrence of the waterbird species

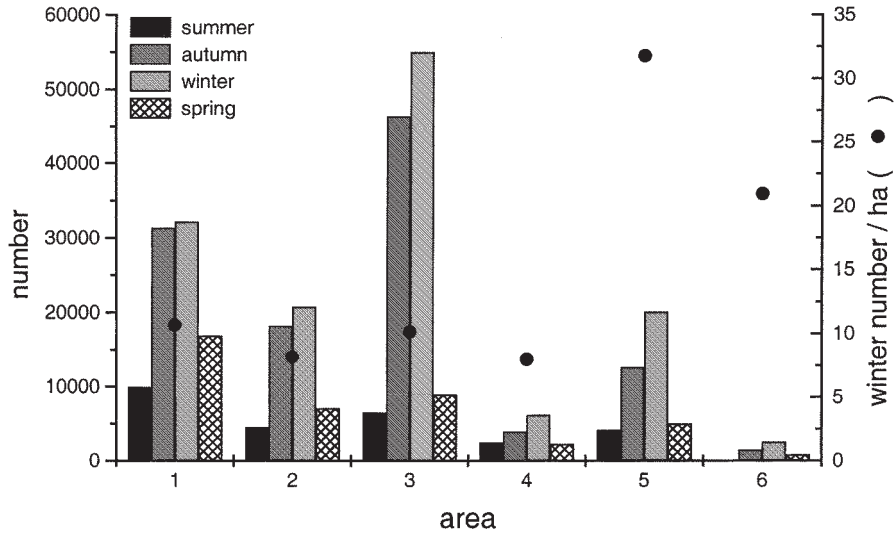


Figure 3. Seasonal mean numbers of waterbirds counted in the six areas along the salinity gradient of the Schelde estuary during summer, autumn, winter and spring. The dots represent the number of birds relative to the available intertidal surface in each area (numbers ha⁻¹ based on winter means).

during the cold winters. Only in area 6 mean total numbers of waterbirds increased significantly (6×) in the severe winters as compared to the mild/normal winters. In the other areas mean total numbers only slightly changed in the severe winters and did not affect the observed pattern of estuarine zonation.

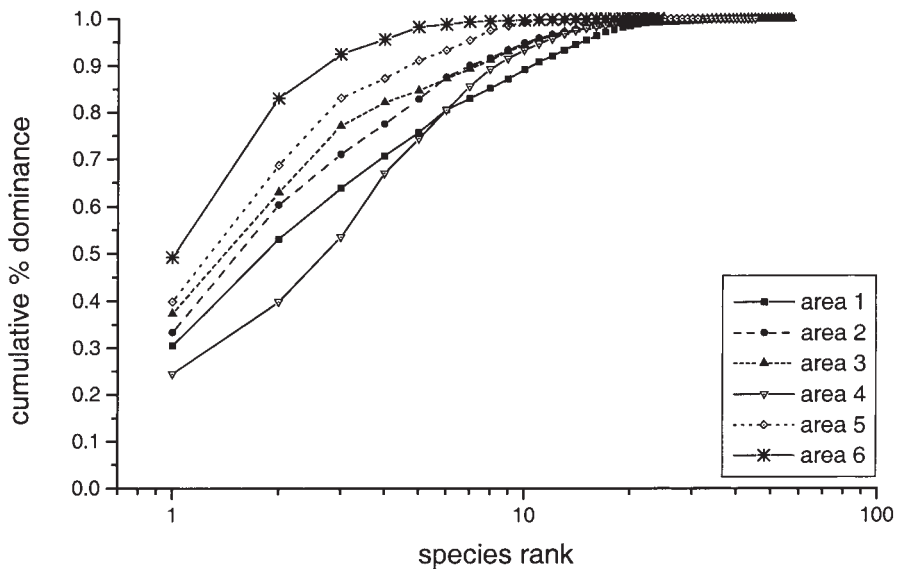


Figure 4. *k*-Dominance curves for the different areas (autumn average).

