A & W ECOLOGISCH ONDERZOEK

Exploitation of intertidal flats in the Oosterschelde by estuarine birds

A&W-report 1657

commissioned by

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Photograph Front
Oystercatchers feeding on the Roggenplaat, with the storm-surge barrier at the background. Photo: Leo Zwarts

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Contents

1 Introduction

1.1 Oosterschelde: from estuary to tidal bay

The Netherlands witnessed a unprecedented natural disaster on the 1st of February 1953. A combination of neglected maintenance of dikes, spring tide and gale force winds caused widespread flooding of the coastal area in the southwest of the Netherlands. A total of 1835 people lost their lives. This event marked the start of a series of coastal engineering works ("Delta Project") to prevent another disastrous flooding in the future.

These large-scale coastal engineering works changed the Oosterschelde in the mid-1980s from an estuary into a tidal bay (Nienhuis & Smaal 1994). The storm-surge barrier in the mouth of the Oosterschelde reduced the exchange of water with the North Sea by 28% (from 1230 km^3 to 880 km^3 during an average tide). As a consequence, the tidal range declined by 0.45 m (from 3.70 m to 3.25 m, on average). Two compartment dams isolated the rear ends of the estuary from the sea, resulting in a total surface area loss of 22% (from 452 km^2 to 351 km^2). However, there were more changes: the residence time of the water became more than twice as long, whereas the freshwater inflow, flow velocity and water turbidity all decreased. The immediate loss of salt marshes and intertidal flats was large: the total surface area of the tidal marshes declined from 17.2 km^2 to 4.5 km^2 (minus 74%) and the intertidal flats from 183 km^2 to 113 km^2 (minus 38%).

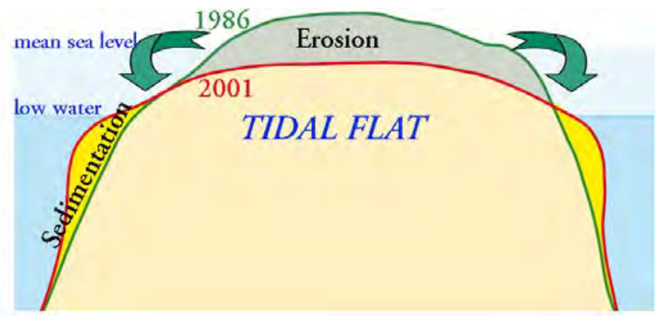
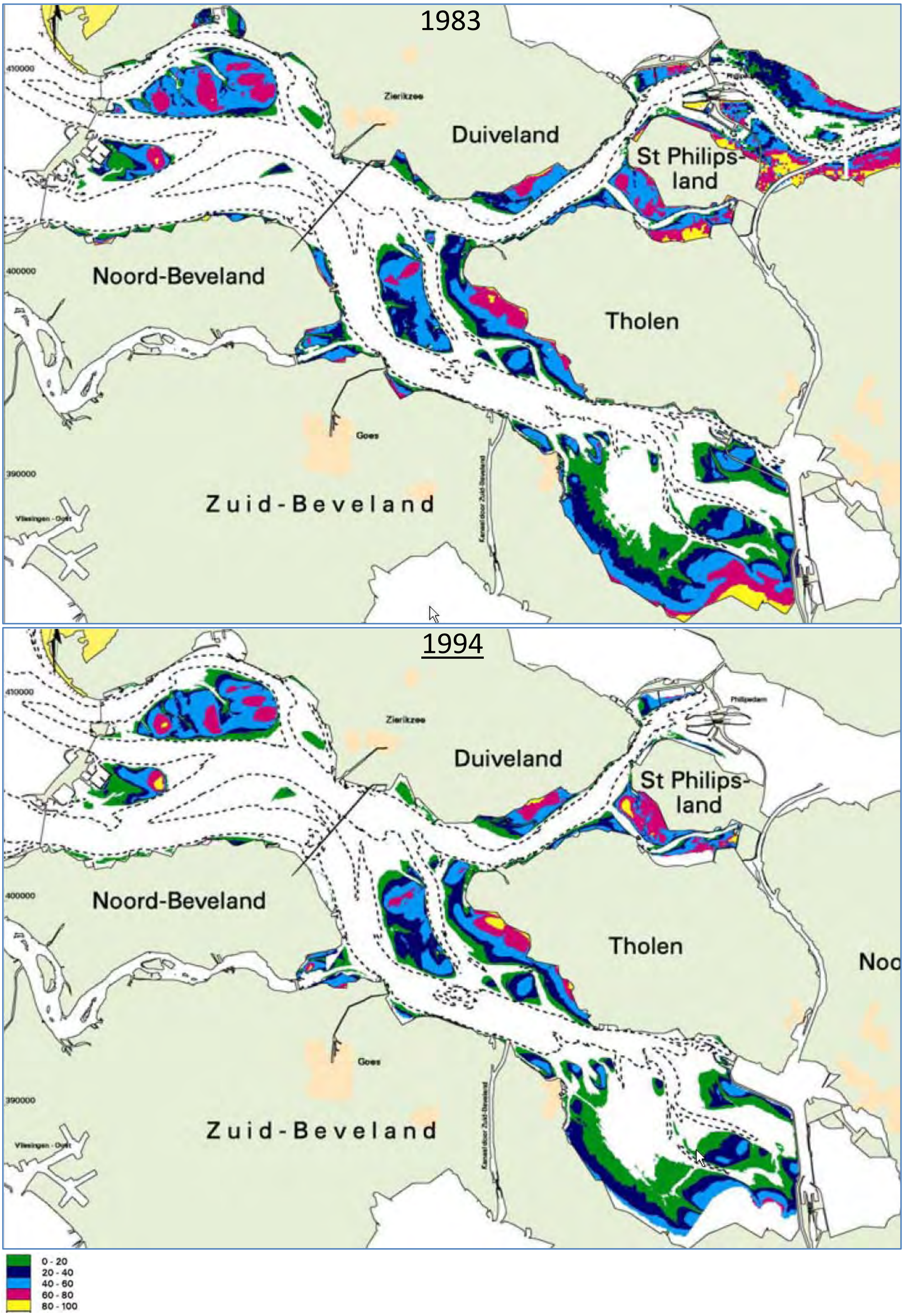


***Figure 1-1** – Ongoing change in the shape of tidal flats in the Oosterschelde. Due to erosion of the flats above the low water line, the tidal flats become lower, smaller and also more flat. From: van Zanten & Adriaanse (2008).*

After all these sudden changes, there was no dynamic equilibrium in the Oosterschelde between hydraulic conditions and geomorphology. The gullies were too large given the reduced tidal volume and lower flow velocity (Louters *et al.* 1998). The tidal currents were strong enough to allow the top layer of the tidal flats to erode, but not strong enough for the necessary sediment transportation from the gullies back to the tidal flats. As a consequence, there was erosion of the tidal flats after each heavy storm (Figure 1-1). In total, the intertidal flats lost 8% of their total surface (from 113 km^2 to 103 km^2) between 1986 and 2001. In the same period, the average height of the intertidal flats declined by 15 cm. Due to these processes the flats lost relief, by which the tidal areas became more flat. The prognosis is that this process of eroding tidal flats will continue (Geurts van Kessel 2004; van Maldegem & Pagee 2005; van Zanten & Adriaanse 2008; Figure 1-2).

1.2 Birds and carrying capacity of the Oosterschelde

The Oosterschelde was, and still is, one of the most important waterbird areas in NW Europe (Meininger *et al*. 1984 – 1998; Berrevoets *et al*. 1999 – 2005; Strucker *et al*. 2005 – 2011). Schekkerman *et al.* (1994) used monthly bird counts between 1978 and 1990 to analyse the impact of the sudden changes on the waterbirds by comparing the numbers and distribution of waterbirds before and after the construction


1983
Zierikzee
Duiveland
St Philips-
land
Noord-Beveland
Tholen
Goes
Zuid-Beveland
410000
400000
390000
1994
Zierikzee
Duiveland
St Philips-
land
Noord-Beveland
Tholen
Goes
Zuid-Beveland
410000
400000
390000
0 - 20
20 - 40
40 - 60
60 - 80
80 - 100

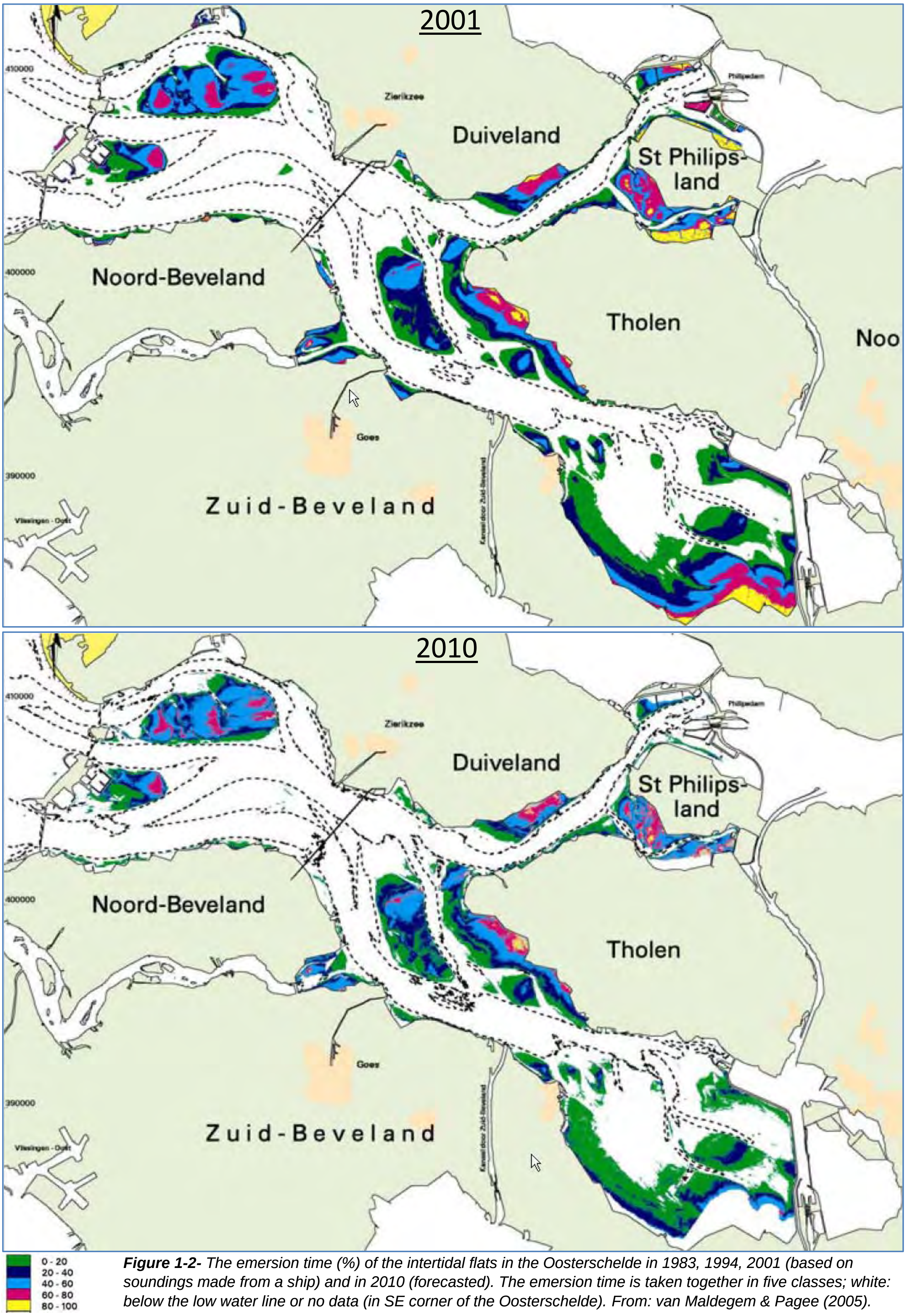


Figure 1-2- *The emersion time (%) of the intertidal flats in the Oosterschelde in 1983, 1994, 2001 (based on soundings made from a ship) and in 2010 (forecasted). The emersion time is taken together in five classes; white: below the low water line or no data (in SE corner of the Oosterschelde). From: van Maldegem & Pagee (2005).*

of the barrier and the secondary dams. Peak numbers during the pre-barrier period (1978/79 – 1982/83) were observed in January with on average 190,000 estuarine waders (mainly Oystercatcher and Dunlin), 57,000 ducks, geese and swans, 40,000 gulls and 3000 other waterbirds. During the post-barrier situation (1987/88 –1989/90), most species that forage exclusively on intertidal flats (such as the estuarine waders) showed a decline, whereas species feeding on open water and in the former estuarine areas remained stable or even showed an increase.

The changed conditions in the Oosterschelde may be considered as a huge and unique field experiment to test the generally accepted idea that the number of birds in the tidal zone is limited by their food supply. If this limitation would not apply, the loss of feeding areas (due to the construction of the barrier and the dams) would be compensated by an increase in the feeding density on the remaining feeding grounds. A comparison of bird counts performed in the pre-barrier (1978-1982) and post-barrier period (1987-1989) revealed that this was obviously not the case (Schekkerman *et al.* 1994). Lambeck (1991) could show with individually marked Oystercatchers that most of the displaced birds were not able to settle successfully in the remaining intertidal areas. This is another, more convincing, argument that the carrying capacity has been reached.

Three factors contribute to an ongoing change in the carrying capacity of the Oosterschelde (Schekkerman *et al.* 1994):

- *Decline in the total surface of the intertidal area.* After the large reduction in the total surface area of the intertidal zone in the mid-1980s, the tidal flats declined annually by 63 ha due to erosion (loss of 942 ha in 15 years; Hesselink *et al.* 2003).
- *Biomass of prey items per unit area*. The prey biomass in the intertidal zone fluctuates form year to year. Hence the carrying capacity fluctuates accordingly (Troost & Ysenbaert 2011), but since estuarine waders are long-lived, the regulation of the population size has to be considered as a long-term process. Schekkerman *et al.* (1994) assumed that the biomass per unit area would not change, but we know now that the Mussel *Mytilus edulis* and Cockle *Cerastoderma edule* have declined on the tidal flats of the Oosterschelde causing a severe reduction in the food supply for birds depending on these prey species (Escaravage *et al.* 2003, Meire & Meininger 1993, Meire *et al.* 1994a).
- *Exposure time of the tidal flats*. Due to the net transport of sediments from the tidal flats to the gullies, the average height of the flats declined by 15 cm between 1986 and 2001, on average 1 cm/year in 15 years (Hesselink *et al.* 2003). This implies that the average exposure time declined by half an hour, on average (see method section). This report focuses on the impact of the continuing loss of available feeding time on the carrying capacity for waders.

Figure 1-3- *Galgeplaat during receding water with Zierikzee at the background.*

1.3 Objectives and scope: impact of erosion of tidal flats on estuarine birds

The Oosterschelde is designated as a Natura-2000 site. Natura 2000 is the centrepiece of EU nature and biodiversity policy. It is a EU-wide network of nature protection areas established under the 1992 Habitats Directive and the 1979 Birds Directive. The aim of the network is to assure the long-term survival of Europe's most valuable and threatened species and habitats.

The Natura 2000 targets for the Oosterschelde comprise habitat types and 15 bird species that depend on intertidal mudflats (Lof 2003). The N2000 targets are focussed on maintaining the quality and quantity in the area, but it is taken into account the intertidal mudflats will decrease annually by 50 hectares due to the geomorphological changes in the area. The question is whether the N2000 objectives are realistic for the Oosterschelde in the long run.

What are the ecological consequences of the ongoing erosion of the tidal flats? The ultimate impact of the erosion of the tidal flats will be a reduction of the time available for feeding in estuarine bird species that crucially depend on tidal flats. Evidently, the available feeding time in the long run will be too short to cover the daily food requirements of these bird species. Hence, tidal flats will lose their function as feeding area before they have entirely disappeared. However, also in the short run, erosion might already have a negative impact. Firstly, the gradual reduction of the feeding time will enhance the risk of not meeting the daily food requirements. Secondly, the same number of birds present has to cope with a reduced feeding area and food supply, by which there will be more mutual competition. Hence, when carrying capacity is lowered, the numbers will decline either because birds have to move to alternative areas or, if they choose to stay, have a higher risk to die of starvation (Goss-Custard 1980).

Despite the ongoing erosion, most estuarine bird species do not (yet) show the expected decline in numbers since the construction of the barrier and the secondary dams. The evidence is otherwise: the monthly bird counts reveal that nearly all species have even increased since 1986 (Strucker *et al.* 2005, 2007, 2009, 2010). How to explain this unexpected result? To answer this question, it is necessary to collect detailed measurements on how the estuarine bird species exploit the intertidal zone. Such basic research has to focus on the following questions:

- Where do they feed within the tidal zone from the moment the higher tidal flats become accessible during receding tide until they become inaccessible by the incoming tide? How long do the estuarine bird species need to feed during the low water period?
- Which prey species are selected by the different bird species and how are the important prey species distributed over the tidal flats?
- What might have changed in the Oosterschelde to explain the population trends during the last 25 years? What might have changed in the way the birds exploit the tidal habitat?

When this information is available, it offers a sound base to indicate the future population trends of the estuarine bird species. However, it has to be taken into account, that the food supply available for waders shows seasonal variation (Zwarts *et al.* 1993). Generally spoken, the winter months are a harsh period, since preys are meagre and most live buried deeper in the sediment and/or are often less active. Moreover, feeding birds are often less successful at night. Hence, it is to be expected that birds have to feed longer in winter to compensate for the presumed lower intake rate during feeding.

There is another reason to expect seasonal variation in the duration of the feeding time. Daily energy requirements reach a high level during the pre-migration period (when the birds need more food to fatten up) and during winter (when they need more energy to keep their body temperature constant). Unless the birds are able to increase their rate of food intake, they have to extend their feeding period to attain the desired food intake. Thus, the winter and the migration periods may be considered as critical periods in their annual cycle. This report describes field work carried out in summer and in two critical periods (winter and migration time) to answer the above mentioned questions.

1.4 Outline of this report

Chapter 2 describes the study sites and the methods used to quantify emersion time, sediment composition, food supply, bird density and prey choice. Chapter 3 deals with the food supply in relation to exposure time and sediment composition and Chapter 4 with the prey selection by the estuarine bird species and to what degree the distribution of the birds over the feeding area may be explained by the spatial variation in their food supply. Chapter 5 is based on the bird counts and describes how the distribution of the bird species changes during the course of the emersion time. Chapters 6, 7 and 8 take all information from Chapters 3, 4 and 5 together to answer the questions posed in the previous section. Chapter 9 gives a summary and indicates the gaps in our knowledge.

Figure 1-5- *No or a few birds feed on the high tidal flats during low water, but its ornithological significance has not to be underestimated since many birds feed on these high flats during receding and incoming tides when the low tidal flats are covered by water.*

2 Methods

2.1 Study sites

The study was performed on 14 sites (Figure 2-1) in three different periods:

- summer (14 July – 28 August 2009)
- winter (21 November – 13 December 2010)
- spring (1 – 15 May 2011).

Five parameters were measured in the sites (being pegged out with sticks in order to be able to measure bird density):

- Exposure time (such as derived from altitude relative to mean sea level); details given in 2.2
- Sediment composition (clay content, median grain size); details given in 2.3
- Prey density (macrozoobenthos and epifauna); details given in 2.4
- Bird density (counts of feeding birds in plots); details given in 2.5
- Prey choice (prey species and prey size taken by different bird species); details given in 2.6.

An exhaustive description of all methods (in Dutch) is given in Zwarts (2009).

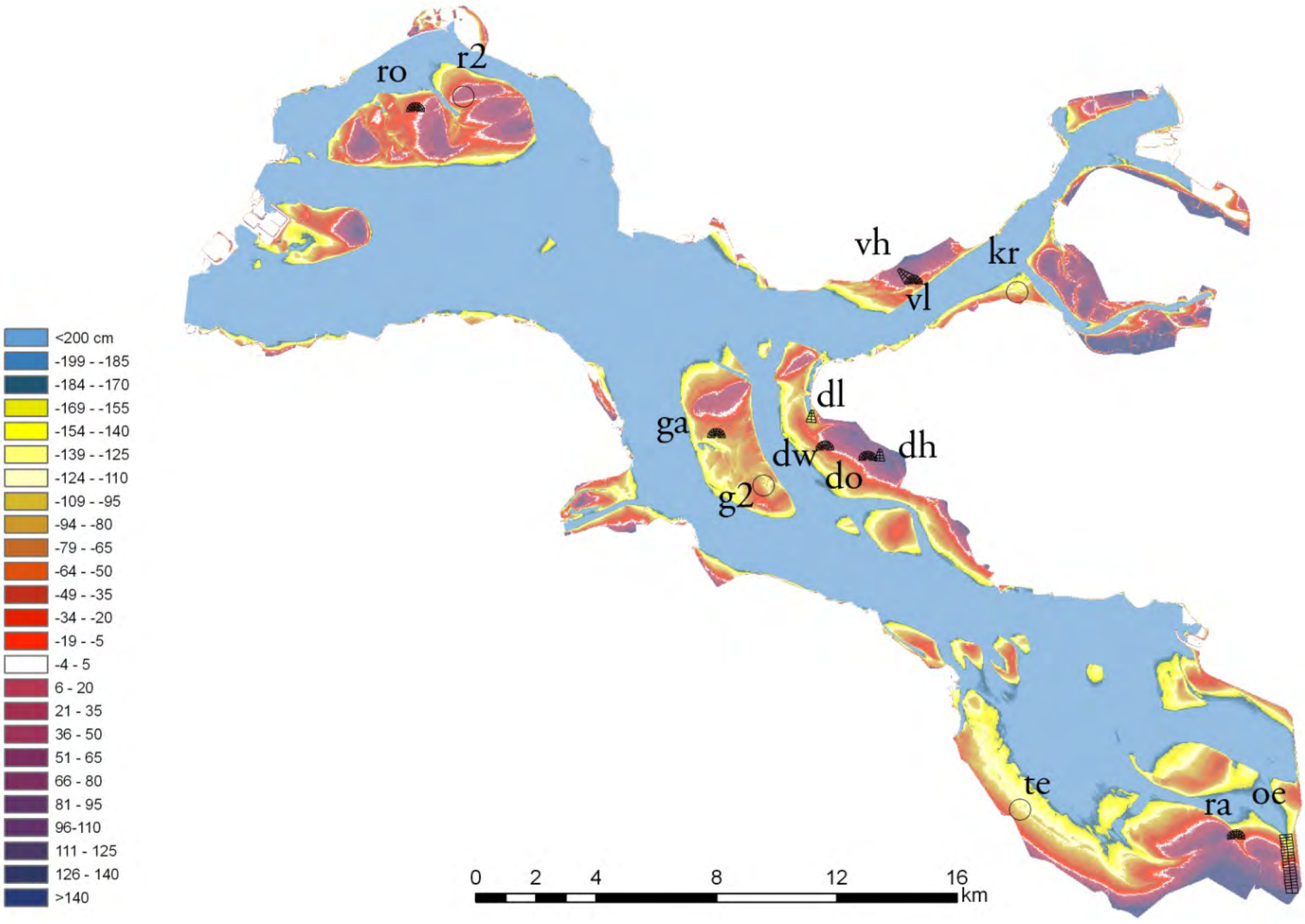


Fig 2-1- *The 14 study sites, shown on a relief map of the tidal flats in the Oosterschelde (altitude in cm relative to mean sea level; based on data from Rijkswaterstaat 2001). Four maps show Roggenplaat, Viane, Dortsman+Galgeplaat and Rattekaai+Oesterdam on a larger scale (see next page).*

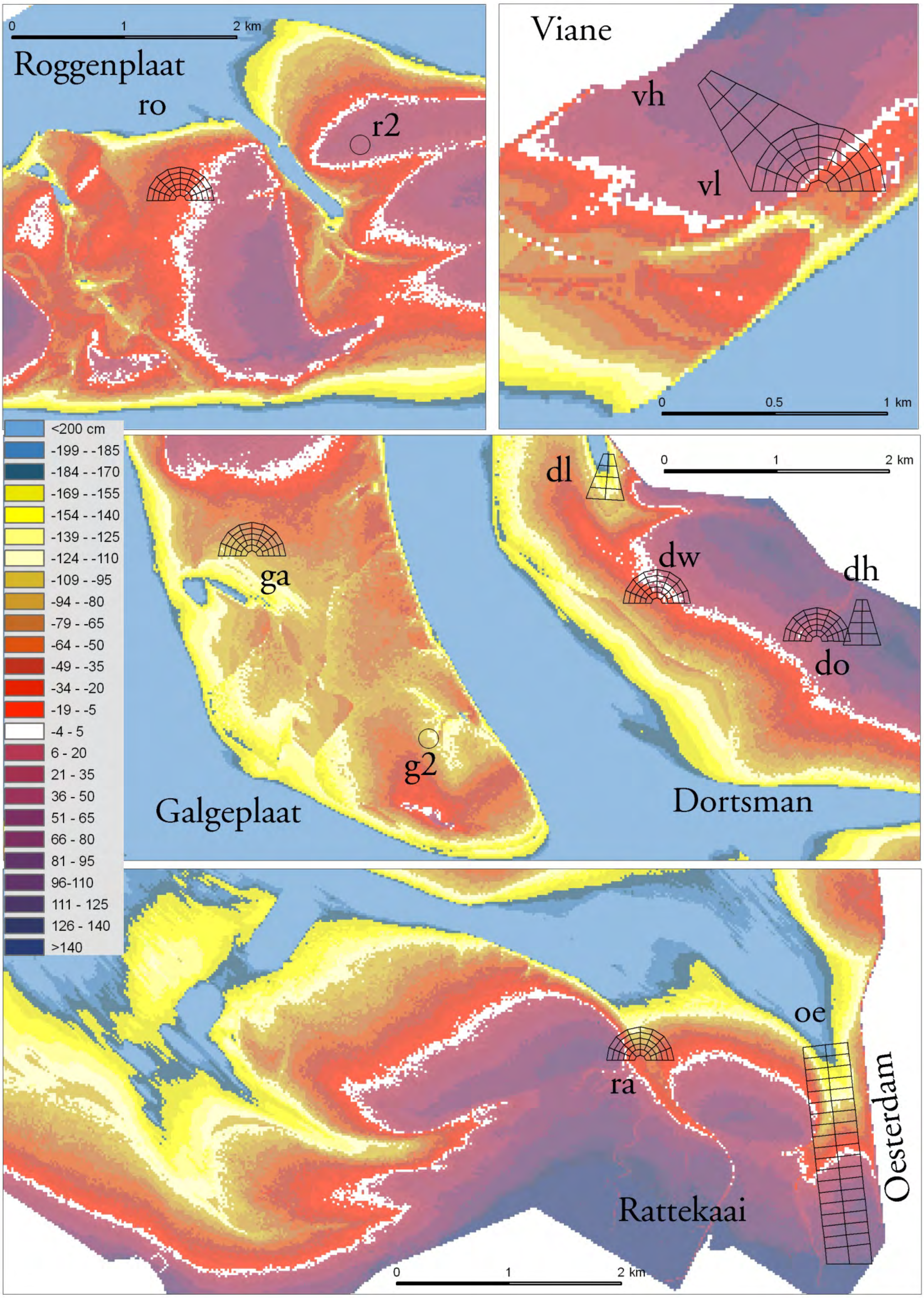

0
1
2 km
Roggenplaat
ro
r2
Viane
vh
vl
0
0.5
1 km
<200 cm
-199 - -185
-184 - -170
-169 - -155
-154 - -140
-139 - -125
-124 - -110
-109 - -95
-94 - -80
-79 - -65
-64 - -50
-49 - -35
-34 - -20
-19 - -5
-4 - 5
6 - 20
21 - 35
36 - 50
51 - 65
66 - 80
81 - 95
96-110
111 - 125
126 - 140
>140
ga
g2
Galgeplaat
0
1
2 km
dl
dw
dh
do
Dortsman
oe
ra
Rattekaai
Oesterdam
0
1
2 km

Figure 2-2- *The boat and the foldable hide used in summer 2009 to do the bird observation on the tidal flats of the Oosterschelde (top) were replaced by a hide on a sturdy boat in winter 2010 (middle). The observations in spring 2011 were done from a small boat (below); the hide was raised before the start of the observations. In all cases we had a beautiful sight over the study area and the wide surroundings.*

The study sites (and the abbreviations used for the various sites) are listed in Table 2-1. The study started in summer 2009 with four sites being intensively studied with regard to the number of parameters and the number of plots (Dortsman west and east, Galgeplaat and Rattekaai, see Table 2-1). At six additional sites data were collected in a single large plot on a selection of parameters (the altitude of the tidal flat, prey selection and the bird density at low water, see Table 2-1). In winter 2010 and spring 2011, the intensive study was continued at eight sites, which partly overlapped with those studied in the summer of 2009.

Site		number of plots	
abbr.	name	2009	2010/11
ro	Roggenplaat	1	36
r2	Roggenplaat-east	1	
kr	Krabbenkreek	1	
vl	Viane-low	1	36
vh	Viane-high		8
dw	Dortsman-west	36	36
do	Dortsman-east	36	
dl	Dortsman-low		8
dh	Dortsman-high		8
ga	Galgeplaat	36	36
g2	Galgeplaat-south	1	
te	Tolseinde	1	
ra	Rattekaai	36	
oe	Oesterdam		38

Table 2-1- *The 14 study sites (Figure 2-1) with the number of plots per site where data were collected in summer 2009 and in winter 2010 / spring 2011.*

The two colours indicate what kind of data were collected (yellow: all five types of data, blue: only altitude, bird density, prey selection).

Measurements available for

	yellow	blue
Altitude	■	■
Sediment	■	
Prey density	■	
Bird density	■	■
Prey selection	■	■

The birds were counted from a flat-bottomed boat on which a small tower with a hide was constructed (Figure 2-2) , but on six sites (kr, vh, dh, dl, te, oe) the observations were carried out from the high sea-wall. More details regarding the counting sites are given in section 2.4.

2.2 Altitude and exposure time

The altitude of the tidal flats has been measured previously by Rijkswaterstaat. The relief map (Figure 2-1) is based on soundings made from a ship, made available as a raster file with a grid size of 20 x 20 m. The altitude of the tidal flats varies between -200 cm and +140 cm relative to mean sea level. Above about + 140 cm the bare tidal flats turn into vegetated saltmarsh. Most of the tidal flats are below mean sea level (Figure 2-3). The average altitude of the study plots was derived from the same relief map and is shown separately for the sites used in 2009 (Figure 2-4) and 2011/11 (Figure 2-5).

The exposure time has been calculated from the altitude using a statistical relationship based on the continuous measurements of the water level in Yerseke (1-1-2008 – 28-7-2009) (Table 2-2).

Table 2-2- *The relationship between exposure time (y, %) and altitude (x, cm relative to mean sea level), based on the continuous measurements of the water level in Yerseke (1-1-2008 t/m 28-7-2009).A fifth degree polynomial was fitted for the range between 230 cm below and 298 cm above mean sea level. For the tidal range between -100 cm and + 100 cm a second degree polynomial suffices.*

-230 cm t/m +298 cm

$y = -3E\text{-}11x^5 + 5E\text{-}09x^4 + 9E\text{-}07x^3 - 0.0004x^2 + 0.2573x + 54.353$

$R^2 = 0.9992$

-100 cm t/m +100 cm

$y = -0.0003x^2 + 0.2522x + 54.191$

$R^2 = 0.9999$

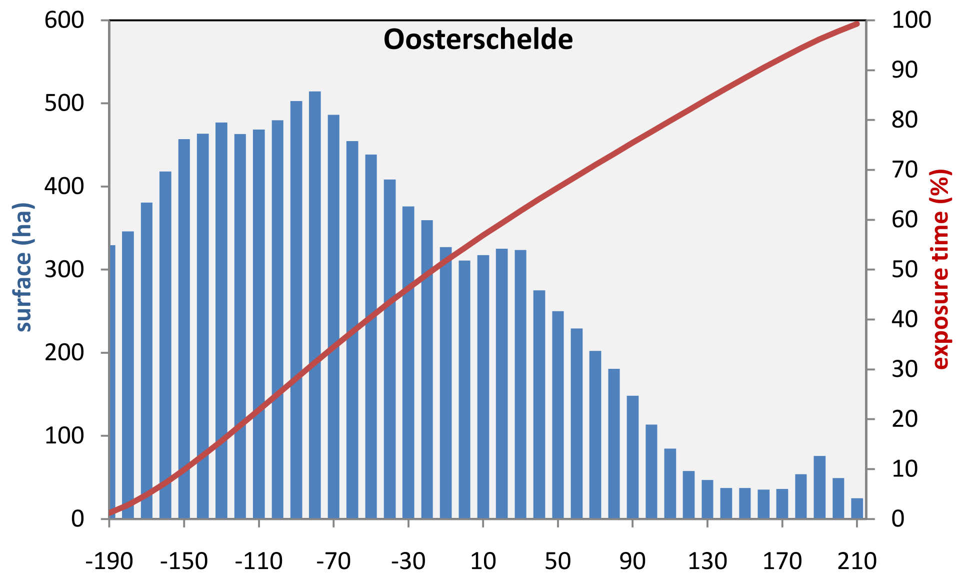


Figure 2-3 *- The surface area of the tidal flats in the Oosterschelde (blue bars, left axis, in hectares) and the exposure time (red line, right axis, in percentage, derived from table 2-2) as a function of altitude (cm relative to mean sea level) in the Oosterschelde.*

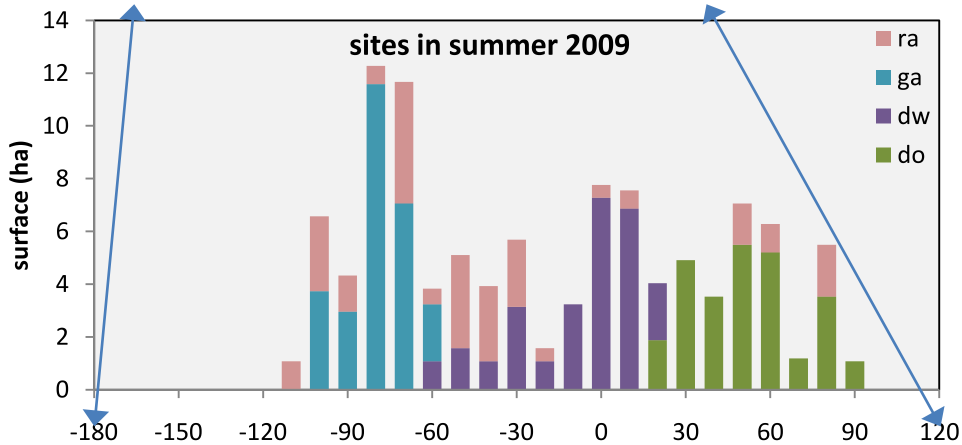


Figure 2-4- *The surface area (ha) of the tidal flats as a function of the altitude (cm relative to mean sea level) for the four study sites in 2009.*

Two arrows are added to show that the scale along the x-axis differs from Figure 2-3.

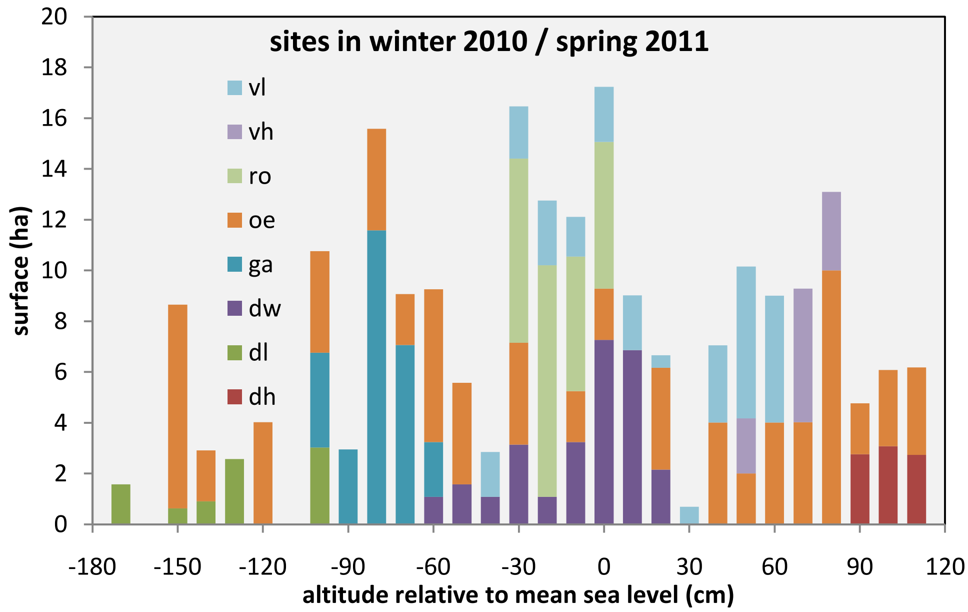


Figure 2-5- *The surface area (ha) of the tidal flats as a function of the altitude (cm relative to mean sea level) for the eight study sites in 2010/2011.*

cm\site	dh	dl	dw	gp	oe	rp	vh	vl	do	ra	total
-210		1									1
-170		1									1
-150		1			4						5
-140		1			1						2
-130		2									2
-120					2						2
-110										1	1
-100		2		5	2					3	12
-90				5						2	7
-80				16	2					1	19
-70				8	1					8	17
-60			1	2	3					2	7
-50			2		2					5	9
-40			2					3		3	8
-30			4		2	8		3		3	20
-20			2			13		3		1	19
-10			5		1	8		2			16
0			10		1	7		3		1	22
10			8					3		1	12
20			2		2			1	3		8
30								1	7		8
40					2			5	5		12
50					1		1	7	7	2	18
60					2			5	7	1	15
70					2		4		1		7
80					5		3		4	2	14
90	3				1				1		5
100	3				1						4
110	2										3
total	8	8	36	36	38	36	8	36	36	36	278

Table 2-3- *The number of the plots per study areas and altitude (dm). Same data as Figure 2-4 and 2-5.*

Emersion time

Table 2-3 gives the number of plots per study sites and per altitude. Since the altitude of a tidal flat has no direct biological meaning as such, we will use in this report the exposure time instead as a relevant biological determinant, using the equation given in Table 2-2 to convert altitude into emersion time. The

dry %	n	mean, cm	min, cm	max, cm
10	10	-154.5	-207	-129
20	10	-109.8	-128	-100
30	42	-82.2	-99	-68
40	30	-53.3	-69	-35
50	72	-16.0	-34	2
60	45	22.2	3	44
70	56	63.7	45	89
80	10	101.9	90	114

Table 2-4- *The number of plots (n) broken down by emersion time. Categories were assigned to the midpoint of a range (for example 20% represents 15% - 25%). In addition the mean altitude per class (cm) and corresponding range of altitudes (min, cm and max, cm) is given.*

emersion times are grouped into eight classes (Table 2-4). Most data are available for plots that are exposed for 30 to 70% of the time (30 to 72 plots), while ten plots are available for each of the two lowest and highest classes.

The 38 plots along the Oesterdam were situated between the high and low water line and here all emersion classes were represented within one study site (Table 2-5). Also the plots on the Rattekaai were well chosen along the tidal gradient. To achieve a similar design elsewhere in the Oosterschelde, plots had to be staked out at additional sites. For instance, it was necessary to peg out four sites on the Dortsman (do, dh, dl and dw) to represent all available emersion classes. The emersion time in the plots varied less in the other study sites. The emersion time of the plots on the Galgeplaat was 20-40% and those on the Roggenplaat 50-60%.

% dry	do	dh	dl	dw	ga	oe	ra	ro	vh	vl	∑
10			5			5					10
20			3		3	3	1				10
30					28	4	10				42
40				5	5	5	14			3	32
50				19		4	5	35		9	72
60	15			12		4	1	1		12	45
70	21	1				10	5		8	12	57
80		7				3					10
∑	36	8	8	36	36	38	36	36	8	3	278

Table 2-5- *The number of plots in the different study sites broken down by exposure time. Same data as Table 2-3.*

Variation in altitude within the plot

The altitude (and thus also exposure time) of the different plots is based on the digital relief map with a resolution of 20 x 20 m. The grid cell values were used to calculate the average altitude per plot, but also the minimal and maximal altitude within a plot and the standard deviation. For most plots the standard deviation was 3 to 10 cm, but it could be higher in the larger plots (*e.g*. Dortsman-low) (Table 2-6). The variation in altitude within the plots was also high in two sites (Oesterdam, Rattekaai) where plots were situated along a tidal creek (see Figure 2-1).

Table 2-6- *The standard deviation (sd) of the altitude measurements (within a plot, averaged per study site; cm). The altitude measurements were taken from the relief map (grid size 20 x 20 m).*

site	do	dh	dl	dw	ga	oe	ra	ro	vh	vl	all
sd	8.43	8.53	20.5	7.19	4.7	19.3	14.4	4.63	5.68	9.15	9.89

2.3 Sediment composition

Sediment samples (upper 15 cm) were taken in all 144 plots of the study sites Galgeplaat, Dortsman-west, Dortsman-east and Rattekaai in August 2009. BLLG (Oosterbeek) determined the clay content (fraction < 2 µm).

Eight plots were sampled from each of the study sites Galgeplaat, Roggenplaat, Viane-low and Dortman-west and in nine plots from study site Oesterdam in April 2011. BLLG (Oosterbeek) determined in these 41 samples the clay content and the particle size distribution of the sand grains.

Figure 2-6- *The animals were separated from the sediment using a 1-mm sieve. They were stored in 1-l bottles with sea water and, after transport, kept at about 5℃.. The animals were sorted out and measured within 24 hours.*

2.4 Macrozoobenthos and epifauna

Macrozoobenthos were sampled using a core sampler (50 cm long; 11.7 cm wide; surface area 90 cm^2). The upper 20-25 cm of the core was washed through a sieve (mesh width 1 mm). The lower part of the core was often not sieved, but broken by hand and inspected (usually when there was much peat in the sample or dead shell material) to collect large animals, such as *Mya arenaria* and *Arenicola marina.*

Four samples were taken per plot and pooled. Samples were taken from all plots on sites Dortsman-west, Dortsman-east, Galgeplaat en Rattekaai on 10-13 August 2009 and in half of the plots on the sites Dortsman-west, Galgeplaat, Oesterdam and Viane-low on 18-21 April 2011. Together, we analysed 548 samples in 137 plots in 2009 and 364 samples in 91 plots in 2001.

The size of the animals was determined by measuring the maximal length (mm) in bivalves and the maximal length (cm) of worms (if possible when creeping along a ruler in sea water). The length of tail and body was separately measured in *Arenicola marina*. The length of broken worms was reconstructed or estimated. To prevent double counts, only fragments including a head were counted. No species was so common that it was necessary to extrapolate the number based on a counted subsample; thus all animals were actually counted. Prey being too small to be a potential prey for estuarine birds (*Bathyporeia* sp. and different small annelids, such as *Polydora* sp, *Spio* sp and *Tharyx* sp*)* were ignored.

The body condition of macrozoobenthos varies during the course of the year, but the differences between years and between sites within western Europe are relatively small (Zwarts 1988, 1991; Zwarts & Wanink 1993). Hence we used existing regression equations (Table 2-7) to convert the size of all animals into biomass (as-free dry weight).

Table 2-7- *Relationship between length (L, mm, but cm in worms) and ash-free dry weight (mg AFDW). The function is given as AFDW = exp(ln((b).L + a). All formulae are based on data collected in the Dutch Wadden Sea. We used for Mytilus, Cerastorderma, Macoma and Mya the formulae given for August.*

name	a	b	source
Arenicola marina	1.198	2.334	Zwarts & Wanink 1993
Heteromastus filiformis	-2.50	2.300	Note 1
Nephtys hombergi	-0.18	2.017	Zwarts & Wanink 1993
Nereis diversicolor	-0.90	2.208	Zwarts & Wanink 1993
Nereis virens	-0.90	2.208	Note 2
Scoloplos armiger	-2.000	2.300	Note 1
Lanice conchilega	-2.500	2.300	Note 1
Crangon crangon	-6.591	2.946	Zwarts 1988
Carcinus maenas	-2.925	2.871	Zwarts & Wanink 1993
Hydrobia ulvae	-5.497	3.500	Zwarts unpubl.
Mytilus edulis	-4.596	2.840	Zwarts 1991a
Cerastorderma edule	-4.429	2.974	Zwarts 1991a
Macoma balthica	-4.759	3.063	Zwarts 1991a
Scrobicularia plana	-5.044	2.900	Zwarts 1991a
Mya arenaria	-5.793	3.153	Zwarts 1991a

Note 1: Separate regressions were not available for the small worm species. A combined regression equation was used for for *Scoloplos* and for *Heteromastus* and *Lanice*; the latter equation was also used for *Capitella capitata* and for *Anaitides* (=*Phyllodoce*) *maculata*.
Note 2: No regression equation was available for *Nereis virens*; the relation for similar shaped *Nereis diversicolor* was used instead.