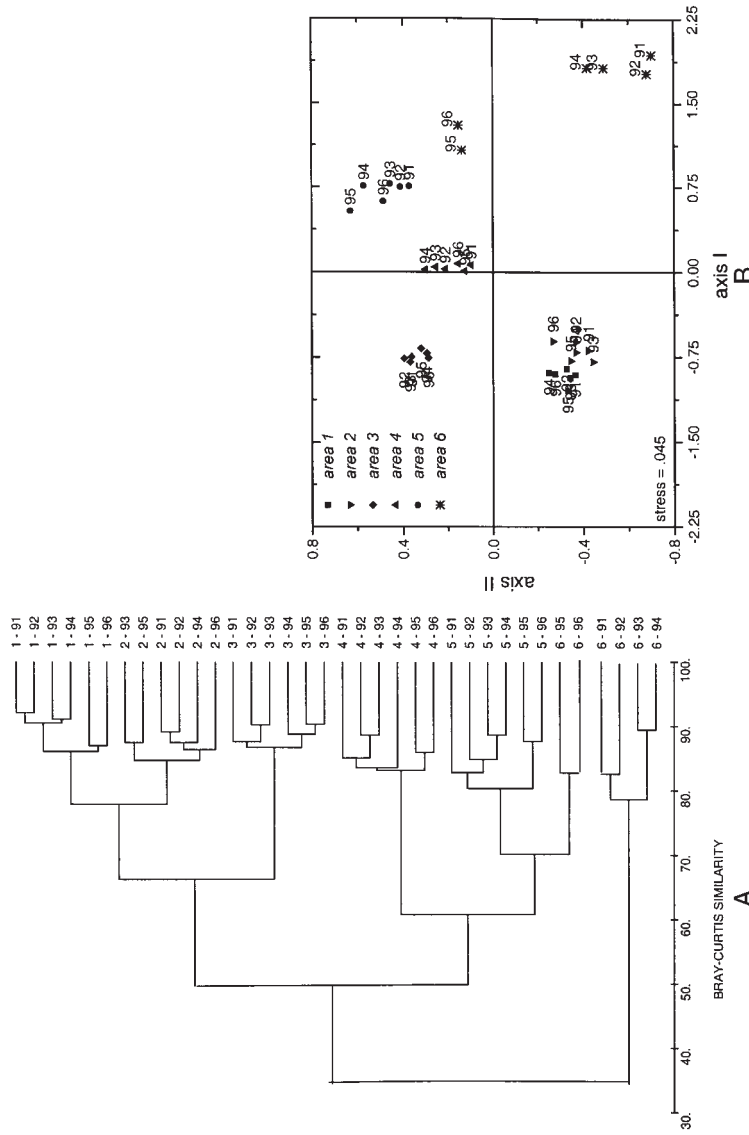


Figure 5. Multivariate analysis based on winter means for the six areas in the Schelde estuary and for the whole study period (seasons 1991/92–1996/97) (A) Hierarchical agglomerative clustering (1–91 = area 1, winter 91/92;...; 2–92 = area 2, winter 91/92;...). The clustering clearly shows a separation of each area along the salinity gradient. (B) Two-dimensional MDS ordination diagram (91 = winter 91/92; 92 = winter 92/93;...). The first axis reflects the salinity gradient, with, on the right side (positive side of the axis), the most upstream, limnetic area 6, and on the left side, the most downstream, polyhaline area 1.

Characterization of waterbird communities along the salinity gradient

Figure 6 summarizes the zonation of the most characteristic waterbird species along the estuarine salinity gradient of the Schelde estuary. The spatiotemporal occurrence of some waterbird species is given in Figure 7.

The polyhaline zone of the estuary (areas 1–2) was dominated by waders and functioned mainly as a migration stop-over and as a wintering area. Oystercatcher and Dunlin accounted for 50–60% of the observed numbers during winter, autumn