Epifauna

Shore crabs (*Carcinus maenas*) and shrimps (*C. crangon*) were collected during the sampling of the macobenthos, according to the standard method described above. Since shorecrabs and shrimps were a major prey for most estuarine bird species in summer, it was decided to do additional estimates of their density. Additional samples were taken on the Dortsman on 20 plots along a transect of 1680 m between the high water line (x = 59877, y= 398733 in the Dutch coordinate system) and the low water line (x = 58479, y = 397808), at an in-between distance of 90 m. The samples, two per plot, were taken on 1 August 2009 and on 7 December 2010 during low tide. We used a round sampler with a diameter of 33 cm (surface area 1/11.69 m^2). The substrate from the upper 2-3 cm was collected and sieved through a 1 mm sieve. We measured the maximal width of the carapax in shorecrabs and the length (from head to tail, without antenna) in shrimps.

2.5 Bird density

Counts

In order to measure the bird density, 278 plots at 10 sites were pegged out with sticks in a grid that was specifically designed for this purpose. The observations were done either from the high seawall (usually from a car or a hide) or from a hide placed on a boat (Figure 2-2). To exclude the impact of disturbance, birds were not counted within a radius of 50 m around the boat and within 200 m from the sea dike. The maximal observation distance amounted to 580 m from the sea dike and 300 m from the boat. The feeding birds in the plots were counted every 15 minutes over the entire low water period, or every 30 minutes if there were too many to finish the count in time. We used binoculars (10 x 40) and zoom-telescopes (15-60 x 70) on sturdy tripods.

As a consequence of the design of the observation-grid, the plots varied in size. The 216 plots counted from the boat measured between 0.5 and 1.1 ha. The 62 plots counted from the sea dike were larger, ranging from 0.6 to 3.4 ha. From earlier experience, we knew that a grid of rectangular plots seems to be lozenges at larger distances, due to perspective distortion. By designing the plots trapezially, birds could be counted easier and were more reliably assigned to the correct plot (Figures 2-1 and 2-8). Tonkin canes (120 cm long; 3 cm thick) were pegged out at in-between distances of 8 m by which always one cane was visible as marker in the view of the binocular or telescope. Hence it was always easy to count the birds in the plots precisely.

All birds were counted from a fixed point of observation, but to count the 38 plots along the Oesterdam it was necessary to replace the car up to nine times, 200 m each, to count the next four plots. Only when the lower plots were covered by water, it was possible to do a full count within 15 minutes, but as soon as also the lower sites were uncovered, a count took up to 30 minutes.

Together, 28029 bird counts were carried out (Table 2-8); counts started when the first bird appeared in a study site during receding water and the count series was finished when the last bird left the study site due to incoming water. The emersion time varied for the different sites between 5 and 9 hours; That explains why fewer counts are available at the beginning of the ebb (5 hours before low water) and at the end of the flood (5 hours after low water). The bird counts were performed during 46 tidal cycles (Table 2-8).

All counts were made during daylight. In addition we counted the birds in the plots up to a distance of 75 m from the boat during two nocturnal low water periods using an infra-red binocular and a light intensifier.

Disturbance

Peregrine Falcons were frequently seen. Twice a wader (an Oystercatcher and a Bar-tailed Godwit) was captured in one of our own plots while doing a count. The wader was eaten on the spot during 30-40 minutes, during which no estuarine birds fed in the direct surrounding (50-100 m). Chasing Peregrines cause a lot of disturbance, by which the distribution of the birds changes continuously. Consequently, the numbers counted in the plots vary from count to count. This applies to all study areas.

It was noted whether the counted number of birds was affected by disturbance. Disturbance by people did not occur on the Roggenplaat, Galgeplaat, Rattekaai and Oesterdam, but was frequent at all other sites. These disturbed sites have all in common that they are all easily accessible for humans from the shore. People are not allowed to be present on nearly all tidal flats in the Oosterschelde, but most are not aware of this ban or know that there is hardly any control.

Figure 2-7- *Running dogs and feeding waders do not go together. The maximum observed was 21 dogs in one time.*

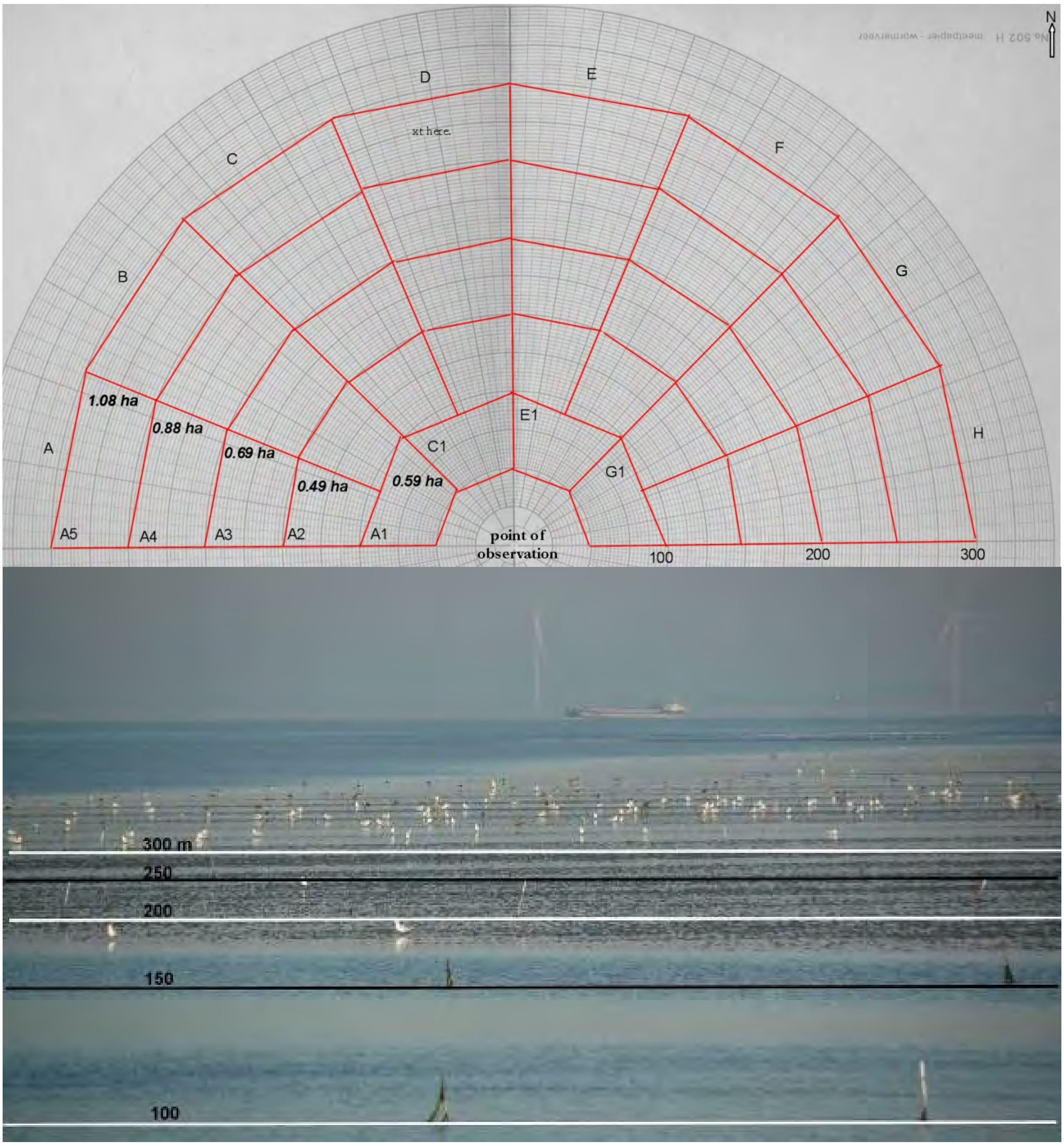


Figure 2-8- *The counts in those study sites that were visited by boat were always done from the same point of observation. To mark the plots, Tonkin canes were pegged out at in-between distances of 8 m; no sticks were needed along the radiate lines. The corners were marked with three sticks. The photo displays the view from the hide at a position of 4 meter above the surface. The white lines are drawn at 100, 200 and 300 m from the hide and the black lines at intermediate distances of 150 and 250 m indicating the boundaries of the plots. Note the apparent narrow plot situated at a distance of 250 – 300 m from the hide. This is the reason why we had no plots designed at larger distances, apart from the (much larger) sites being counted from the sea wall. In that case, the higher position (10 m above the surface) allowed us to count birds and assign them to the correct plot up to a distance of 580 m.*

Most people present on the tidal flats made a walk, often with a horse or one or more dogs, or stayed for hours to search for lugworms or check fishing lines (or make new ones). The birds chased from the plots did usually not return before the incoming water. All counting series on the Dortsman (west and east) were disturbed during the summer. The disturbance in winter and spring was less, but (to our surprise) not absent.

The data shown in this report are based on all counts including these disturbed ones.

Table 2-8- *Number of bird counts carried out in the plots during the course of the tidal cycle. The data are given separately per season and emersion time (% dry). Note that in summer 2009 no plots with an emersion time of 10% and 80% were available.*

period	% dry	Time relative to low water water (hour)										
		-5	-4	-3	-2	-1	0	1	2	3	4	5	Total
summer 2009	20		4	12	39	33	21	30	42	12	8		201
	30		40	120	372	316	202	288	400	120	80		1938
	40		61	203	253	243	176	238	258	208	137	5	1782
	50		38	193	212	212	159	212	212	212	135	19	1604
	60		91	216	228	228	171	228	228	228	188	57	1863
	70		125	228	228	228	171	228	228	228	208	63	1935
	Total		359	972	1332	1260	901	1224	1368	1008	756	144	9324
winter 2010	10	5	25	15	28	44	70	74	49	35	15		360
	20	3	15	9	24	48	66	66	48	21	9		309
	30	4	20	12	72	184	192	164	160	28	12		848
	40	5	28	62	77	108	115	113	105	90	38		741
	50	4	29	321	430	432	431	405	427	330	97		2906
	60	4	32	155	162	190	186	197	182	180	72		1360
	70	10	80	133	144	165	179	200	178	175	98	6	1368
	80	3	29	44	26	19	39	46	43	77	65	42	433
	Total	38	258	751	963	1190	1278	1265	1192	936	406	48	8325
spring 2011	10	10	40	25	40	40	20	40	45	50	40	40	390
	20	6	24	15	39	48	27	48	39	39	24	24	333
	30	8	32	16	156	240	148	240	132	112	32	32	1148
	40	10	58	84	106	108	83	108	104	114	85	40	900
	50	8	98	450	511	464	456	464	505	497	191	32	3676
	60	8	80	214	204	168	160	168	208	227	164	32	1633
	70	21	130	194	190	194	182	178	212	235	196	92	1824
	80	13	66	26	26	26	20	26	29	56	80	108	476
	Total	84	528	1024	1272	1288	1096	1272	1274	1330	812	400	10380

Figure 2-9- *Oystercatchers, Curlews and Bar-tailed Godwits following the water's edge, being chased away (photo next page) just before the birds would enter the plots. Only Black-headed Gulls remained to feed at a distance of 100 m.*

Date \ site	dh	dl	do	dw	ga	oe	ra	ro	vh	vl
14-7-2009							x			
16-7-2009					x					
27-7-2009							x			
28-7-2009			x							
29-7-2009				x						
31-7-2009					x					
4-8-2009					x					
5-8-2009				x						
6-8-2009			x							
7-8-2009							x			
21-11-2010									x	
22-11-2010	x	x								
23-11-2010					x					
24-11-2010									x	x
25-11-2010	x	x		x						
26-11-2010								x		
8-12-2010					x					
9-12-2010	x	x				x		x		
10-12-2010						x			x	x
11-12-2010						x				
2-5-2011	x					x				
3-5-2011	x	x			x					
4-5-2011									x	x
5-5-2011				x					x	
6-5-2011								x	x	
7-5-2011						x				
9-5-2011								x		
10-5-2011				x						
11-5-2011										x
12-5-2011					x					

Table 2-9- *Days during which a series of bird counts were carried out during the low water period in the ten study sites.*

Daily variation in emersion time

Bird numbers in the plots fluctuate in the course of the tidal cycle due to the variation in water level. In order to quantify this variation in bird density, we have grouped all counts in discrete hours relative to the time of low water.

The emersion times differ for neap and spring tide and deviate most for the lower and higher tidal flats. In addition, there is also a daily variation due to wind force and wind direction. There is, however, no need to take this variation into account for this report. All data were collected at the same stage of the lunar cycle (the first week after spring tide). Moreover, all our observation days were carried out during relatively quiet weather conditions, without strong winds from the NW (that give rise to water levels above the forecasted level based on the lunar cycle) or from the SE (resulting in lower water levels).

2.6 Prey choice

Prey selection by the different estuarine bird species was determined in individual birds feeding close to the hides. Notes were made of the prey species taken, the prey size and the plot where the bird was actually feeding. Prey size was converted into biomass using the equations given in Table 2-3. The prey selection was noted separately for (short-billed) male and (long-billed) female Curlew and Bar-tailed Godwit. We switched from one individual bird to another as soon as some prey were taken.

Figure 2-10- *Oystercatchers feeding on Cockles are easy to distinguish, even at a large distance, from birds feeding on burrowing bivalves and worms. Cockle-feeding Oystercatchers search by sight, at least by day, for prey with slightly open valves. While searching they make shallow pecks at the surface and never probe the bill far into the substrate. Characteristic is the way in which the birds often turn around after they have stabbed their bill between the valves. Elsewhere in Europe, Cockles may also be opened by hammering a hole in the valve, but this has never been observed in the Oosterschelde.*

Reliable observations on prey selection are determined - apart from the skills and experience of the observers - by the distance, the focal bird species and the type of prey. For instance, for Oystercatchers up to a distance of 400 m, feeding on cockles can still be reliably quantified (Figure 2-10). When the same species is foraging on worms at a similar distance, quantification of prey selection is impossible. The observations must be carried out within about 100 m to distinguish *Nereis diversicolor.* from (small)

Table 2-10- *Total number of prey observed to be taken by different bird species per study site in summer 2009, winter 2010 and spring 1011.*

bird species\site	do	dh	dl	dw	g2	ga	kr	oe	r2	ra	ro	rw	to	vh	vl	sum
oystercatcher	7			62	48	39	42		6	102		89	35		112	542
curlew	46			291	208	328	125		157	192		156	253		187	1943
whimbrel	10			204	10		9					5			26	264
bar-tailed godwit				16		31			13	1		51				112
redshank					7		7					15			39	68
greenshank							8					24				32
knot												13				13
grey plover							1		4			10				15
black-headed gull	100			192	55	28	75		53	29		34	45		66	677
herring gull				2	10	3	77		5	47		3	12		2	161
common gull				19	10					1		2			6	38
spoonbill							62									62
little egret							12									12
SUMMER 2009	**163**			**786**	**348**	**429**	**418**		**238**	**372**		**402**	**345**		**438**	**3939**
oystercatcher		72		89		23					39				134	357
curlew		3	7	81		37					36				12	176
bar-tailed godwit						7					13					20
redshank		1				9										10
dunlin				5												5
knot															5	5
grey plover				9		12					50					71
herring gull		1														1
brent goose		34														34
WINTER 2010		**111**	**7**	**184**		**88**					**138**				**151**	**679**
oystercatcher		1	4											9	23	37
curlew		1		9		17		2			56			6	12	103
whimbrel			6													6
bar-tailed godwit															9	9
redshank				7												7
greenshank			1	175												176
dunlin														1		1
knot											8					8
sanderling											1					1
grey plover				19							24			7		50
black-headed gull			2	70		50										122
herring gull			2	5		3		6							19	35
spoonbill		1														1
SPRING 2011		**3**	**15**	**285**		**70**		**8**			**89**			**23**	**63**	**556**

Arenicola marina. Smaller bird species in general need to be more nearby. Fortunately, it is not necessary to observe the prey in the bill of a bird in order to know the species taken. Behavioural cues can also additionally be used to quantify the prey selection. For instance, to distinguish whether a bird fed on *Crangon* or small *Carcinus*, it was sufficient to pay attention to a few simple cues: (1) the way of searching - birds feeding on *Crangon* are more mobile than if they feed on *Carcinus*, (2) handling time - relatively short in *Carcinus* being picked up compared to *Crangon* that struggles upon capture (3) whether the prey was systematically taken from water (*Crangon*) or from water as well as from dry substrate (*Carcinus*). Using similar cues, several prey species could be distinguished. It is not possible, however, to quantify the prey selection. For some species foraging on tiny worms, notably Dunlin and sometimes Bar-tailed Godwit and Grey Plover, the quantification of the prey selection can be problematic, especially if prey were eaten piecemeal. Prey eaten beneath the surface may be difficult too (Oystercatcher feeding on (small) *Scrobicularia* or *Macoma*).

Much time was spent to study the prey selection in summer 2010. In 13 bird species we could note 3939 times the prey species taken. Fewer observations are available for the winter and summer period (Table 2-10). Besides the prey systematically registered (Table 2-10), we saw birds eating prey while doing the counts. That is why we know that, for instance, all Oystercatchers on the Roggenplaat preyed on *Cerastoderma* in spring, although we did not register the prey selection of any Oystercatcher.

Figure 2-11- *The different estuarine bird species could be observed very well from the observation hide, also a shy species such as the Curlew (foreground left). The prey selection was determined separately for male and female Bar-tailed Godwit (right and left on the foreground). Oystercatchers and Black-headed Gulls are visible on the background.*

3 Results: food supply

3.1 Macrozoobenthos

The results of the sampling programmes in summer 2009 and spring 2011, although partly referring to different sites, roughly draw the same picture: the same species are common and deliver a dominant contribution to the total biomass (Table 3-1). The differences are even smaller when a comparison is made between the two sites being sampled twice (Galgeplaat and Dortsman-west; data not shown). The largest difference was that nearly half of the *Cerastoderma* on the Galgeplaat and Dortsman had disappeared between 2009 and 2011, but since they had grown some mm, the decline in total biomass was small. In the further analysis the data for both sampling programmes will be combined.

year	August 2009			April 2011		
species	n/m^2	g/m^2	mg	n/m^2	g/m^2	mg
Harmothoe impar	0.0			1.0	0.00	3.7
Nereis diversicolor	30.2	0.42	14.0	18.9	0.24	12.7
Hediste virens	0.2	0.02	117.4	0		
Phyllodoce maculata	2.4	0.01	2.7	5.3	0.02	3.7
Nephtys hombergii	8.1	0.27	33.5	7.1	0.19	26.5
Glycera convoluta				0.2	0.00	4.0
Scoloplos armiger	170.8	0.57	3.3	92.7	0.35	3.8
Heteromastus filiformis	51.9	0.52	9.9	50.5	0.51	10.0
Arenicola marina	107.9	4.76	44.1	45.2	3.15	69.5
Lanice conchilega	109.1	1.82	16.7	22.3	0.80	36.0
Littorina littoralis	0.2	0.01	50.8	31.2	0.48	15.4
Hydrobia ulvae	62.5	0.04	0.6	188.7	0.09	0.5
Crepidula fornicata	0.2	0.23	1118.6			
Acmaea virginea				0.2	0.00	5.1
Mytilus edulis	0.2	0.06	286.9	0.6	0.19	304.9
Cerastoderma edule	33.5	6.65	198.7	26.2	6.05	231.1
Venerupis pullastra				0.6	0.04	60.3
Macoma balthica	9.1	0.19	21.1	28.8	0.94	32.7
Scrobicularia plana	0.8	0.13	154.1	2.0	0.40	195.1
Ensis siliqua	0.2	0.04	200.0			
Mya arenaria	1.8	3.89	2132.1	2.4	5.36	2200.8
Gammarus locusta	0.0			0.2	0.00	0.6
Crangon crangon	3.9	0.03	8.5	3.0	0.01	4.5
Corophium volutator	0.0			2.6	0.00	0.7
Carcinus maenas	3.9	0.27	70.8	0.6	0.01	12.7
TOTAL	598.6	19.9		530.7	18.8	

***Table 3-1-** Average numerical density (n/m^2), biomass (g AFDW/m^2) and average individual weight (AFDW, mg) of macrobenthos found in the samples taken on four site in August 2009 (Galgeplaat, Dortsman-west & east, Rattekaai) and on five sites in April 2011 (Roggenplaat, Viane, Galgeplaat, Dortsman-west and Oesterdam).*

The average values are based on 548 and 364 samples, taken in 2009 and 2011, respectively. The total surface area investigated was 5.11 m^2 and 3.28 m^2, respectively.

Bathyporeia pelagica *(not counted in 2009 and also not included in the table) reached in 2011 an average density of 94.3 individuals per m^2 and, given an estimated average weight of 0.15 mg, an average biomass of 0.01 g/m^2.*

The average biomass amounted to 21.8 g/m^2. Dominant species were *Cerastoderma* (7.4 g/m^2) and *Mya* (4.4 g/m^2). Together with two worm species (4.9 g/m^2 for *Arenicola* and 1.3 g/m^2 for *Lanice*), these four species contributed 83% to the total biomass (Figure 3-1). For nine species the contribution to the total biomass was larger than 1%.