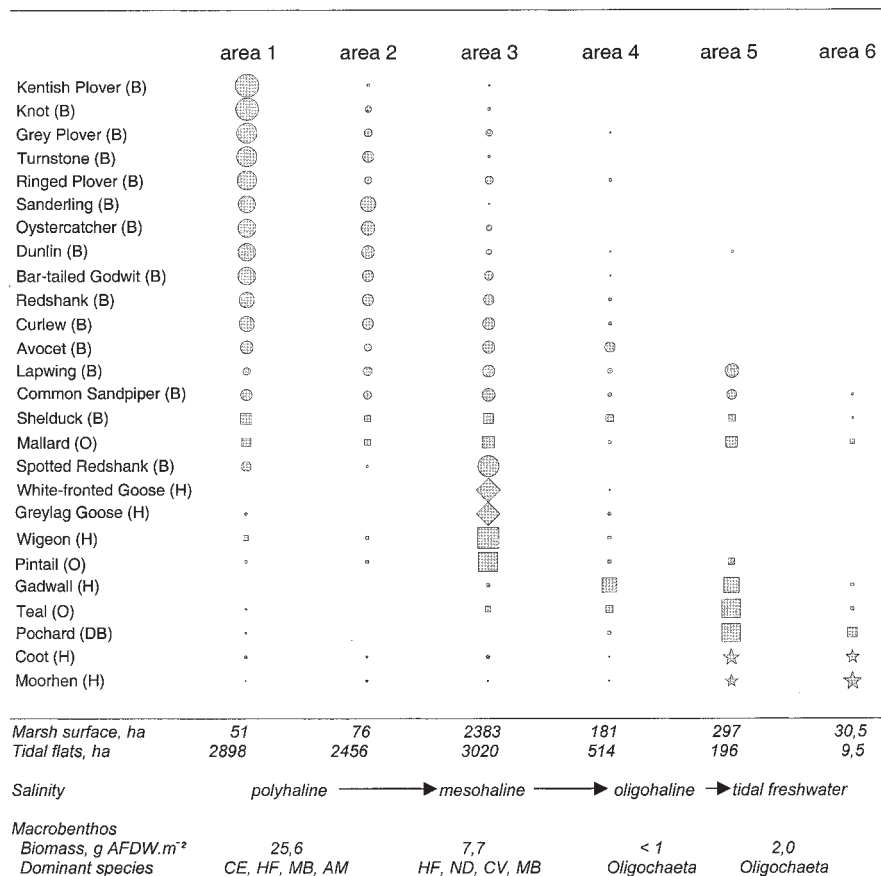


Figure 6. Zonation of the most characteristic waterbird species (B = benthivores, H = herbivores, O = omnivores, DB = diving benthivores) along the salinity gradient of the Schelde estuary (scaling based on annual mean numbers). Circles = waders, Squares = ducks, Diamonds = geese, Stars = other waterbird species. For each area marsh and tidal flat surfaces (ha) are given. For each salinity region mean total macrobenthic biomass is given, together with the dominant macrobenthic species present (CE = *Cerastoderma edule*, MB = *Macoma baltica*, HF = *Heteromastus filiformis*, AM = *Arenicola marina*, ND = *Nereis diversicolor*, CV = *Corophium volutator*). Macrobenthos data based on Ysebaert and Meire (1999) and Seys et al. (1999).

and spring. In summer Oystercatcher (37%), mainly non-breeding subadults, and Shelduck (22%) dominated. Typical migrating waders were Kentish Plover, Knot, Grey Plover, Turnstone, Ringed Plover, Sanderling and Bar-tailed Godwit.

In the mesohaline zone of the estuary (area 3) both waders and ducks occurred. Here the waterbird community was mainly related to the presence of the very large brackish marsh Saeftinghe (Table 1). The area mainly functioned as a wintering area. During winter the bird community was dominated by the herbivores Greylag Goose (37%) and Wigeon (36%). Greylag Geese, which feed mainly on roots of *Scirpus maritimus*, were only since 1990 present in such large numbers. During migration periods large numbers of Grey Plover, Bar-tailed Godwit, Redshank and Curlew were observed and the area appeared typically suitable for Spotted Redshank. During late autumn migration the Avocet reached highest numbers in area 3. During summer large numbers of Shelduck were observed (41%).

In area 4, a transition zone between the brackish area 3 and the freshwater tidal area 5, the waterbird community was composed of species found in areas 3 and 5. During winter Teal (25%), Mallard (14%), Greylag Goose (14%), and Wigeon (13%) were the most important species. Typically, the Gadwall was observed to feed almost exclusively on the man-made hard substrates (rubbles). During spring and summer Shelduck dominated, accounting for 40% of the total numbers observed in this area. During summer Avocet reached highest numbers in area 4.

In area 5 several duck species occurred. The area mainly functioned as a wintering area. During winter Teals (41%) were mainly observed on mudflats, feeding along the low water line. Like in area 4, Gadwalls were feeding on hard substrates. The Pochard, the only common diving duck observed in the freshwater tidal area, was observed in large numbers during the severe winters of 1995/96–1996/97 (maximum of 11,000 ind.) as compared to normal winters (maximum of 2150). During autumn and especially during summer Mallard dominated in area 5 (77%).