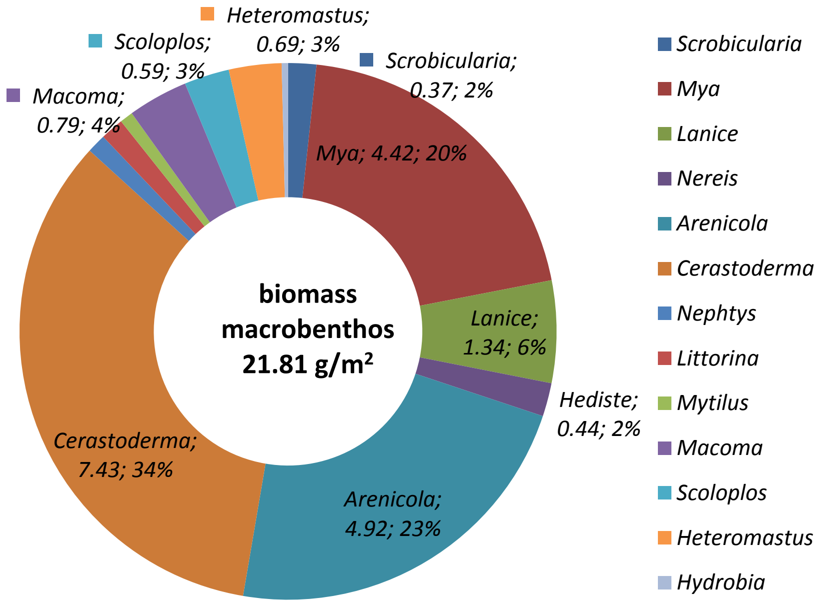


Figure 3-1- *The absolute (g/m^2) and relative (%) contribution to the average total biomass for the 13, in terms of biomass, most important species. Combined data from samples taken in August 2009 and April 2011; same data as Table 3-1.*

The total biomass differed per site (Figure 3-3). The Roggenplaat was rich, while the Rattekaai was poor in terms of biomass. Also the species composition differed: the biomass of *Mya* was high on Roggenplaat and Galgeplaat but low elsewhere. *Macoma* had a high biomass on the Roggenplaat and *Lanice* on the Galgeplaat but both species were hardly found at the other five sites. The relative contribution of *Arenicola* to the total biomass varied for the sites between 11 and 39%, but the variation was still larger in *Cerastoderma* (12 - 65%) and *Mya* (0 - 42%). In the next two sections we analyse to what degree these differences are due to differences in emersion time and sediment composition.

Figure 3-2*- A relatively poor sample of the lower shore, with many* Lanice *and a single* Nephtys *and* Arenicola*.*

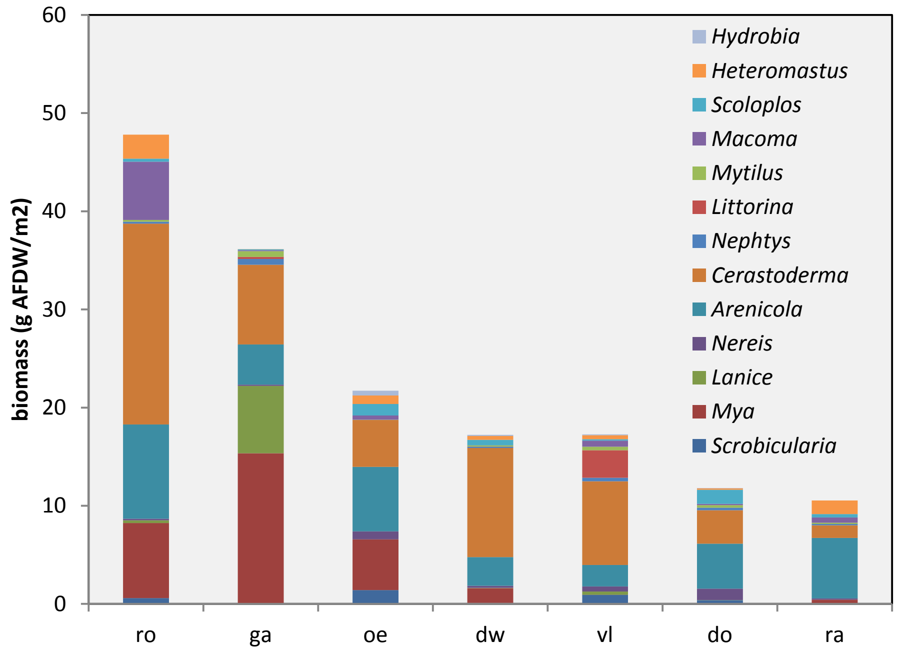


Figure 3-3- *The biomass of 13 major species on 7 different sites, sorted from rich (Roggenplaat) to poor (Rattekaai); data are combined for the samples taken in August 2009 and April 2011.*

Emersion time

A large part of the differences between sites may be related to the emersion time. When the data are broken down by emersion time (Figure 3-4), the sites with a long emersion time (such as Dortsman-east, Rattekaai) appear to be poor compared to sites that have short emersion times or are located at or below mean sea level (such as Roggenplaat and Galgeplaat). *Mya* was dominant on the low tidal flats. *Cerastoderma* and *Arenicola* occurred throughout but especially around mean sea level. *Macoma*, *Heteromastus* and *Hydrobia* were found on the higher flats.

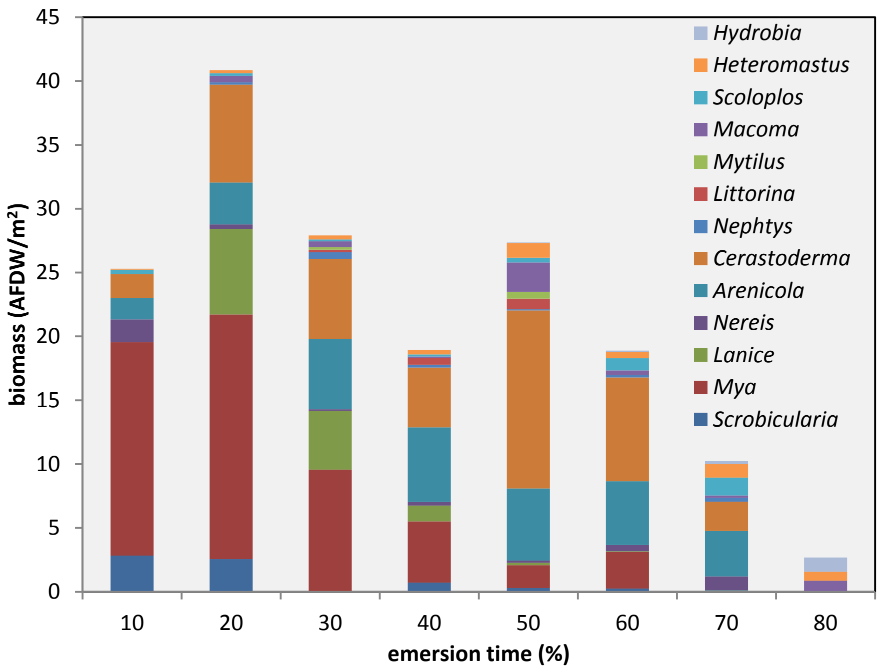


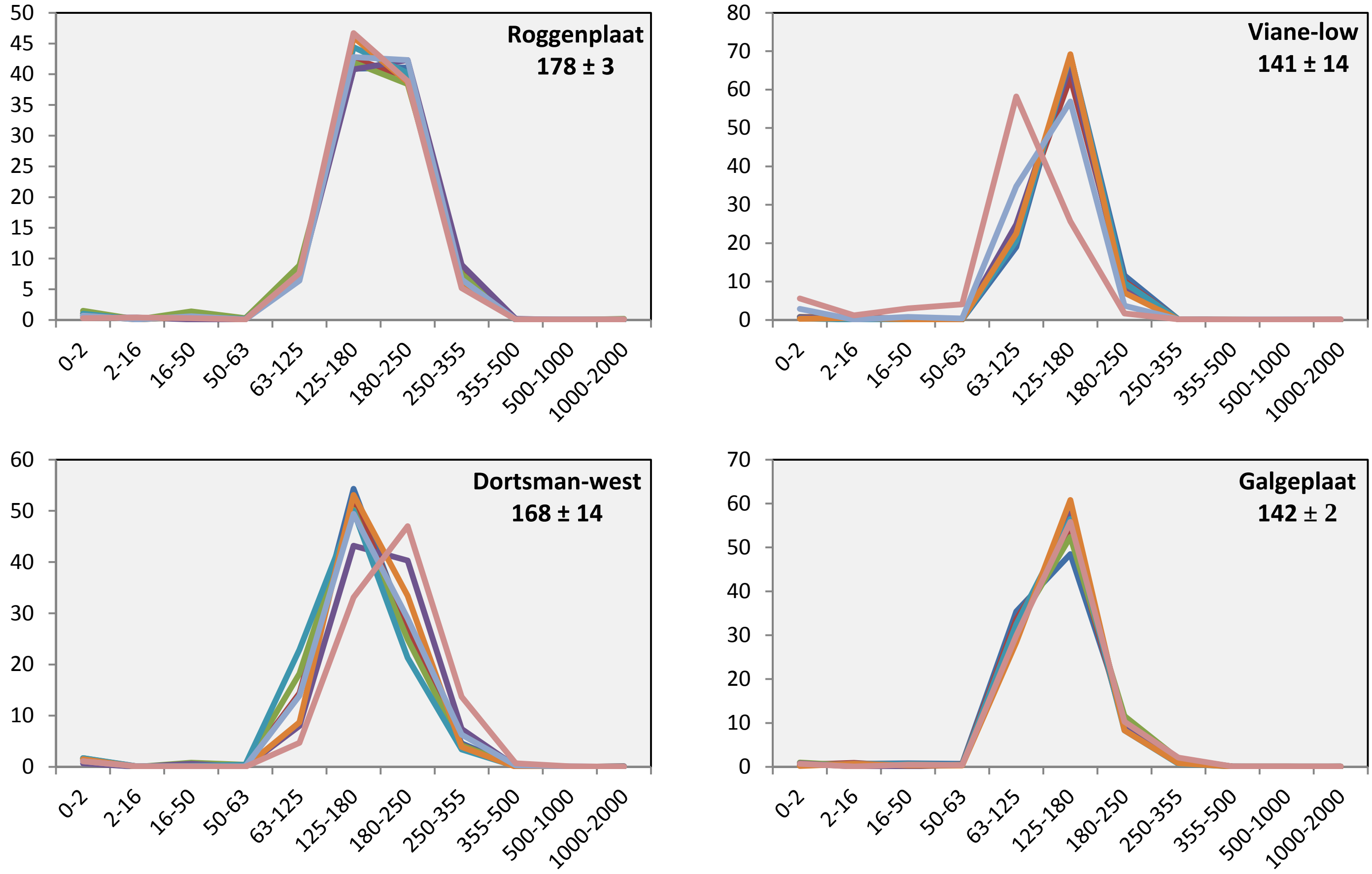
Figure 3-4- *The biomass per m^2 of 13 major species as a function of emersion time (%); data are combined for the samples taken in August 2009 and April 2011.*

Sediment

The clay content (< 2 µm) was less than 1% in 142 out of the 144 sediment samples collected in 2009; it was slightly higher than 1% in two plots of the Rattekaai site.

The tidal flats in the Oosterschelde consist of very fine, fine and middle fine sand (Figure 3-5). The Roggenplaat and Dortsman-west consist of middle fine sand (180-250 µm) and fine sand (125-180 µm), Viane-low and Galgeplaat of fine sand and the Oesterdam of very fine sand (63-125 and 125-180 µm). Thus, the dominant sand fraction is middle fine in the mouth of the former estuary and very fine at the rear end.

The median particle size, varying between 98 and 198 µm, appeared to explain a small part of the variation in biomass, in addition to emersion time. Figure 3-6 shows the biomass of the 13 major species



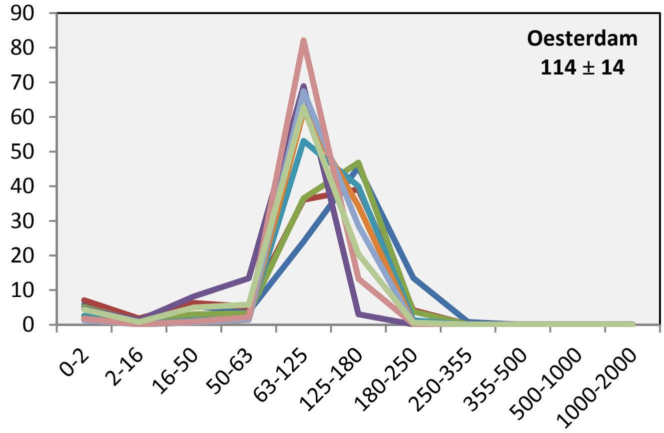


Figure 3-5- *The particle size distribution (%) in different sediment samples (upper 10 cm) taken in five different sites; 8 samples were taken per site, but 9 on the Oesterdam. The median particle size (average ± sd) is given in the upper right corner.*

as a function of the median particle size. The four low and two high sites (emersion time 10 and 80%, respectively) were omitted in this analysis in order to exclude the effect of emersion time. There is a negative relationship between biomass and median particle size in the worm species (Figure 3-7). These trends remain present if the highest and lowest sites are included or if the analysis was done on a more restricted set of data (40-60% emersion time). The correlations are non-significant in all other species.

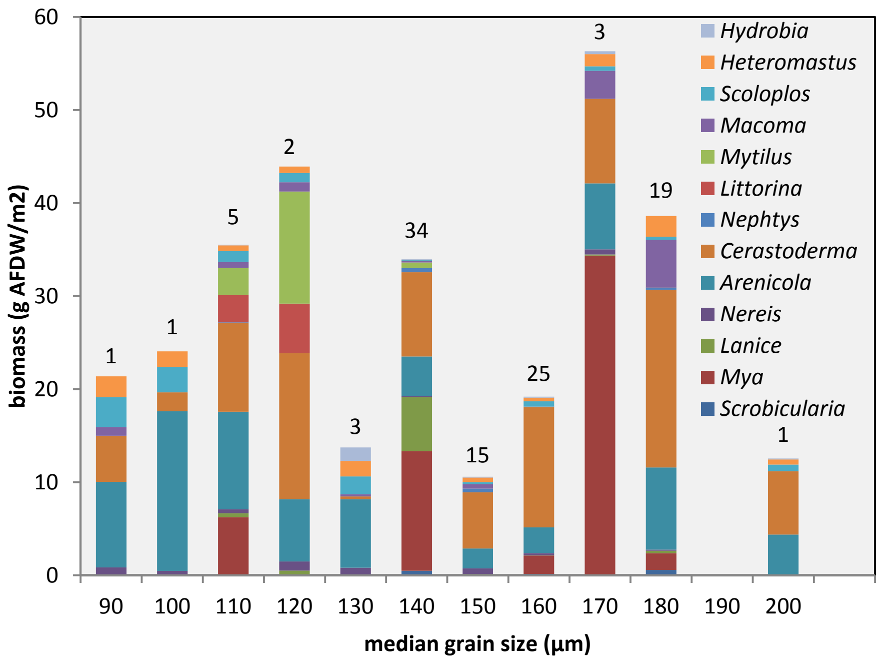


Figure 3-6- *The biomass per m^2 of 13 major species as a function of the median grain size (µm); data are combined for the samples taken in August 2009 and April 2011.*

The number of plots per category is given.

A selection has been made of sites where the emersion time varied between 30 and 70%.

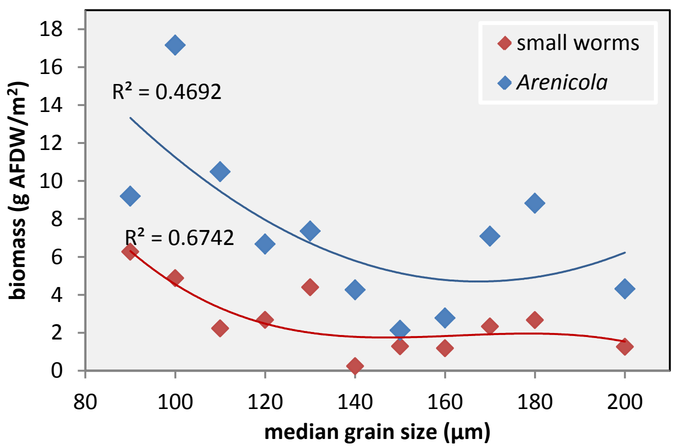


Figure 3-7- *The biomass per m^2 of* Arenicola *and small worms (*Nereis + Scoloplos + Heteromastus*) as a function of the median grain size (µm); data are combined for the samples taken in August 2009 and April 2011.*

Local variation

Emersion time explained a large, and sediment composition a small, part of the variation in biomass. However, there remain local differences between sites which cannot be related to emersion time or sediment. For instance, *Macoma* was only common on the Roggenplaat and *Lanice* only on the Galgeplaat. *Arenicola* is another example. This species reached a high biomass on the Oesterdam in plots being uncovered for 20-70% of the time (Figure 3-8 left). Comparable biomass was found on the

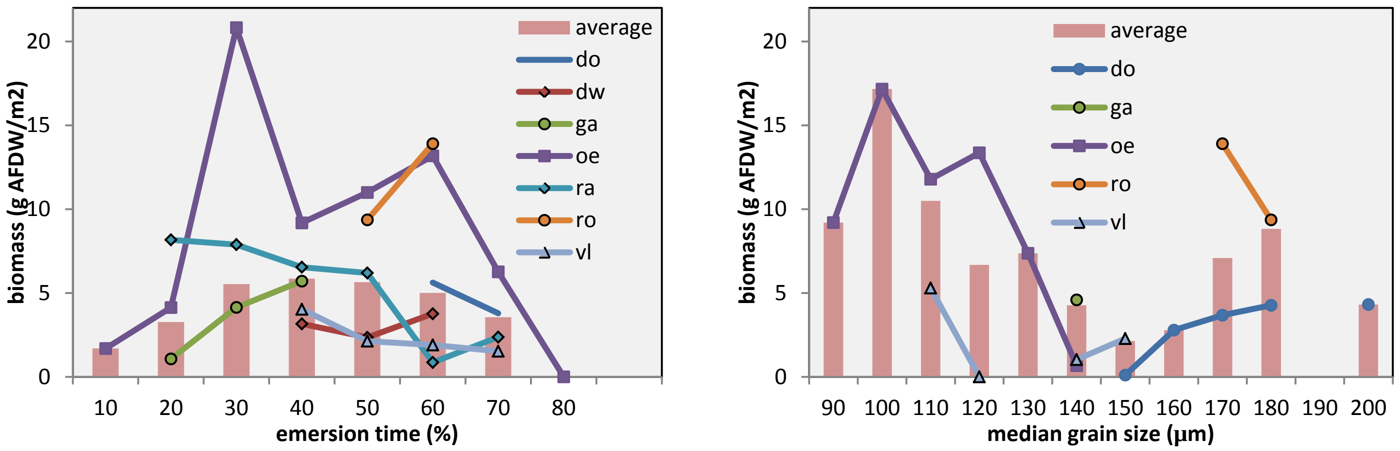


Figure 3-8- *The biomass of Arenicola as a function of emersion time (left; same data as Figure 3.2)) and median grain size (right; same data as Figure 3.5), given separately for the different sites; data are combined for the samples taken in August 2009 and April 2011.*

Roggenplaat, but at all other sites the biomass of *Arenicola* was lower. Similarly, the Oesterdam and Roggenplaat were rich in terms of biomass compared to plots from other sites with comparable sediment composition (Figure 3-8 right).

3.2 Epifauna

The standard method to sample macrobenthos is less suitable for mobile species such as *Carcinus* and *Crangon*, since these animals may walk or swim away just before the core sampler is pushed into the ground. The alternative method is to capture these mobile prey with a larger core sampler (Figure 3-9).

Crangon found on the tidal flats of the Dortsman on 1 August 2009 ranged in size between 7 and 12 mm long and *Carcinus* between 5 and 7 mm wide. Smaller size classes were not found, but they may have

Figure 3-9- *A core sampler (diameter 33 cm) was used to measure the density of the epifauna at low water. It suffices to collect the sedi-ment from the upper few cm to collect all* Carcinus *and* Crangon*.*

passed through the 1 mm sieve. The tidal flats on the Dortsman are sandy and rippled. The ripples are usually dry at low water, but the space in-between the ripples is covered by water. The water coverage was on average 81% in the samples and the average water depth measured 12 mm. Small *Crangon* were found in these shallow water pools along the entire range from high to low water line. The density was below average near the low and the high water line and also where there was less water on the surface (Figure 3-10).

The average density was 79.8 *Crangon*/m^2 and 9.4 *Carcinus*/m^2 in August. For *Crangon* this is 20 times as high as found with the corer used to sample the benthic fauna (Table 3-1).

Three *Carcinus* (8-10 mm) and 13 *Crangon* (8-19 mm) were found along the same transect on 7 December 2010 (again 40 samples on 20 sites). This is equivalent to an average density of 0.88 *Carcinus*/m^2 and 3.8 *Crangon*/m^2. In contrast to the summer samples, all *Crangon* were found on flats being exposed for less than 50%. Moreover, they were much larger. The water coverage (76% on average) and water depth (12 mm on average) did not deviate from the measurements in August 2009.

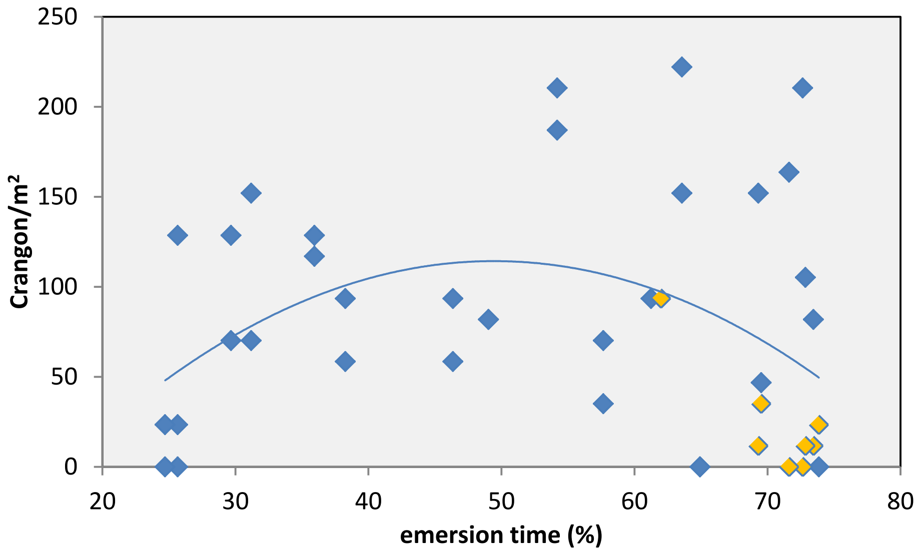


Figure 3-10- *The density of* Crangon *on the Dortsman on 1 August 2009. The yellow symbols refer to 8 sites where the cover by water was 0-30% (17% on average); for the other 33 plots the water coverage was 80-100% (96%, on average). The polynomial line is calculated over all 41 plots.*

Figure 3-11 *Water coverage at low water was measured on the Dortsman in August 2009 and December 2011. In both cases, the water coverage was the same (76-82%) as well as the average water depth (12 mm).*

4 Results: birds and their estuarine prey

4.1 Prey selection

Meire *et al.* (1994a) mentioned for the tidal flats in the Oosterschelde 62 macrobenthic species and Schaub *et al*. (2003) even 210 species for the entire Oosterschelde. Estuarine bird species prey only on a small fraction of these prey. Some are too rare, but most are simply too tiny to be a profitable prey, even for small waders such as the Dunlin. The total biomass of the macrobenthos is dominated by only a few species (Table 3-1). To know which species are actually taken by the different bird species, we registered the prey and size selection (sampling details in Table 2-10).