Area 6 was characterised by very low numbers of waterbirds. Only two species dominated during all seasons, Mallard (40–50%) and Moorhen (25–40%). Only in severe winters an influx was observed from other species like Pochard and Teal.

The zonation was also translated in different trophic groups among areas (Figure 8). In mild/normal winters as well as in autumn benthivores dominated in areas 1–2, herbivores in area 3, both herbivores and omnivores in area 4 and omnivores in the freshwater tidal areas 5–6. In severe winters the proportion of herbivores increased in the polyhaline and mesohaline zones of the estuary (areas 1–4), whereas an increase in diving benthivores was observed in the freshwater tidal areas. Piscivores were nearly absent in all areas. During spring the proportion of benthivores increased in the areas 1–4 up to more than 80% during summer. In the freshwater tidal areas 5–6 omnivores (Mallard) dominated during summer (>80%).

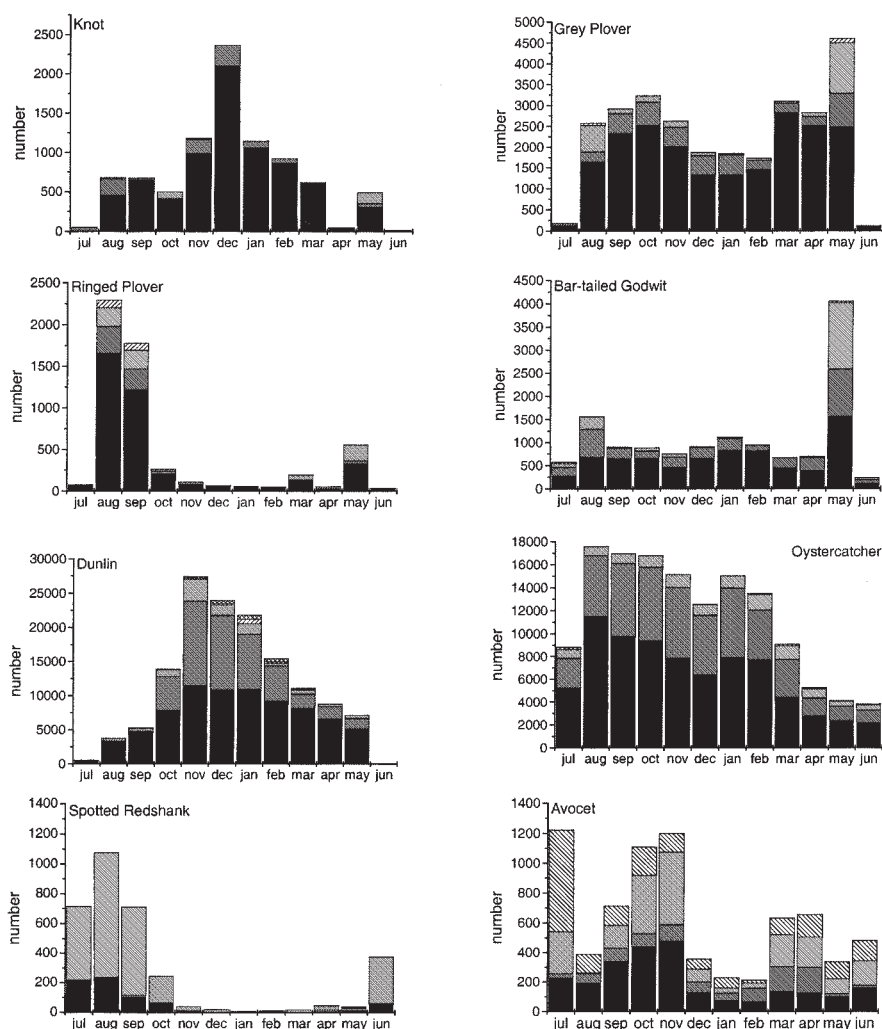


Figure 7. Monthly mean numbers per area of some characteristic waterbird species counted in the Schelde estuary during the whole study period (1991/92–1996/97).

International importance of the Schelde estuary

For the study period considered the Schelde estuary appeared to be of international importance for 21 waterbird species (Table 2). In the Westerschelde (areas 1–3) the internationally most important species were Greylag Goose, Pintail and Wigeon, the absolute maximum number of which exceeded for the whole Schelde estuary the 1% level respectively 25.5, 7.6 and 5.4 times. These species mainly occurred in area 3, demonstrating the extremely high importance of the marsh of Saeftinghe. Important waders were Ringed Plover, Grey Plover, Dunlin and Oystercatcher, the absolute

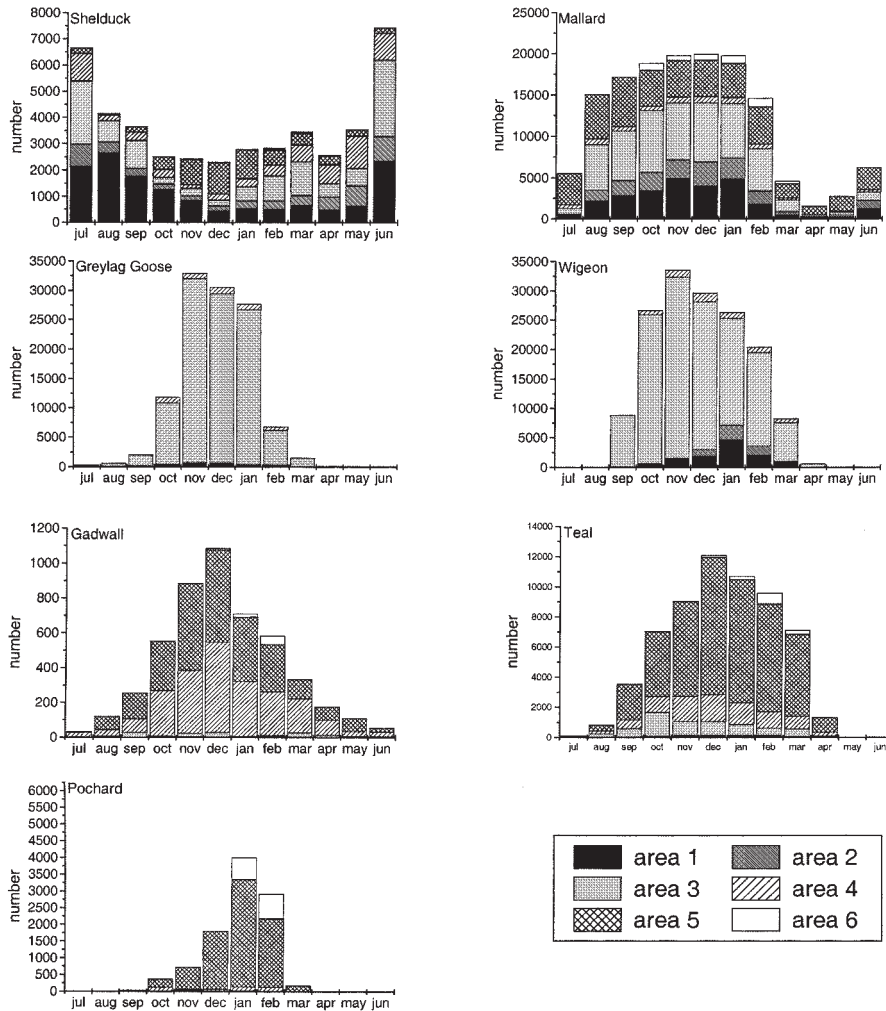


Figure 7. Continued.

maximum number of which exceeded the 1% level respectively 7.5, 6.0, 3.1 and 2.6 times. These species mainly occurred in area 1. Typical migratory species (e.g. Spotted Redshank, Sanderling) only shortly exceeded the 1% level. In the Zeeschelde (areas 4–6) internationally important species were Gadwall and Teal, the absolute maximum number of which exceeded the 1% level respectively 5.8 and 4.5 times. During severe winter months the 1% level was exceeded for the Pochard. In area 6 no important waterbird populations were observed. For the whole Schelde estuary, the frequency of occurrence exceeding the 1% level was highest for Grey Plover and Oystercatcher (seven months a year on average). Other species exceeding the 1% level regularly were Greylag Goose and the ducks Teal, Gadwall, Shelduck and Wigeon.