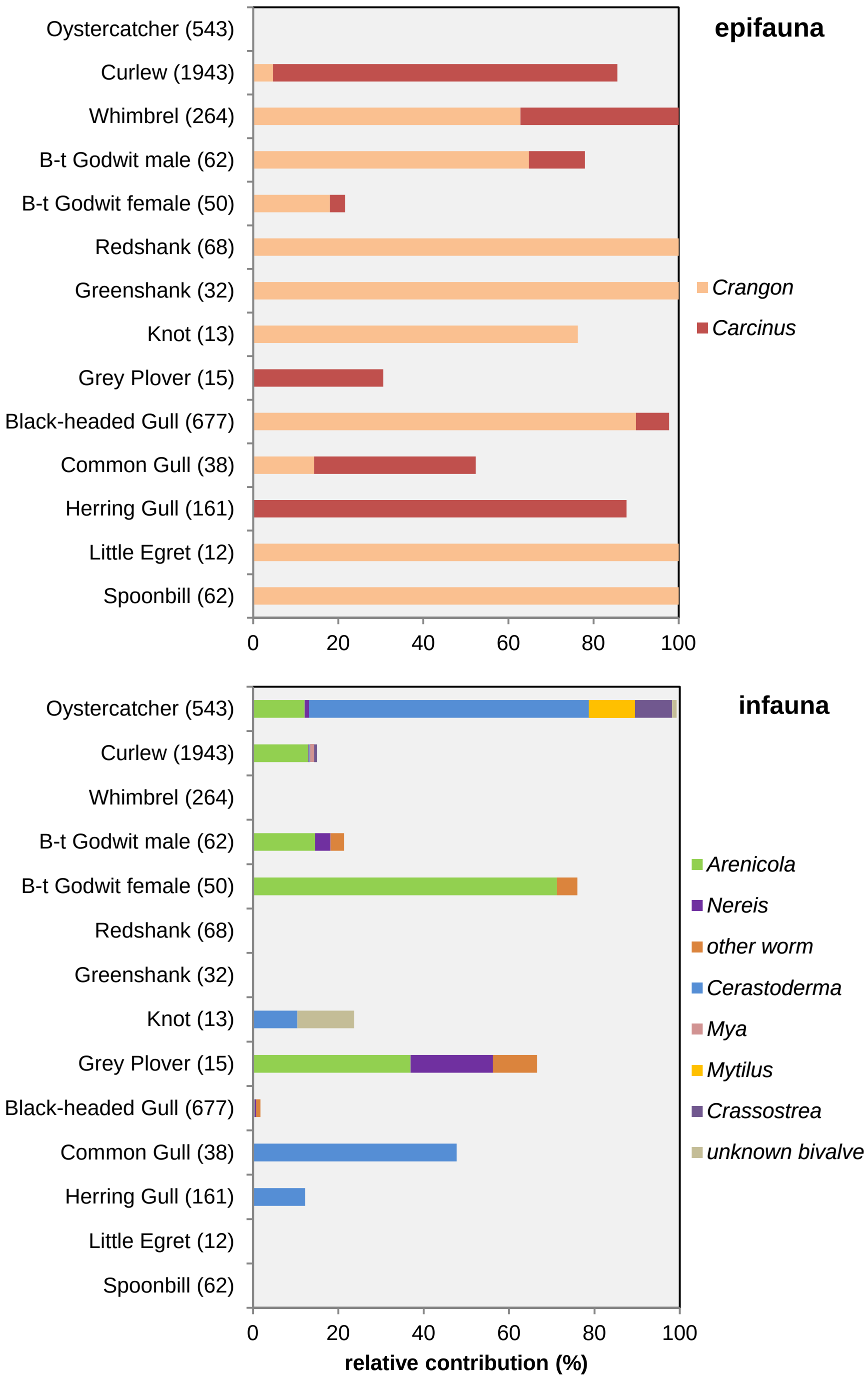


Figure 4-1*- Relative contribution (%) of different prey to the diet (g AFDW) of 13 different bird species in July-August 2009.*
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Prey living at the surface (Crangon and Carcinus) and prey living in the sediment (infauna) are shown in separate panels; together adding up to 100%.

The data for male and female Bar-tailed Godwit are given separately.

Between brackets the number of registered prey.

Figure 4-1 gives an overview of all data collected on 10 different sites during 17 low water periods in July and August. The single *Nephtys* taken by a Curlew and the few smaller worms selected by Bar-tailed Godwit, Grey Plover and Black-headed Gull (*Lanice*, *Scoloplos* and *Heteromastus*) are joined as “other worm”. The unknown bivalves taken by Oystercatcher and Knot were either *Macoma* or small *Cerastoderma*. Not included in Figure 4-1 are two other prey species: one *Ensis* and one flatfish eaten by Oystercatcher and one flatfish eaten by a Curlew. Together, 14 different prey species were eaten, but it is obvious that the diet of the bird species during the summer is dominated by only two prey: *Carcinus* and *Crangon*. The Oystercatcher is the only exception. This species has a diet of bivalves (mainly *Cerastoderma*) and worms (mainly *Arenicola*). The diet of male and female Bar-tailed Godwit differed: males took *Crangon*, while females preyed upon (small) *Arenicola*.

The diet of some bird species varied locally. Herring Gulls preyed on large *Carcinus* everywhere, but in the Krabbenkreek they took *Cerastoderma* of 15-25 mm (being swallowed whole, including the shell). The many Oystercatchers on Galgeplaat, Viane and Roggenplaat preyed upon *Cerastoderma* and only rarely on *Arenicola*. The diet of the few Oystercatchers on the Rattekaai consisted of *Arenicola* (84% of the prey biomass taken); they had no other choice since alternative prey, such as *Cerastordema*, were hardly present (Figure 3-3).

Figure 4-2- *Large* Carcinus *were the major prey for Herring Gulls feeding on the tidal flats of the Oosterschelde.*

Fewer observations are available for winter and spring. The most striking results are:

- Oystercatchers fed on *Cerastoderma* (80 and 86% of their total diet in winter and spring) and hardly on *Arenicola* (14% in winter and 1% in spring). On the Roggenplaat, 100% of their prey in winter were *Cerastoderma*, but in the same period (the few) Oystercatchers on the Dortsman sites had a mixed diet (49% *Cerastoderma*, 41% *Arenicola* and 8% *Mytilus*). Some Oystercatchers (females with a long bill) on Viane-low preyed in May upon *Scrobicularia plana*, while we saw a few birds on the Roggenplaat and Dortsman-low in May feeding on *Macoma* and *Mytilus*, respectively.
- The major prey for the Curlew was *Carcinus* (81% in summer, 39% in winter and 82% in spring); *Crangon* was hardly taken (5%, 0% and 1% in summer, winter and spring, respectively); *Arenicola* was a winter prey (37% against only 13% in summer and 11% in spring). Also *Mya* (large individuals) were important in winter (22% of the prey biomass).
- All Whimbrels observed in spring ate *Carcinus* but no *Crangon* (in summer: 37% *Carcinus* and 67% *Crangon*).
- All Redshank seen near the hides walked in shallow water and took, as far as we could see, *Crangon* only.

- Also all Greenshank took *Crangon* in summer and in spring, although one small fish, most likely *Pomatoschistus microps*, was eaten in spring.
- Dunlins had to feed very close to the hide to see what kind of prey was extracted from the substrate. Most likely, they took mainly *Scoloplos armiger* in winter and small *Nereis diversicolor* in spring.
- We were not able to see the (small) prey taken by Sanderlings feeding around the hide on the Roggenplaat, but saw once a bird spending much time to eat a large *Crangon*.
- We saw only a few Knot nearby the hide on the Roggenplaat. All birds swallowed *Macoma* of 12-15 mm, but more often we saw that they refused, after some handling, larger *Macoma* (14-18 mm; being too large to be swallowed). Indeed, only a small minority of the *Macoma* found in our April samples appeared to be of the “right size” for Knot.
- Grey Plover preyed in winter and spring on worms. The majority of their prey were *Nereis* in spring, but they took also *Scoloplos* in winter.
- The diet of Black-headed Gulls consisted in spring, just as in summer, of *Crangon*, although they ate some *Arenicola* present at the surface (we also found ourselves many *Arenicola* in apparent poor condition at the surface in April and May).
- Herring Gulls only took relatively large *Carcinus* in winter as well as in spring.
- Spoonbills (observed in spring while doing the regular bird counts), swallowed small items (fish or *Crangon* < 3 cm) but several times also larger flatfish.

4.2 Numerical response

Estuarine birds distribute themselves over the emerging tidal flats, but the feeding density shows a large variation (as found already by Geene & Goedbloed 2007). This is also evident from the data collected for this study. For instance, the feeding density of the estuarine birds in winter was more than ten times higher on the site near the Oesterdam than on Dortsman-west (Figure 4-3). The variation was even larger at species level. All Shelduck in winter were concentrated on the Oesterdam site, but they were absent from all other sites.

Some bird species changed their distribution between seasons (Figure 4-3). The Galgeplaat attracted many birds in summer, while this site was sparsely used in winter and spring. Many Dunlins were seen on Roggenplaat and Viane-high in winter as well as summer, but they were absent along the Oesterdam in spring, but common in winter. Oystercatchers on the Roggenplaat were more common in spring than in winter, while it was the other way round on the two Viane sites.

One might expect that the distribution of the birds on the tidal flats can be explained by the distribution of their prey and that a seasonal shift in the distribution of the birds, can be attributed to a change in their diet. That is always difficult to show, however, since the diet of estuarine birds consists often of several prey species. That is why the “numerical response” (density of a predator as function of density of one single prey) is difficult to show. For three other reasons, we did not expect to find numerical responses in our data: (1) the prey density was not very accurate due to the low number of samples per plot; (2) the bird density was not accurate due to frequent disturbance by human and Peregrine Falcon; (3) the birds moved over the flats between receding and incoming tide, causing a large variation in bird densities during the series of counts. Nevertheless, some nice numerical responses could be detected (Figure 4-4). Apparently, the relationships between food supply and bird density were so evident, that they overrule all the just mentioned contaminating variables. To rule out the impact of emersion time, the bird density was calculated for counts made between 2 hours before and 2 hours after low water.

The winter density of the Oystercatcher was correlated with the density of *Cerastoderma* (Figure 4-4 left). Similar relationships were found for the summer and spring (not shown). The winter density of the Curlew depended on the biomass of *Arenicola* (Figure 4-4 right), but such a relationship was fully absent in summer and spring. However, that was not to be expected, since they took another prey, *Carcinus,* in both seasons.

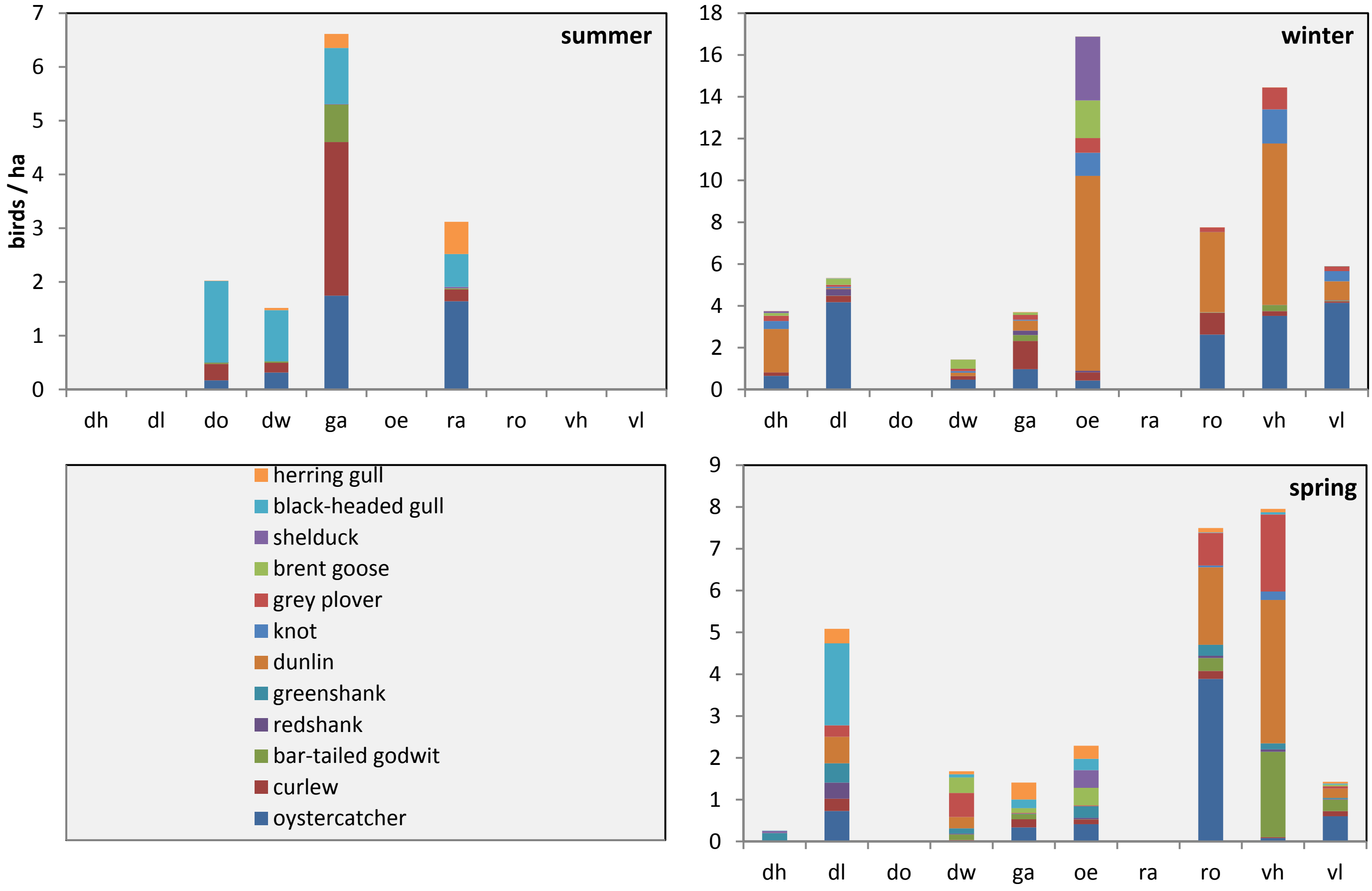

Figure 4-3- *Average bird density in four study site in summer and eight study sites in winter and spring.*

Cerastoderma were not the only prey for Oystercatcher and *Arenicola* not the only prey in winter for Curlew. This explains why still so many birds were present in plots where their main prey was fully absent (Figure 4-4). The lower the density of the major prey, the higher the fraction of birds feeding on alternative prey. Oystercatchers switched on the higher flats being exposed more than 70% (where *Cerastoderma* were less common) to *Arenicola* as alternative prey. *Mya* and *Carcinus* were in winter an important prey for Curlews, also in areas where they fed on *Arenicola*, although both alternative prey were mainly taken on the lower flats.

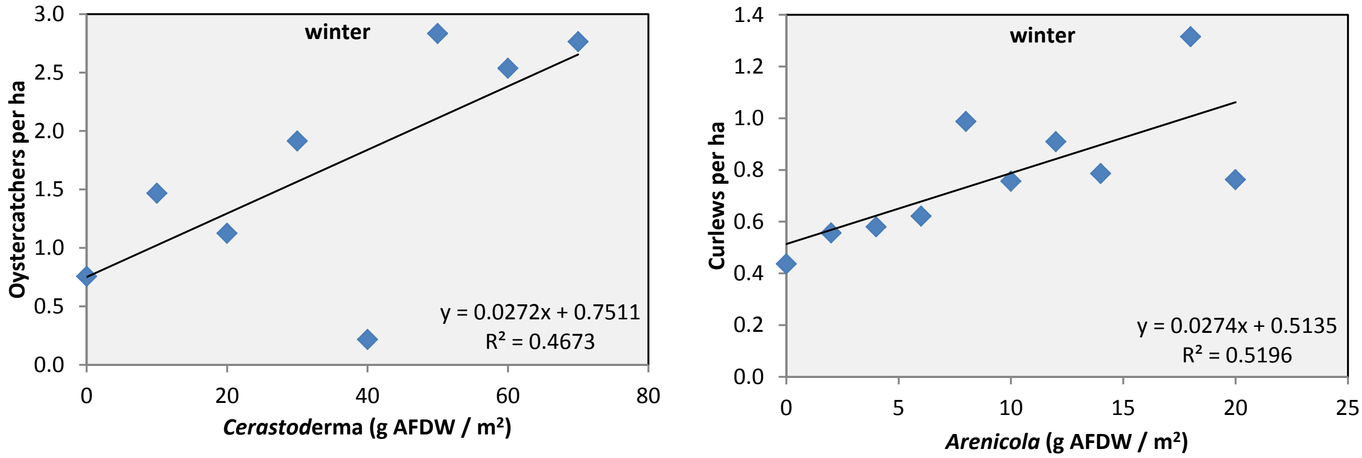

Figure 4-4- *Average bird density at low water (-2 hours to +2 hours relative to low water) in winter as a function of the biomass of their main prey: Oystercatcher vs.* Cerastoderma *(left) and Curlew vs.* Arenicola *(right).*

The feeding densities of Grey Plovers and Dunlins were related to the biomass of *Nereis*, but the fit improved when the prey biomass of *Nereis* was combined with those of two other, small worms, *Scoloplos,* and *Heteromastus* (Figure 4-5). The numerical responses were found in winter as well as in spring.

We found no convincing numerical response in Knot. This species reached in winter a high density on the high flats near the Oesterdam, where *Hydrobia* was abundant. The birds were present here, however, only at receding and, still more, at incoming tide. At low water the birds spread over the lower tidal flats where they must have taken other prey than *Hydrobia*. That is why the low water density of Knot was not related to the biomass of *Hydrobia*. However, when the density of Knot was calculated over all counts being done during the exposure time, the expected relationship became apparent (Figure 4-6), but not as convincing as in Oystercatcher, Curlew, Grey Plover and Dunlin.

Shelduck were concentrated in the same area being visited by Knot during receding and incoming tide. Most of them stayed there the entire low water period. The feeding density of Shelduck was nicely related to the biomass of *Hydrobia* (Figure 4-6). Figure 4-6 is based only on low water counts, but the graph is nearly the same when all Shelduck counts from the ebb and flood are included. The feeding density of Shelduck in spring was not related to biomass of *Hydrobia*.

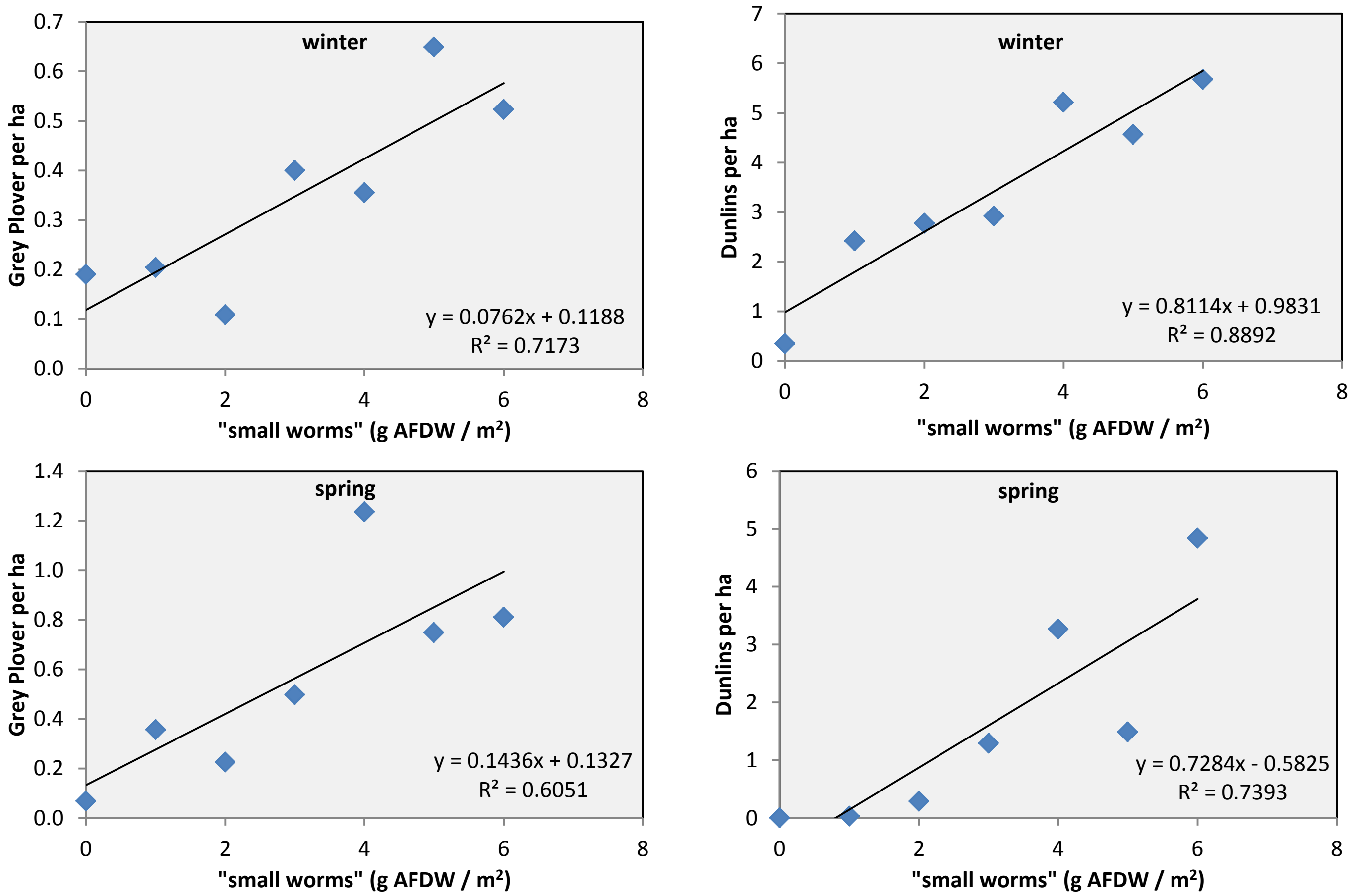

Figure 4-5- *Average bird density at low water (-2 hours to +2 hours relative to low water) in winter (top) and spring (bottom) as a function of the biomass density of their main prey: Grey Plover (left) and Dunlin (right) . The biomass of* Nereis, Scoloplos *and* Heteromastus *has been taken together as “small worms”.*

For the summer period, we found no numerical responses in any combination of bird density and prey biomass, beside the relationship between Oystercatcher and *Cerastoderma.* That was also not to be expected since nearly all bird species preyed in that time of year on *Carcinus* and *Crangon* (Figure 4-1), species for which we hardly know the spatial variation in density.

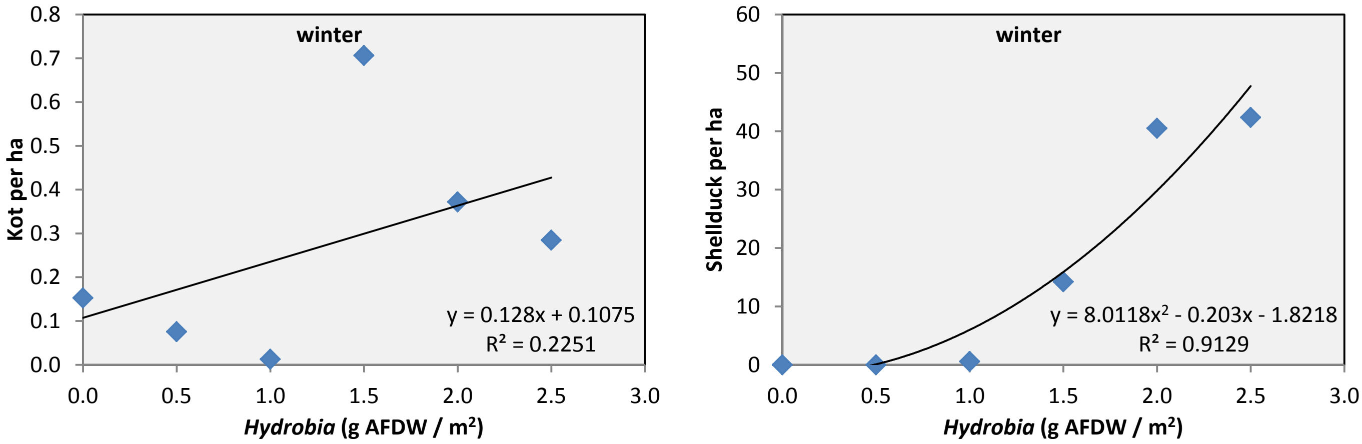

Figure 4-6- *Average density of Knot (left; entire low water period) and Shelduck (right; based on counts from -2 hours to +2 hours relative to low water) in winter as a function of the biomass of their main prey,* Hydrobia.

4.3 Seasonal variation in prey choice

The data collected on prey choice are not more than preliminary but in combination with the shown numerical responses, they indicate that there was hardly a seasonal variation in the prey selection in Curlew, Redshank, Greenshank, Black-headed Gull and Herring Gull. *Carcinus* are the entire year the major prey for Herring Gull present on the tidal flats and the same holds, to a lesser degree, for Curlew. Greenshank and Black-headed Gull prey predominantly on *Crangon* in summer as well as in spring. Redshank does so the entire year.

The prey selection changed seasonally in some other species. Given the distribution of Shelduck they must have fed on *Hydrobia* in winter but have switched to other (unknown) prey in spring.

There was a seasonal change in the distribution of Grey Plover and Dunlin (from Oesterdam in winter to Roggenplaat and Viane in spring). There was also a likely shift in their diet (from mainly *Scoloplos* in winter to mainly *Nereis* in spring). The sampling data of the benthic infauna (Figure 3-3) do not suggest that *Nereis* was more common on the Roggenplaat and *Scoloplos* on the Oesterdam site. Thus, it is still unclear why the Dunlins used different parts of the Oosterschelde in winter and spring.

Why Grey Plovers and Dunlins moved from the Oesterdam to the Roggenplaat is still the question, but for Knot a similar seasonal shift seems to be reasonable (Zwarts & Blomert 1992). *Hydrobia* is the entire year an easy accessible prey for Knot. *Macoma* is a prey being more profitable than *Hydrobia*, but it lives too deeply buried in winter to be accessible for Knot. This changes in early spring when *Macoma* reduce their burying depth and most individuals become to live within reach of the bill of the Knot. When Knot switch from *Hydrobia* to *Macoma* in spring, they achieve a higher intake rate, but they have to move from the Oesterdam (where *Macoma are* rare) to the Roggenplaat (where *Macoma* are common; Figure 3-3).

4.4 Bird predation on epifauna and infauna

Estuarine birds depend for their living on an amazing small part of the potential prey items present in the sediment or living at the surface. The little we know about the predator-prey relationships in the Oosterschelde reveal that this is not different in this area. *Mya* were 7-10 cm long in 2009-2011 and lived 15 to 25 cm beneath the surface. Except for long-billed Curlews these prey were of no interest for the other estuarine birds. Nearly all *Cerastoderma* were larger than 15 mm, being a highly profitable prey for Oystercatchers, but not for any other bird species. Thus, for any bird species only a small fraction of the biomass is harvestable.

Crangon and *Carcinus* belong for most bird species to the harvestable fraction of the biomass, *e.g*. the prey species being detectable, accessible, ingestible, digestible and profitable. The total biomass of the infauna and epifauna was 21.5 g/m^2 and 0.3 g/m^2, respectively (Table 3-1; Figure 3-1). Even if we assume

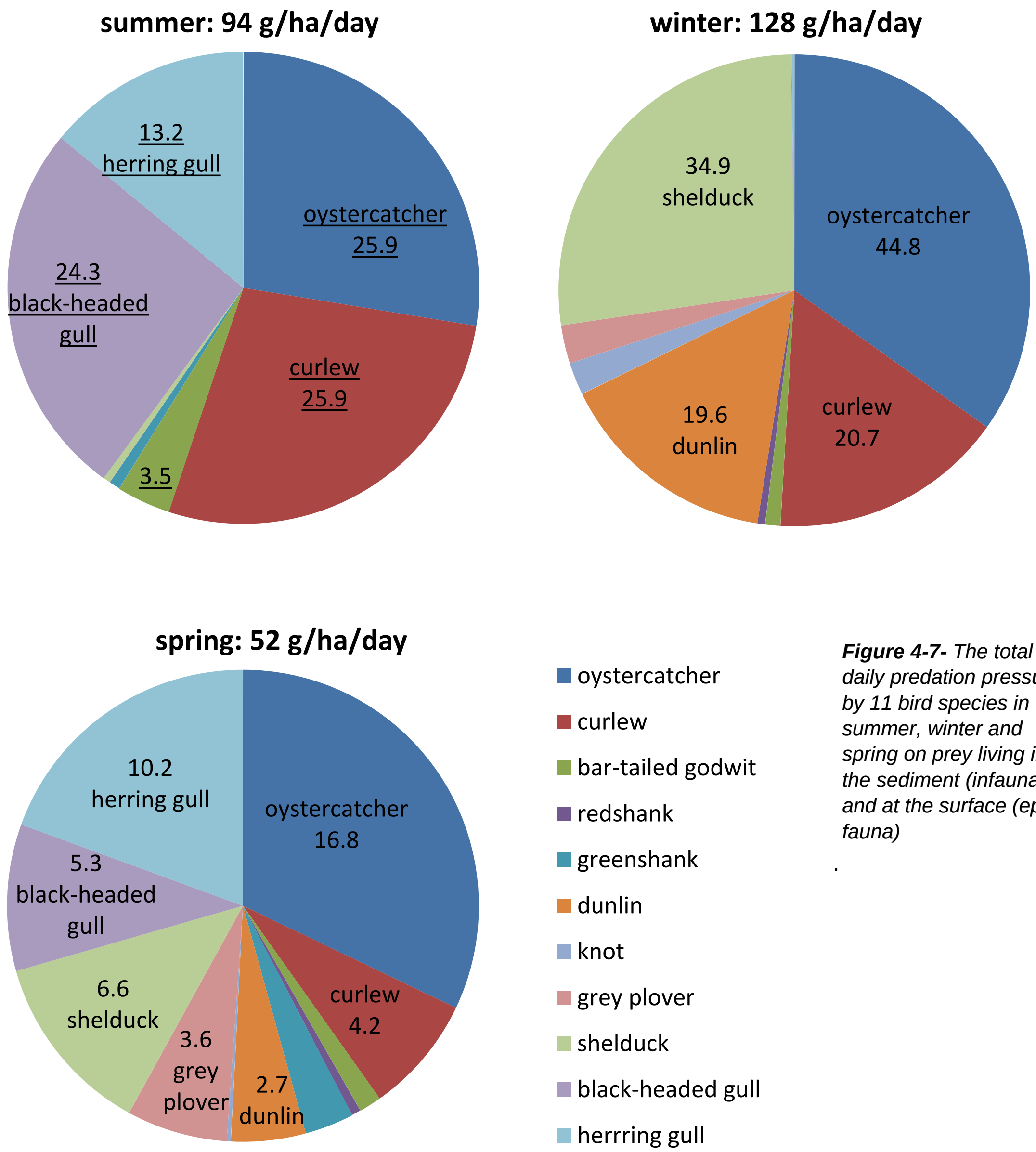

Figure 4-7- *The total daily predation pressure by 11 bird species in summer, winter and spring on prey living in the sediment (infauna) and at the surface (epifauna)*

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that the biomass of *Crangon* was ten times higher (see section 3.2), the biomass of the infauna remained very low compared to the biomass of the epifauna.

The predation pressure on the infauna and epifauna can be estimated from the product of (1) the average bird density on the study sites (Figure 4.2) and (2) the daily consumption (g AFDW) of the birds (being a function of the body weight (W, in gram): $0.322W^{0.723}$; Zwarts & Wanink 1993). The daily predation pressure by the estuarine birds varied seasonally between 52 g/ha in spring and 128 g/ha in winter (Figure 4-7). The summer predation was dominated by four species: Oystercatcher, Curlew, Black-headed Gull and Herring Gull. The latter three species fed on *Carcinus* and *Crangon*.

The total summer predation on the epifauna amounted to 60 g/day/ha, or 0.006 g/day/m^2. The total predation would arrive at 0.5 g/m^2 for a period of three months (July-September). This is even larger than the prey biomass present in August. Of course, the entire bird predation on the total population of *Crangon* and *Carcinus* in the Oosterschelde as a whole (including the gullies) is relatively small, but it remains remarkable that the birds removed such a large part of these prey from the tidal flats and that so many bird species depend in summer on these prey species (Figure 4-1). Even in winter, when the density of *Crangon* and *Carcinus* on the tidal flats were much lower, Redshank and Curlews still take relatively many.

The predation pressure on the infauna was in winter higher than in the rest of the year and amounted to, in total, 1 g/m^2 for these 100 days (Figure 4-7). That is 5% of the total biomass.

The large difference between the relative predation pressure on infauna and epifauna raises two questions: Why do birds switch from benthic prey to *Crangon* and/or *Carcinus*? And why do so many birds make this switch in the Oosterschelde, by which even species such as Bar-tailed Godwit, Grey Plover and Knot, known elsewhere as birds preying on worms, bivalves and snails, were seen to feed on *Crangon* or *Carcinus*.

The answer on the first question is that waders searching for one prey may adjust their feeding behaviour (*e.g.* walking faster) to increase the encounter rate with other prey. They only do so if the alternative prey are profitable and easy to detect. *Carcinus* present at low water on a bare tidal flat are such easy, profitable prey and this also applies for *Crangon* present in the shallow water remaining on the tidal flats at low tide (Figure 3-11). A Curlew searching for worms or *Mya* walks more than 3 km per low water period and encounters many *Carcinus*, even if their density is low, *e.g.* 0.1/m^2. If this alternative prey occurs in a higher density, Curlews can decide to ignore the worms and *Mya* and only search for *Carcinus*.

Why do so many birds make such switch from benthic prey to epifauna in the Oosterschelde? The only feasible answer is that these prey are apparently abundant making it worthwhile to change their diet. The question is then: are these species indeed so much common as, for instance, in the Wadden Sea? Is that something new in the Oosterschelde and if so: what has changed in the Oosterschelde? Section 7.1 will deal with these questions.

Figure 4-8- *Black-headed Gulls feeding on* Crangon *during receding water; Galgeplaat; August 2009.*

5 Results: bird exploitation of the tidal flats

5.1 Emersion time

Tidal flats are only a part of the time available as feeding area for bird species which feed on the uncovered flats. How long they are able to feed depends on which part of the tidal zone is used. In theory, they may feed 100% of the time if they continue to feed at high tide along the water's edge, but since these high flats are not attractive as feeding area due to the poor food supply (Figure 3-4), most birds are inactive in the hours around high water and are concentrated on high water roosts.

As soon as birds start to feed on the emerging flats, they follow the water's edge, not only species such as Greenshank which feed in shallow water, but also birds which are distributed over the uncovered tidal flats. All estuarine bird species move during receding, but also during incoming, tide, over the tidal flats. As an example, Figure 5-1 shows the average feeding density of Oystercatcher in winter in plots with a different emersion time. Oystercatchers start to feed two hours after high water (4 hour before low water) on flats being uncovered for 60, 70 and 80% of the time. They do so in an average density of 5 birds/ha. An hour later, most of the birds have moved to flats being exposed for 50% and again an hour later they feed on still lower flats being exposed for 40%. At low water most birds feed on flats with an emersion time of 20%. In reverse order, the same movement can be seen during incoming water.

Figure 5-3 shows the feeding density in the course of the tidal cycle for 12 bird species in winter and on the next page the same for spring. The density is given separately for sites being uncovered for 10 to 80%.

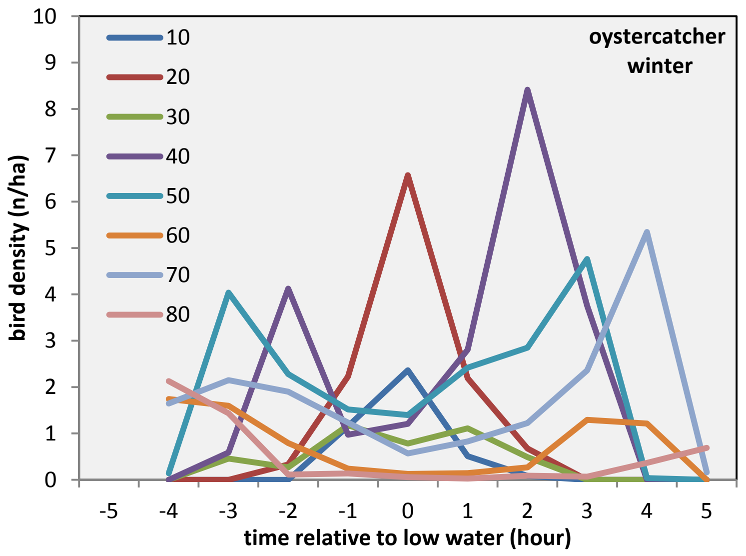


Figure 5-1- *The feeding density of Oystercatcher in winter during the course of the tidal cycle, given separately for tidal flats being uncovered for 10 to 80%.*

Tidal flats with an emersion time of 10%, will be dry for about 80 minutes, on average, so we expect that waders will feed here from 1 hour before to 1 hour after low water. Figure 5-3 suggests that it is a bit longer, which is due to variation in altitude within some low lying plots situated along tidal creeks (Table 2-6).

Gulls and geese arrive earlier than waders and stay longer since feeding waders have to walk, but gulls and geese may feed while they swim (head dipping and upending in Shelduck and Brent Goose) or capture their prey by making plunge-dives (Herring and Black-headed Gull).

Tidal flats with an emersion time of 80% are covered by water for only 2 hours per tidal cycle and thus available as feeding area for waders for 10 hours. Estuarine bird species feed on these high flats in winter as well as in summer, but most species only do so during receding and incoming water.

Figure 5-3 also shows how the different estuarine species exploit the tidal zone during the low water period. The next sections will deal with the different species. Two graphs were made. One type of graphs show the estimated number of birds in the Oosterschelde feeding on flats situated at different height. To do so, the average densities (as shown in Figure 5-3) were multiplied with the total surface of flats with a different emersion time (Table 5-1).

Table 5-1- *Surface area of the tidal flats in the Oosterschelde per relative emersion time; 10% = 5-15%, 20% = 15-25%, and so on. Surface area derived from same data as shown in Figure 2-1.*

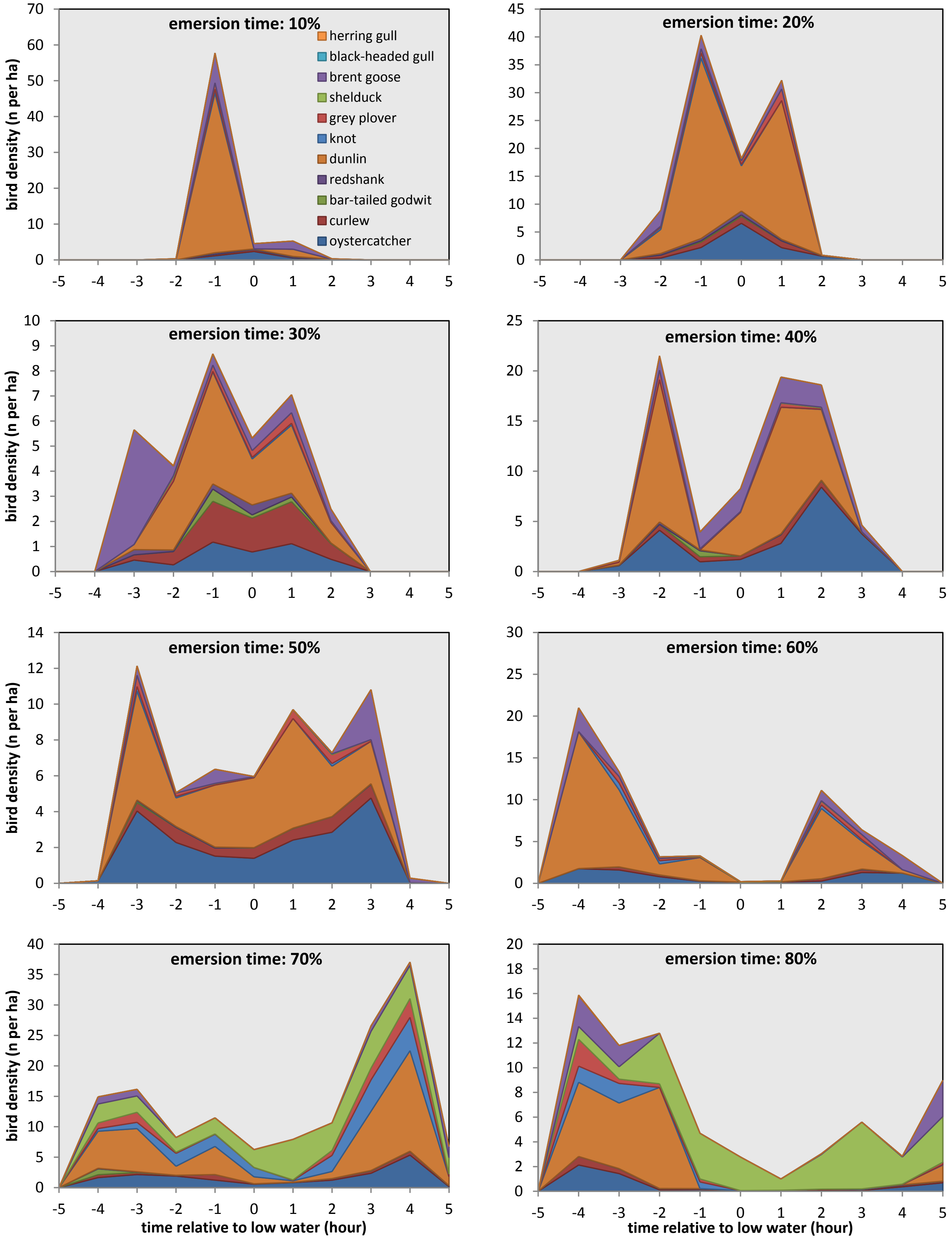
emersion time, %	10	20	30	40	50	60	70	80	total
ha	1338	1407	1962	1291	1339	1226	993	298	9854

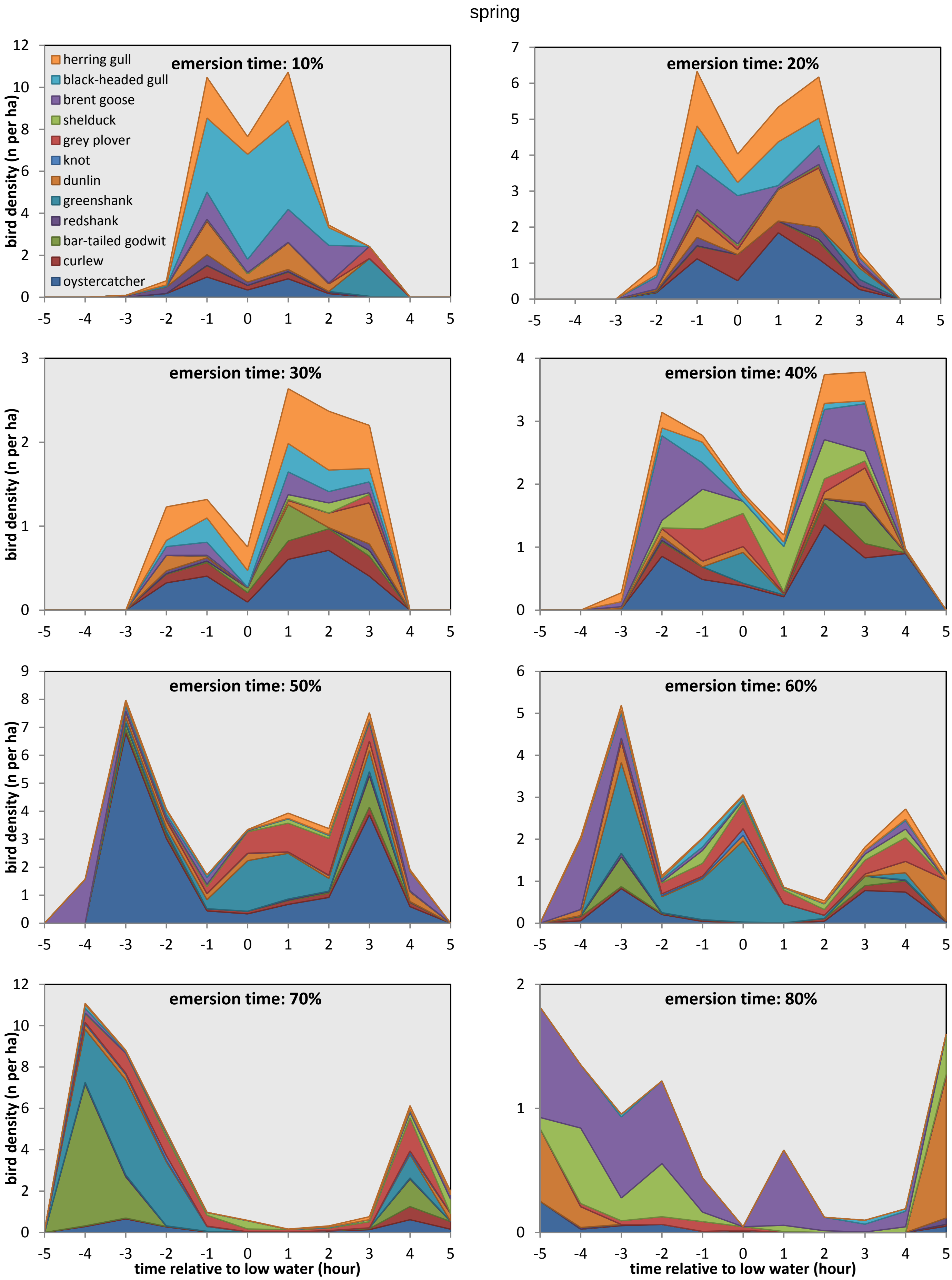
The other graph shows the exploitation in terms of “bird hour” per ha. An evaluation of the ecological significance of tidal flats along the tidal gradient should not only be based upon bird density but also on the time the feeding birds are present. Bird exploitation is expressed as bird hour per ha, being the average density per ha per hour summed over all hours within the entire low water period.