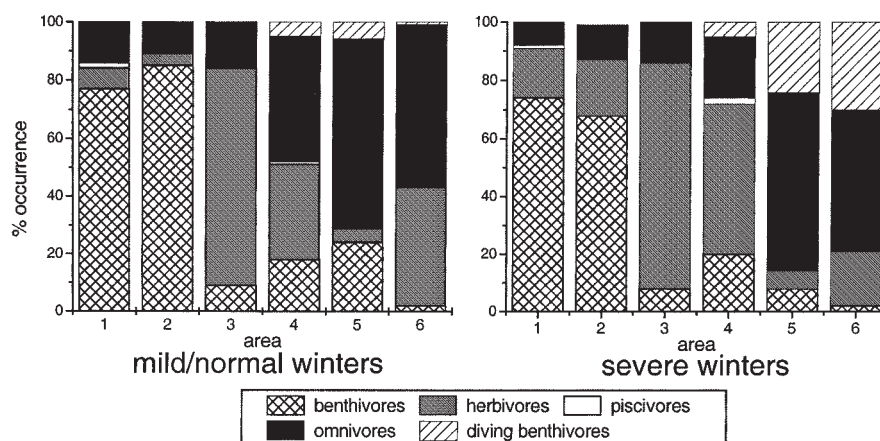


Figure 8. Proportion of different trophic groups in each area along the Schelde estuary in mild/normal (1991/92–1993/94) and severe winters (1995/96–1996/97) (based on winter means).

Discussion

Zonation of waterbirds along the Schelde estuary

In this paper the zonation of non-breeding waterbird communities along an estuary with a complete salinity gradient, the Schelde estuary, has been described in detail for the first time. Estuaries with a complete salinity gradient, including an extensive freshwater tidal area, are nowadays very rare habitats in NW-Europe. In the past, several such estuaries have been cut off from the sea (e.g. Rhine-Meuse Delta, Ferguson and Wolff 1983; Smit et al. 1997b), or have been regulated completely, resulting in an accelerated sedimentation (e.g. Seine estuary, Avoine et al. 1981).

The most important factors affecting the distribution of waterbird species along an estuarine salinity gradient are habitat diversity and habitat suitability. For wintering and migrating waterbirds food availability appears to be the main factor determining habitat suitability (Evans et al. 1984). Many benthivorous waterbird species depend on the estuarine intertidal areas for their survival, as they feed on the tidal flats on macrobenthic invertebrates which become available during low water (Evans and Dugan 1984; Goss-Custard 1985; Piersma et al. 1993; Zwarts 1997). In the Schelde estuary a significant decrease of both biomass and diversity of macrobenthos in the intertidal zone was observed in upstream direction (Ysebaert et al. 1993, 1998a; Ysebaert and Meire 1999; Seys et al. 1999). The intertidal macrobenthic biomass was mainly determined respectively by molluscs and large polychaetes in the polyhaline zone (with locally biomasses of 250 g AFDW m⁻² in cockle beds), by smaller polychaetes and amphipods in the mesohaline zone and by few oligochaetes in the oligohaline zone (Figure 6). The freshwater tidal zone had impoverished communities dominated by oligochaetes. The distribution of the benthivorous waterbirds observed

in this study was clearly related to this macrobenthic gradient (Figure 6) (see also Wolff 1969). High numbers of waders, especially those feeding mainly on bivalves (e.g. *C. C. edule*, *M. balthica*) and large polychaetes (*Nereis* spp.), such as Oystercatcher, Knot, Grey Plover, Bar-tailed Godwit and Curlew (Zwarts and Blomert 1992; Piersma et al. 1993; Zwarts 1997) were observed in the polyhaline areas 1–2. Species, like Avocet and Spotted Redshank, feeding on small crustaceans (*C. volutator*), spionid polychaetes and oligochaetes in soft and silty sediments (e.g. Moreira 1995) were more concentrated in the mesohaline zone. Shelducks, feeding to a large extent on diatoms, the mudsnail *Hydrobia ulvae*, small oligochaetes, *C. volutator* and green algae (Buxton 1981; Thompson 1982; Meininger and Snoek 1992), were observed in large numbers from the polyhaline zone up to the freshwater tidal zone. Shelducks were most abundant during summer in the Schelde estuary, especially in areas 1, 3 and 4, using the estuary also as pre-moulting and moulting sites (2000–3000 moulting ind.) (Meininger and Snoek 1992). During winter total numbers decreased but the relative importance of area 5 increased, with Shelducks mainly feeding here along the low water line.