Figure 5-2- *Waders have to keep walking away from the incoming water line in order to continue foraging; Oystercatcher, Bar-tailed Godwit, Sanderling, Grey Plover and Greenshank on the Roggenplaat, May 2011. Since we counted the birds every 15 minutes, there was for each plot usually only one count per tidal cycle during which birds were driven by the incoming water, - and usually present in a (very) high density.*

Figure 5-3- *The feeding density of 12 estuarine bird species during the course of the tidal cycle in winter (page 41) and spring (page 42). Each panel gives the bird density of plots with a variable emersion time. Number of plots per emersion category has been given Table 2-5.*

winter


emersion time: 10%
herring gull
black-headed gull
brent goose
shelduck
grey plover
knot
dunlin
redshank
bar-tailed godwit
curlew
oystercatcher
emersion time: 20%
emersion time: 30%
emersion time: 40%
emersion time: 50%
emersion time: 60%
emersion time: 70%
emersion time: 80%
bird density (n per ha)
time relative to low water (hour)


spring
herring gull
black-headed gull
brent goose
shelduck
grey plover
knot
dunlin
greenshank
redshank
bar-tailed godwit
curlew
oystercatcher
emersion time: 10%
emersion time: 20%
emersion time: 30%
emersion time: 40%
emersion time: 50%
emersion time: 60%
emersion time: 70%
emersion time: 80%
bird density (n per ha)
time relative to low water (hour)

Before the graphs per species are shown, five remarks have to be made:

- the counts refer to *feeding* birds. The increase in numbers during the ebb is due to birds which have left the high-tide roost and the decline during the flow is due to birds which had gathered on the tidal roost. However, birds may also have a resting period on the feeding area and even form large resting groups, mainly at low and incoming water.
- no data for summer are available for the emersion class 10% and 80%. Thus, the estimated total numbers of feeding birds in summer are slightly underestimated.
- the density counts show a large variation due to (human) disturbance. This impact was larger in species feeding in flocks (Dunlin, Knot, Bar-tailed Godwit) and less in birds being widely distributed (Curlew).
- we assembled data from different sites of which we know already that the bird density differed significantly (Figure 4-2). This may contaminate the graphs since the number of plots per emersion category differ per study site (Table 2-5). The alternative would have been to show the same graphs per site, but that would give many more pages with graphs.
- the estimated total number of feeding birds may be compared to the total number actually counted at high water. In theory we would expect that, due to inactive birds, the high water number would be, on average, 10-20% higher than our estimate. A good fit is not be expected, however, since our study sites are not representative for the tidal flats in the Oosterschelde as a whole. Oyster beds, for instance, are underrepresented in our sites. Thus, the estimated number has to be interpreted as a relative rather than as an absolute number.

5.2 Oystercatcher

Oystercatchers stayed 7-8 hours on the tidal flats, in winter 1 hour longer than in summer (Figure 5.3). The flats being exposed for 80% were hardly used. The birds moved from the higher to the lower flats during the ebb and other ways around during the flood. There were some remarkable differences between the seasons. Relatively many Oystercatchers fed in summer on the lower tidal flats, but in winter and spring most were found at flats being exposed for 40% and 50%, respectively.

The graph of the spring period seems to be a bit odd given the extremely low number at low water. There are three explanations. (1) it was true that the birds were very lazy and large numbers were seen in resting flocks during low water; (2) it is feasible that local breeding birds only fed some hours on nearby flats during receding and incoming water; (3) Oystercatchers were present in only low numbers in all study sites, except the Roggenplaat where their feeding density was even higher than in winter (Figure 4-3). The emersion time of the study site on the Roggenplaat was 50% (Table 2-5), so the graph is dominate by the fluctuating number in this one site; at low water a large part of these birds fed on the lower tidal flats just outside the counting plots.

Oystercatchers fed predominantly on Cockles and to a much lesser degree on *Arenicola* and *Mytilus*, thus prey species being not, or hardly, found at flats being exposed for 70 or 80% (Figure 3-2). The biomass of prey relevant for Oystercatchers is mainly found at flats being exposed for 20-60%. That is also the zone where the total predation by Oystercatcher reached its maximum in winter and spring. More Oystercatchers were found at the lower shore in summer, due to the frequent human distribution on the higher flats.

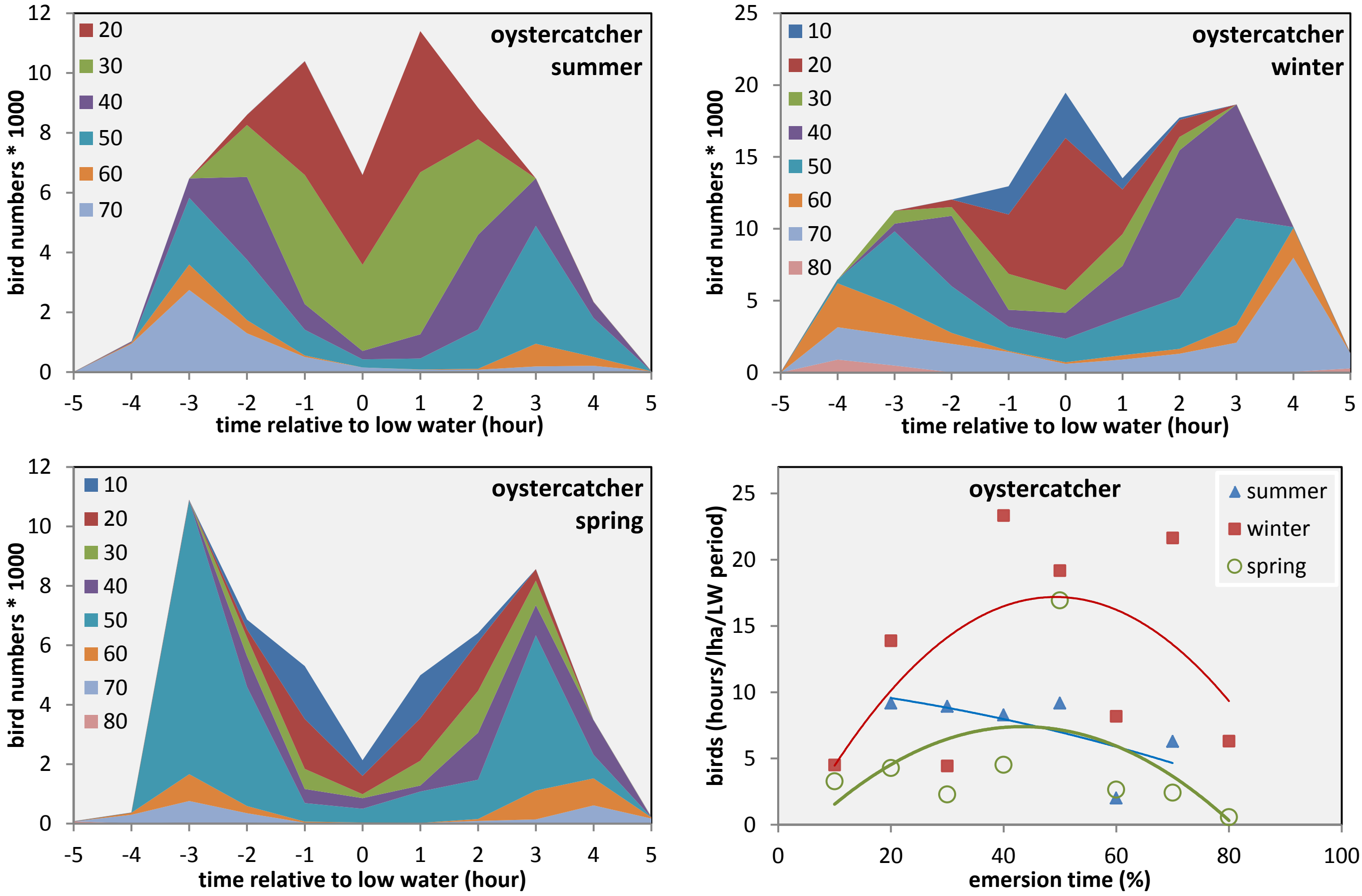


Figure 5-4- *Number of feeding Oystercatchers on the tidal flats and the total explotation (bird hour/ha) on the feeding area during the course of the low water period in summer, winter and spring, given separately for tidal flats with a different emersion time.*

5.3 Curlew

Curlews spent 5 to 7 hours on the tidal flats to feed, in winter and spring evidently longer than in summer, when large flocks of roosting Curlews were gathered during incoming water from two hours after low water onwards, as a consequence of which the feeding numbers started to decline already from 1 - 2 hours after low water (Figure 5-5. Curlews follow more or less the moving water line during incoming and receding tide, but many Curlews remain to feed for hours on the same spot. We saw several individual birds for many hours on the same counting plots near the hides. At least a part of the Curlews were territorial, given the frequency at which the bubbling- call was heard, border disputes were seen and apparent intruders were chased away.

The flats below mean sea level (emersion 50% and less) were exploited most. *Carcinus* were the main prey of the Curlews, especially in summer and spring. In winter, the long-billed females fed on large *Mya*, but *Arenicola* was the most important prey for Curlew, which also explains why the feeding density in win-ter was related to this prey species (Figure 4-3).

It was unexpected that *Arenicola* was the main prey in winter. *Arenicola* can only be taken by birds when the worms come to the surface to defecate. The defecation rate is low from October onwards (Roukema 1984). Apparently enough *Arenicola* remain active in the Oosterschelde to be a prey for Curlews during the winter months (see also Verbiest 1988). Most likely, *Arenicola* is not a reliable food source in winter (being inactive at low temperatures; Cadée 1976). Hence *Carcinus* must be an essential supplement to meet their daily food requirements.

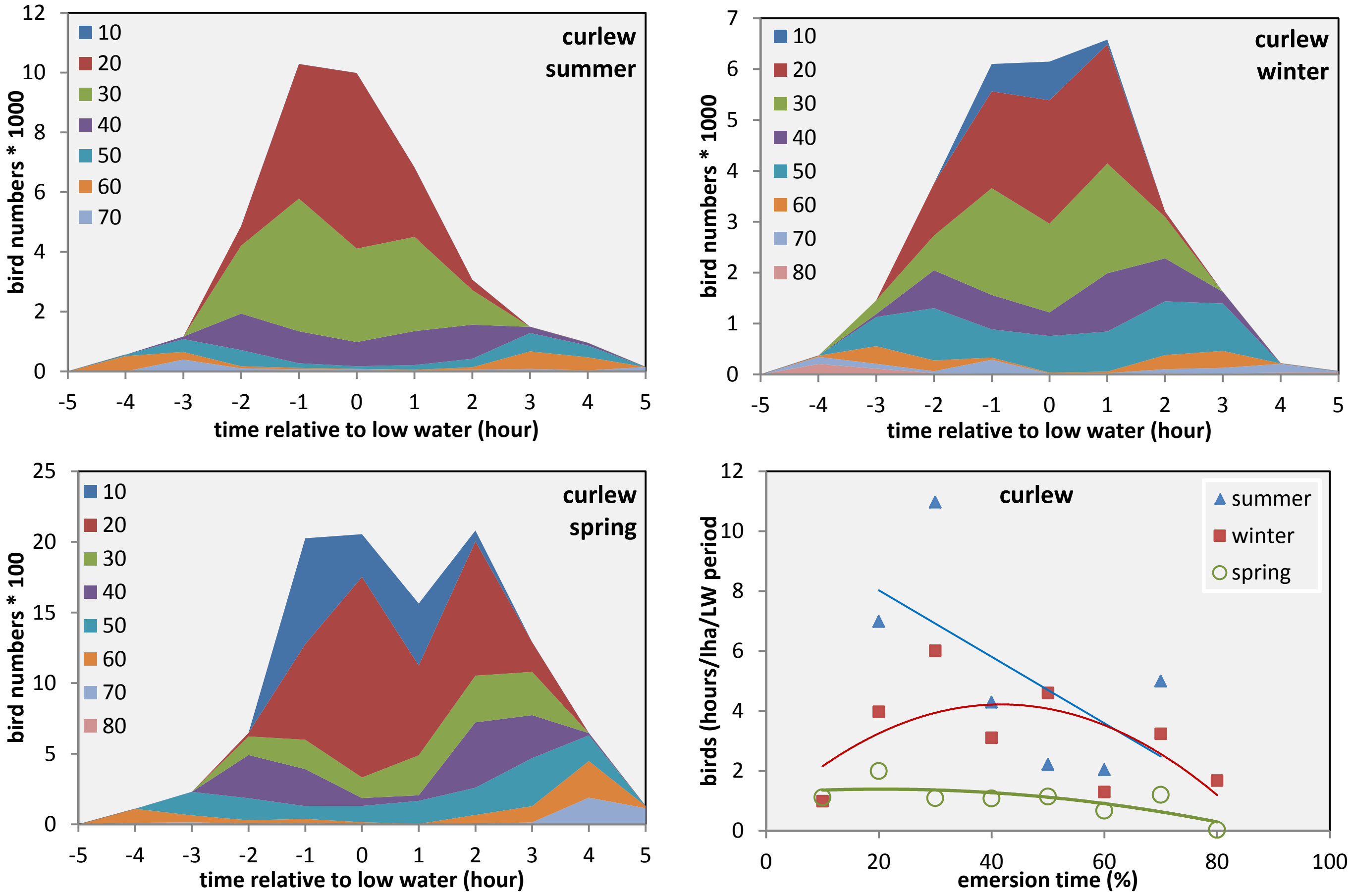


Figure 5-5- *Number of feeding Curlews on the tidal flats and the total explotation (bird hour/ha) on the feeding area during the course of the low water period in summer, winter and spring, given separately for tidal flats with a different emersion time.*

Figure 5-6- *As the tide receded, Curlews walked from the tidal roost to the emerging tidal flats, where most birds took another break. Few Curlews started to feed and followed the receding water's edge, but they had a low feeding success, which explains why the majority of the Curlews waited till more tidal flats had become available for feeding.*

5.4 Bar-tailed Godwit

Figure 5-7 suggests that Bar-tailed Godwits feed for 5 hours and ignore the flats above mean sea level and that they feed during an even shorter time in winter. In contrast, the species would only exploit the high flats in spring. The Bar-tailed Godwits feed in loose flocks and follow the water's edge during receding and incoming tide. That is why they may easily be missed in our system of fixed study sites during a part of the tidal cycle. For instance, the large number of Bar-tailed Godwit present on Viane in spring passed our plots on the high flats, but did not arrive in the lower plots since they foraged in the hours around low water elsewhere on Viane. Thus, although not apparent from the counts, we know from what could be seen from the hides that Bar-tailed Godwit spent 8 hours on the feeding area during spring.

Whether Bar-tailed Godwits feed no more than 5 hours in summer is difficult to say. As far as we could see from the seawall and the boat, birds were so often disturbed by people that they had no chance to feed on the high flats, even in the early morning and late evening. That is why birds flew from the (often disturbed) Dortsman to the (undisturbed) Galgeplaat as soon as the highest part of the latter area was uncovered (2.5-3 hour before low water). In this way they may have extended their total feeding time to 5-6 hours per low water period. Bar-tailed Godwits seen in winter did not feed on the exposed flats but remained to feed in shallow water and thus passed our study sites in a short time. That is why the series of density counts of Bar-tailed Godwits give an incomplete picture of their exploitation of the tidal flats during the winter.

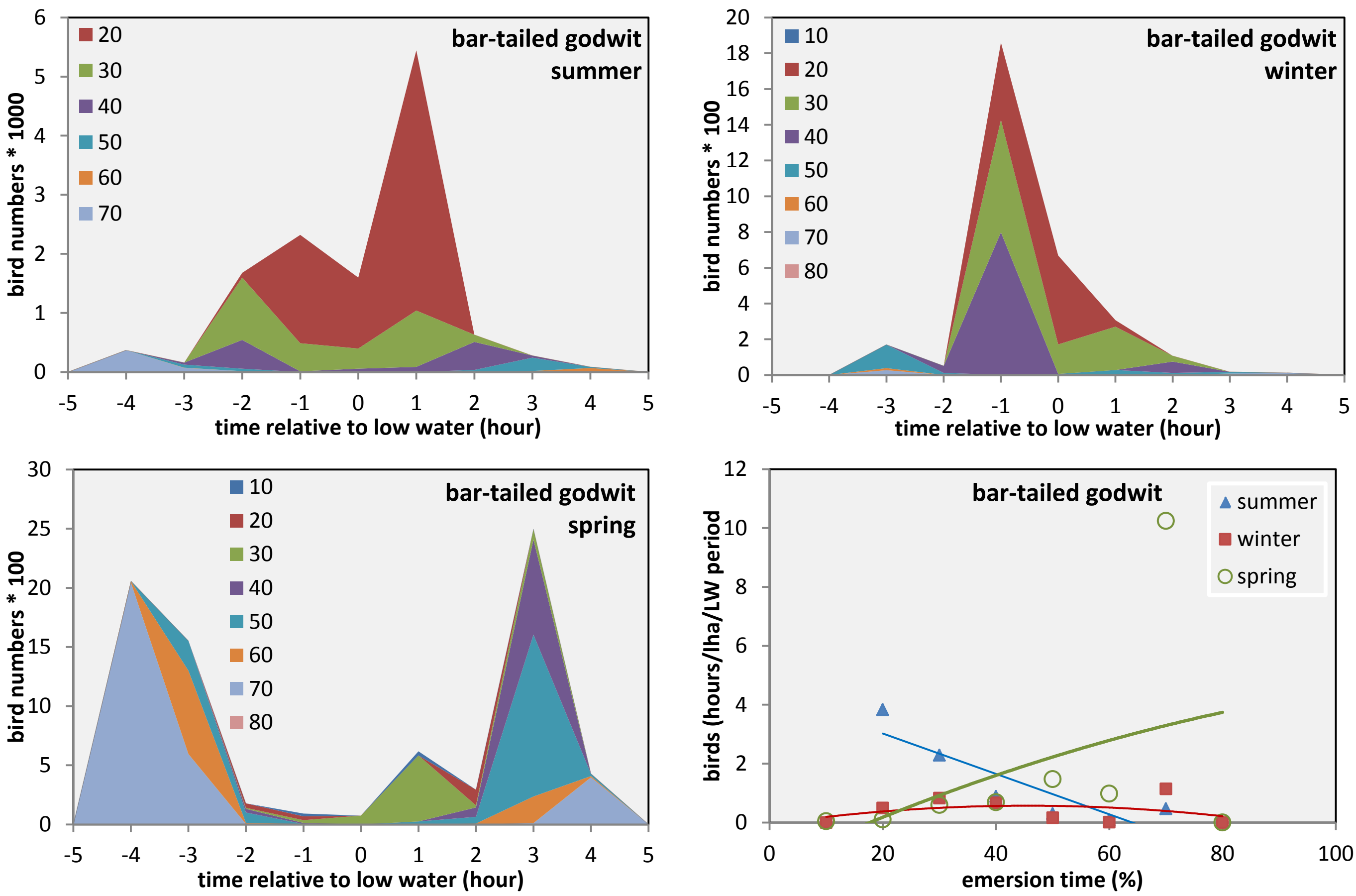
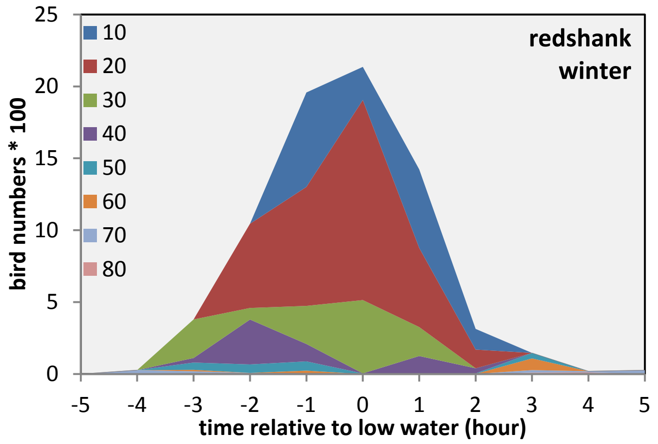


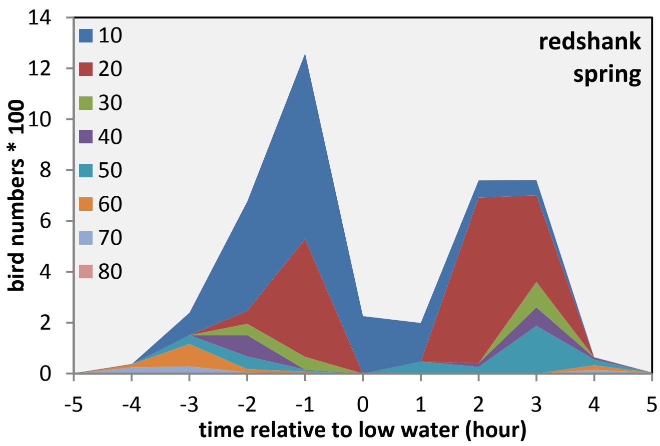
Figure 5-7- Number of feeding Bar-tailed Godwits on the tidal flats and the total explotation (bird hour/ha) on the feeding area during the course of the low water period in summer, winter and spring, given separately for tidal flats with a different emersion time.