In the freshwater tidal zone the combination of excess organic material (derived from natural input as well as from human waste loads) and of low but sufficient oxygen supply locally resulted in mass populations of tubificid (peak densities of 3×10^6 ind m^{-2} , Seys et al. 1999). Such mass populations of tubificid oligochaetes and small polychaetes present in polluted bottoms were demonstrated to be an important part of the diet of estuarine birds in polluted estuaries (Gray 1976), and more specifically of the diet of ducks (Zwarts 1976; Rofritz 1977; Warnes 1981; pers. observ.). This was confirmed for the Schelde estuary by the occurrence of several duck species (especially Teal, Mallard and Shelduck) in area 5, feeding along the low water line while dabbling in the soft muds. Studies in the Biesbosch and the Oude Maas indicated that the presence of tidal flats was the determining factor in the presence of duck species like the Teal. These formerly freshwater tidal areas from the Rhine-Meuse delta in the southwestern part of The Netherlands, with at that time often more than 10,000 wintering Teals, were cut off from the tide in 1970, resulting in the permanent disappearance of most of the Teals within a few weeks (Lebret 1979; Strucker et al. 1994). Loss of suitable foraging habitat was given as the main reason for this decrease.

Marshes are especially important for waterbirds as resting, refuge and roosting areas, but also as feeding areas for grazing waterbirds (e.g. Evans and Dugan 1984; Aerts et al. 1996). In the Schelde estuary the small available marsh area in the polyhaline zone (areas 1–2) was reflected in low numbers of herbivores (Figure 6). The mesohaline area 3, with its large marsh surface, appeared a suitable feeding area for herbivorous waterbird species. On the large marsh of Saeftinghe, with a vegetation dominated by *Phragmites australis*, *Elymus athericus* and *Scirpus maritimus*, very high numbers of herbivores such as Wigeon and Greylag Goose were observed, giving this area a characteristic and distinctive waterbird community. The relatively high vegetation with willow scrubs and reed beds on the marches of the freshwater

tidal area of the Schelde estuary appeared not suitable for feeding waterbirds, but mainly functioned as resting and refuge areas. The man-made constructions in the Zeeschelde, such as dikes with rubble, were especially important as a feeding area for Gadwalls, foraging along the low water line on green algae, seeds and detritus (pers. observ.). However, Gadwalls were completely absent on hard substrates in the most upstream, narrow areas of the Zeeschelde where disturbance by e.g. shipping was high. Other waterbird species (e.g. Teal, Mallard and Lapwing) also occurred on hard substrates, but mainly using them as resting places. Also external factors were responsible for the occurrence of certain waterbird species in the Schelde estuary, e.g., the spectacular increase of the Greylag Goose on the marsh of Saeftinghe (area 3) could be explained by a general increase of the NW-European population, a shift from traditional wintering grounds in Spain towards wintering grounds in NW-Europe, and the abandonment of hunting in the Saeftinghe area (Nillson et al. 1999).

International importance and conservation of the Schelde estuary

With a maximum of 188,000 individuals observed in midwinter the Schelde estuary is one of the most important NW-European estuaries for waterbirds as compared to other important estuaries in the region, such as the Oosterschelde (175,000 ind.) in The Netherlands (Meininger et al. 1997) and the Wash (180,000 ind.) and Morecambe Bay (140,000 ind.) in Great Britain (Davidson et al. 1991). The importance of the Schelde estuary for waterbirds is further evidenced by the 1% level criterion, which is exceeded for 21 waterbird species (Table 2).

Today, several parts of both the Westerschelde (areas 1–3) and the Zeeschelde (areas 4–6) are protected (Table 3), but this is mainly due to independent measures from The Netherlands and Belgium. Thus far, no mutual communication aiming at the protection of the unique estuarine salinity gradient has been organised. Independently, the complete intertidal area of the Zeeschelde has been proposed in 1996 as SCI by the Flemish government and recently the complete Westerschelde (excluding the shipping lanes) as Ramsar site, SPA and SCI by the Dutch government. As such, the intertidal zone along the whole Schelde estuary will have an international conservation status in the near future. However, the Schelde estuary also has different, often conflicting, functions that have an impact on the normal functioning of the estuarine ecosystem as a whole. As a result of human expansion, 150 km² of tidal area was lost due to land claim the last 200 years. The last decade several new harbour infrastructures were constructed along the estuary due to industrial expansion of the harbour of Antwerpen. This resulted in the direct loss of several parts of the previously protected (Ramsar, SPA) intertidal areas. Moreover, other human impacts, such as increased sedimentation and dredging activities and pollution, further degraded the estuarine ecosystem. Since the 1960s, riverine mud input, deriving from wastewater, surface erosion and precipitation, has increased, and together with the large amount of dredging and dumping and the modest attempts of regulation, has resulted in an

Table 3. List of the current status of the conservation measures taken in the Westerschelde and Zeeschelde respectively (intertidal areas only).

Conservation measure	Westerschelde (The Netherlands)	Zeeschelde (Belgium)
International (worldwide)		
Ramsar	Area 1: all* Area 2: all* Area 3: 3500 ha, all*	Area 4: 398 ha Area 5: – Area 6: –
International (EC)		
Wild Birds Directive: SPA sites 'Special Protection Area' (Council Directive 79/409/EEC)	Area 1: all* Area 2: all* Area 3: 3500 ha, all*	Area 4: ±450 ha Area 5: ±360 ha Area 6: ±33 ha
Habitat Directive (SCI proposals) 'Site of Community Importance' (Council Directive 92/43/EEC)	Area 1: all* Area 2: all* Area 3: 3500 ha, all*	Area 4: all** Area 5: all** Area 6: all**
National/Regional		
National Act on Nature Conservation (The Netherlands)	Area 1: all* Area 2: all*	Area 4: –*** Area 5: 40.5 ha***
State Nature reserves (Belgium)	Area 3: 3600 ha, all*	Area 6: –***
Nature reserves owned and/or managed by nature conservation organisations	Area 1: 966 ha Area 2: 163 ha Area 3: 3922 ha	Area 4: 312 ha Area 5: 93 ha Area 6: 24 ha

* The complete intertidal and shallow subtidal area of the Westerschelde has been proposed by the Dutch Government as Ramsar, SPA and SCI site, and to be put under the National Act on Nature Conservation.

** The complete intertidal area of the Zeeschelde (±1200 ha) has been proposed by the Flemisch Government as SCI site.

*** The complete intertidal area of the Zeeschelde (±1200 ha) will become a state nature reserve.

increased sedimentation in the intertidal areas. For example, the flood volume in the marsh of Saefthinghe has decreased from more than 60 million m³ to less than 10 million m³ in 1990 (Smit et al. 1997a). The extensive dredging in the shipping channel to Antwerpen, being 10–15 × 10⁶ m³ per year at present, has resulted in several changes in the morphology of the estuary (Vroon et al. 1997). Future plans include a further deepening of the estuary, which will increase the dredging activities by more than 50%. Especially the upper and freshwater tidal parts of the estuary are heavily polluted by domestic, industrial and agricultural waste loads (Wollast 1988; Van Damme et al. 1995; Van Eck et al. 1998) and the concentrations of PCBs, PAHs and cadmium are high (Van Zoest and Van Eck 1993; Zwolsman 1999).

Estuarine management

Despite several international conservation measures, protected areas in industrialized and densely populated areas, e.g. estuaries, are still under the risk of habitat degradation, fragmentation and loss (see also Prater 1981; Davidson 1991; Davidson

et al. 1991; Gray 1997). The compensation of habitat loss, as regulated by the international conservation measures, may result in the conservation of other areas with high ecological values. However, this can never replace a unique estuarine salinity gradient. The entire Schelde estuary should be conserved since changes in one area may have an impact on another. Furthermore, the mosaic of habitats must be protected to achieve a complete protection of biodiversity (Perrings et al. 1992; Gray 1997).

Estuaries often have a 'naturally' limited number of species or have species which are spatially restricted (Wolff 1973; Day et al. 1989). This is also confirmed in this study where only a few waterbird species dominate in each of the six areas along the salinity gradient. Thus, priorities for marine diversity conservation cannot be based simply on habitats with high diversity (Prendergast et al. 1993; Gray 1997). Besides biological community structure (species conservation, based on the species present, their abundances and biomasses and the diversity of the community) and quality and maintenance of habitats (habitat conservation), also the functioning of the estuarine ecosystem should be included in the management of estuaries. Indeed, natural ecosystems also perform fundamental life-support services (Daily et al. 1997). For estuaries these fundamental life-support services are very important (e.g. production of ecosystem goods (fish, shellfish, shrimp), cycling and movement of nutrients, purification of water, maintenance of biodiversity,...), but often these values are ignored by the short-term goals of economic developments. It should be one of the challenges of the scientific community to demonstrate to the human society and policy makers the value of these fundamental life-support services and the long-term benefits gained from them (Costanza et al. 1997).

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