5.5 Redshank

Like Bar-tailed Godwits, Redshank feed in loose flocks near the water's line (Figure 5-9). We counted hardly any Redshank in summer. The species was mainly seen on tidal flats below mean sea level, and in spring even only at the lowest part of the tidal flats. They seem to feed remarkably long on the lower flats. The explanation is that most Redshank fed in plots situated along tidal creeks where the altitude within the plots varied more than in the other sites (see section about "Variation in altitude within the plot" on page 13). We still do not know whether Redshank indeed do not feed on the high flats 3-4 hours before and after low water. We also did not observe feeding Redshank outside the study sites.

Figure 5-8- *Number of feeding Redshank on the tidal flats and the total explotation (bird hour/ha) on the feeding area during the course of the low water period in winter and spring, given separately for tidal flats with a different emersion time.*





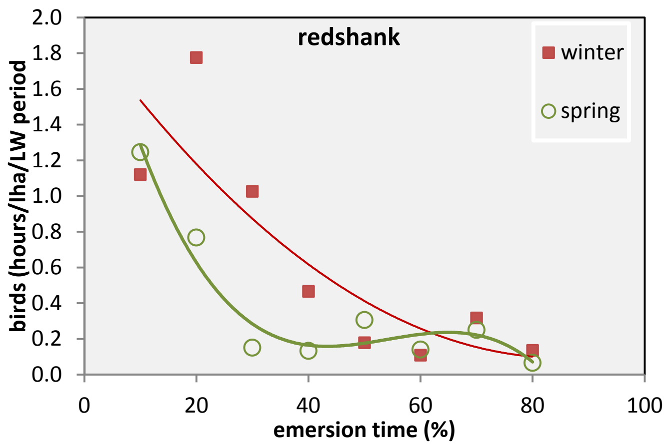


Figure 5-9. *A flock of redshank feeding in shallow water during incoming tide. Note that the birds do not feed in the tidal rim (behind the incoming water line), but remain to feed on the tidal flats just not yet covered by the flood.*

5.6 Greenshank

Greenshank were only seen in some numbers in spring (Figure 5-10). It was the first species to start feeding at receding tide and also the last still present when the highest parts of the tidal flats were covered by water. Thus, it is likely that Greenshank fed more than 10 hours per tidal cycle. Some of them searched for prey in the shallow water along the water's line, but most foraged for 1-2 hours after a flat was uncovered, where they preyed upon small shrimps found in the very shallow water between the sand ripples.

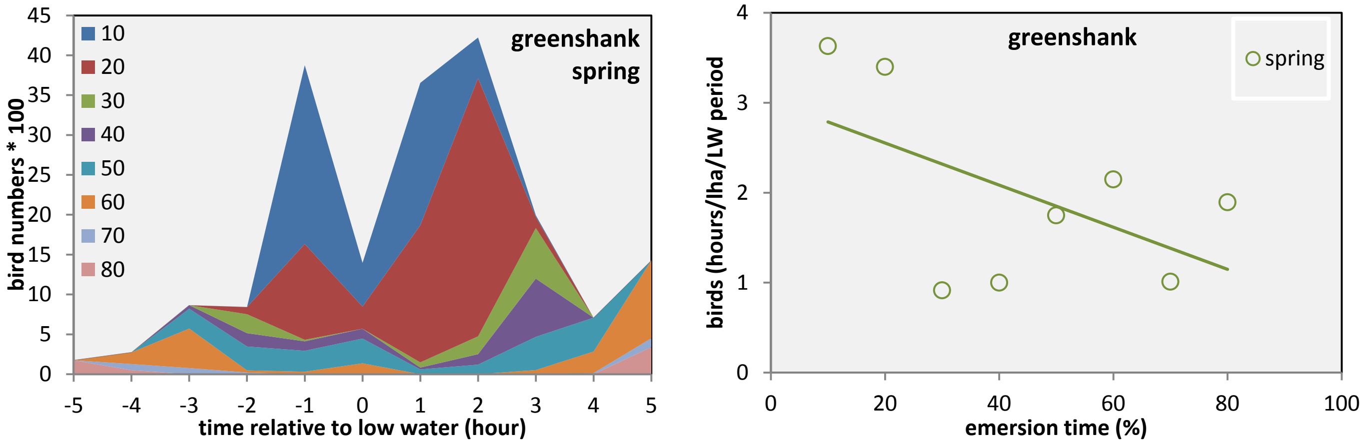


Figure 5-10- *Number of feeding Greenshank on the tidal flats and the total explotation (bird hour/ha) on the feeding area during the course of the low water period in spring, given separately for tidal flats with a different emersion time.*

5.7 Dunlin

Dunlins foraged in flocks moving over the tidal flats. That is why the registered numbers fluctuated from count to count. Nevertheless, it is obvious that Dunlins in winter exploit the entire tidal zone from the high to the low water line (Figure 5-11). Their total feeding time amounted to 8-9 hours.

Dunlins fed on worms (*Scoloplos, Nereis* and possibly also *Heteromastus*) which they can find along the entire range between the high and the low water line (Figure 3-4).

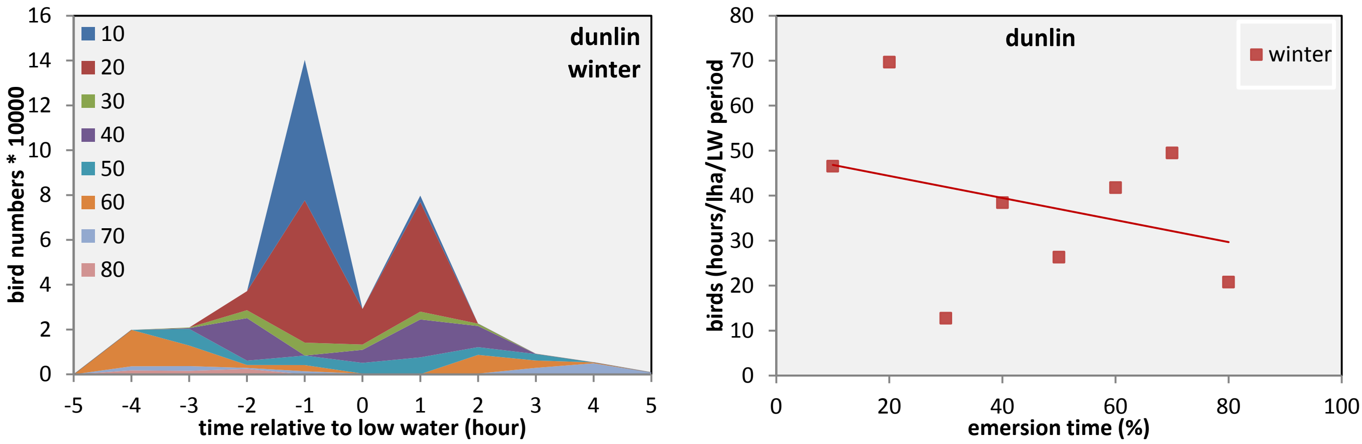


Figure 5-11- *Number of feeding Dunlins on the tidal flats and the total explotation (bird hour/ha) on the feeding area during the course of the low water period in winter, given separately for tidal flats with a different emersion time.*

5.8 Knot

Nearly all Knot we saw in winter were concentrated along the Oesterdam, of which most on the high flats (Figure 5-12) where *Hydrobia* was common (Figure 4-5). At low water most of them moved to tidal flats just outside the counting plots. *Hydrobia* only occurred on the high flats (Figure 3-4), thus Knot must have switched to an alternative prey for some hours at low water. Knot in spring were concentrated on the Roggenplaat where they took *Macoma*. Their presence in the study site was irregular.

The total feeding time amounted to 9 hours in winter.

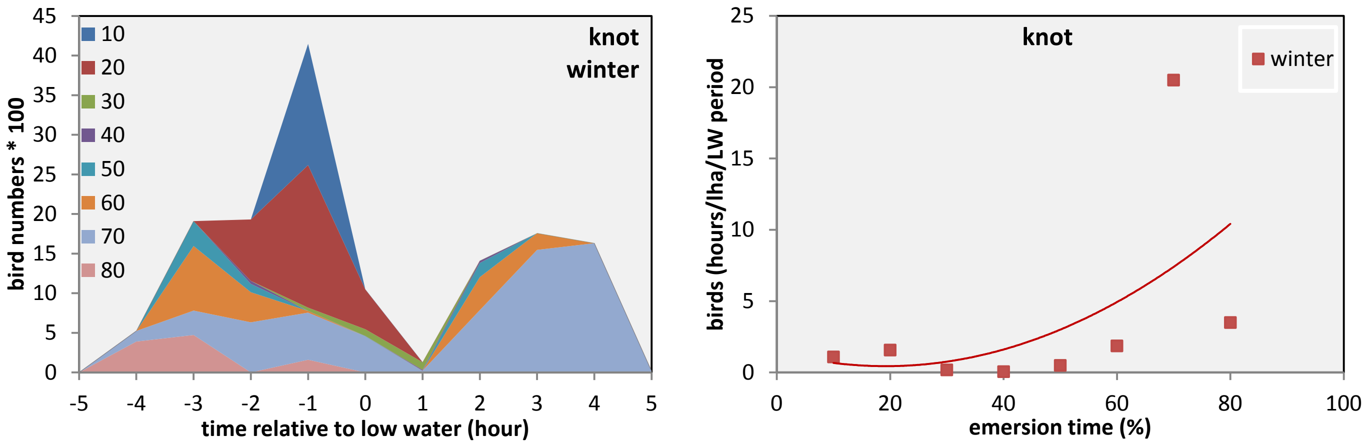


Figure 5-12- *Number of feeding Knot on the tidal flats and the total explotation (bird hour/ha) on the feeding area during the course of the low water period in winter, given separately for tidal flats with a different emersion time.*

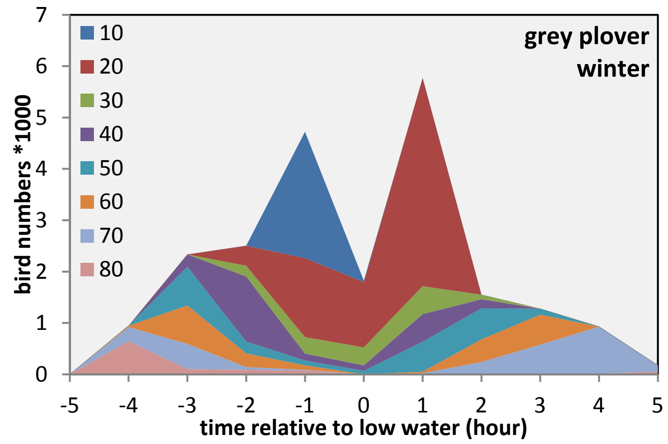
Figure 5-13 *Knot preying on* Hydrobia *had to feed on the high flats nearby the saltmarsh and the seawall, a landscape having not much in common with the vast wide-open tidal flats where they usually are found.*

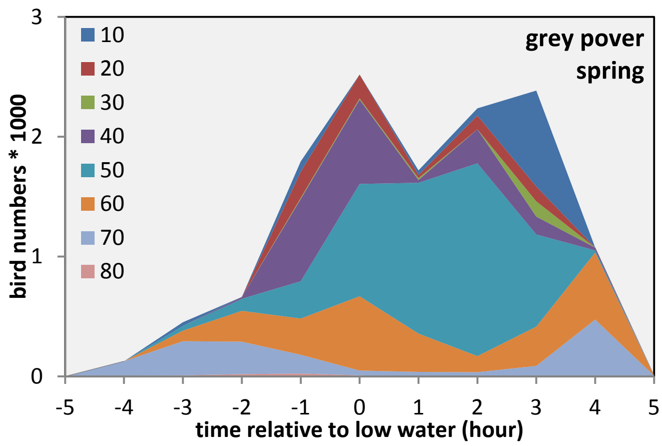
5.9 Grey Plover

Grey Plovers follow the receding water line, but with a retardation of an hour. That is why they were sometimes the only birds feeding in plots being exposed already for some time. They start feeding when the flats being exposed for 70% (spring) or 80% (winter) become available (Figure 5-14) and continue to do so until these high flats are immersed again. Their total feeding time amounted to 8-9 hours in winter and that is probably the same in spring.

Grey Plovers preyed on *Arenicola*, *Nereis* and smaller worms. These prey can be found on the lower as well as higher flats (Figure 3-4).

Grey Plovers are the only wader species for which the intertidal flats at, and above, mid sea level (emersion time of 50-70%) are more important than the flats below mean sea level, at least in winter and spring. This preference may be a problem in summer, given the frequent disturbance of the upper tidal flats along the shore. Unfortunately, Grey Plovers were hardly seen in summer, but it is not possible to indicate their use of high and low flats at different tidal states.





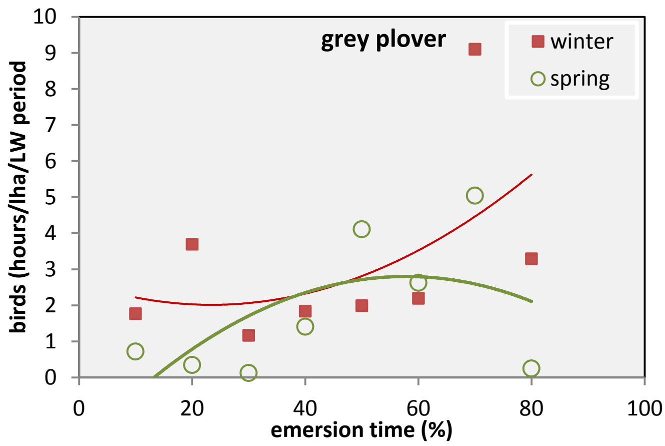


Figure 5-14- *Number of feeding Grey Plovers on the tidal flats and the total explotation (bird hour/ha) on the feeding area during the course of the low water period in winter and spring, given separately for tidal flats with a different emersion time.*

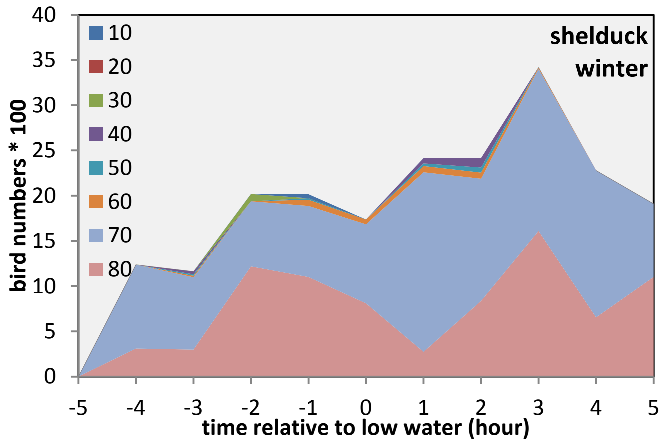
5.10 Shelduck

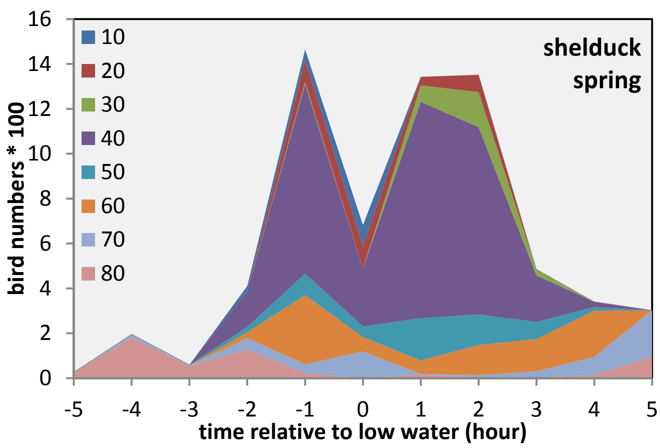
Shelduck was absent from most study sites, but many birds were concentrated near the Oesterdam. In winter, the birds selected within this site the higher flats, also at low water. In contrast, the few birds still present in spring followed the water line between high water line and tidal flats being exposed for 40% (Figure 3-17). The Shelduck in winter were concentrated where *Hydrobia* were the most common (Figure 4-5), but in spring they must have taken other prey given the lack of overlap in the distribution of Shelduck and *Hydrobia*.

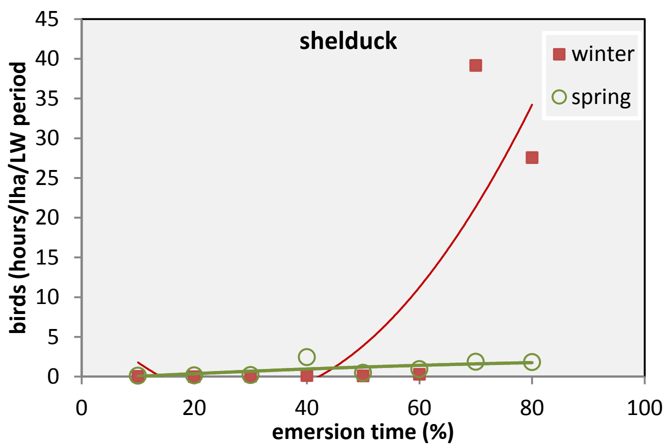
The total time spent on the tidal flats amounted to 10 hours in winter and 5 hours in spring. That does not imply that the actual time spent feeding was in winter twice as long as in spring. Shelduck spent in winter much time on the tidal flats, but many birds were inactive between two hours before to two hours after low water. In contrast, all Shelduck were actively feeding in spring during the five hours they were present on the tidal flats.

Hydrobia is the staple food of Shelduck in NW Europe, also in the Oosterschelde (Meininger & Snoek 1992). It is an unreliable food resource, however, showing a large year-to-year variation in their density. Their density in the Oosterschelde was very high in 1985 (14000 snails/m^2 on average), but low in 1989 1000/m^2) and even much lower in our own sample programme (62/m^2 in 2009 and 189/m^2 in 2011; Table 3-1).

Figure 5-15- *Number of feeding Shelduck on the tidal flats and the total explotation (bird hour/ha) on the feeding area during the course of the low water period in winter and spring, given separately for tidal flats with a different emersion time.*





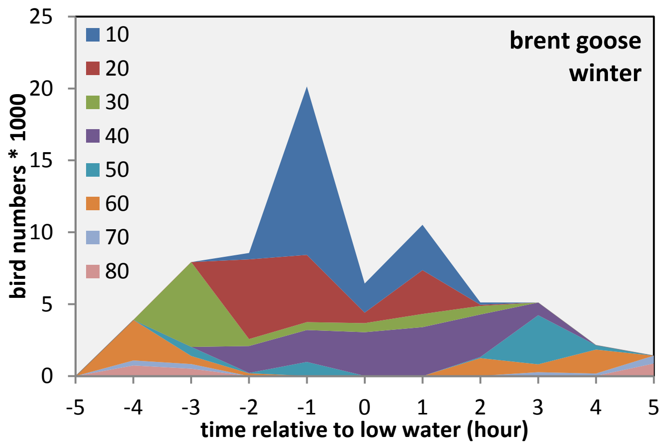


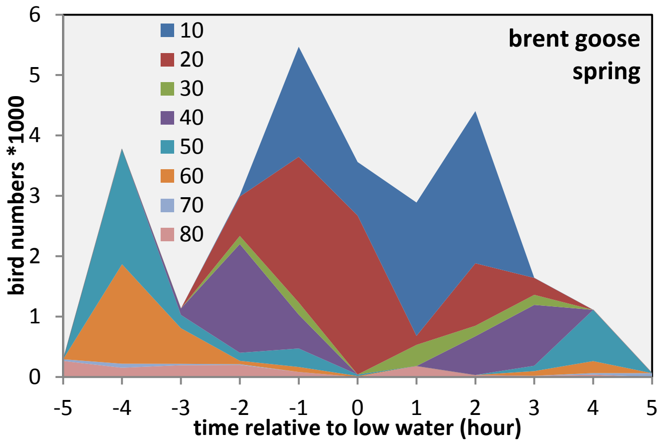
5.11 Brent Goose

Bent Geese in our study sites fed on *Ulva* and other marine green algae. They prefer to feed in shallow water and not on dry sediment. That is why they move continuously depending on the tidal stage (Figure 5-16). They may also feed in deeper water with head and neck below surface. That is why Brent Geese were usually the first birds seen in the counting plots during the ebb and the last ones to leave at incoming water. The total time spent on the feeding area is estimated at 7-8 hours in winter 8 hours in spring.

Brent Geese exploited the entire range of the tidal zone between high and low water line, but the grazing pressure on the lower shore was a bit higher than on the higher shore.

Figure 5-16- *Number of feeding Brent Geese on the tidal flats and the total explotation (bird hour/ha) on the feeding area during the course of the low water period in winter and spring, given separately for tidal flats with a different emersion time.*





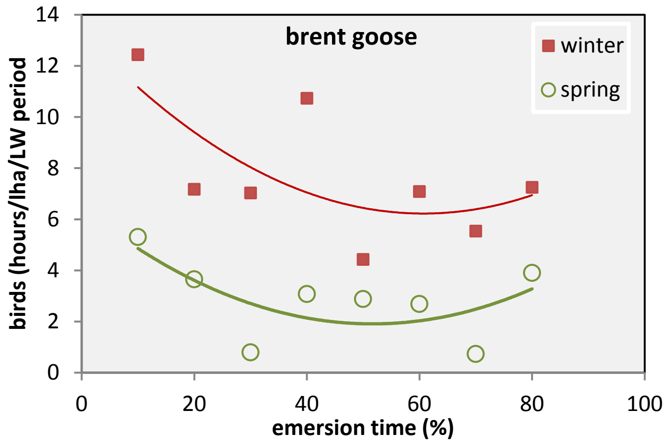


Figure 5-17- *Brent Geese, and a single Shelduck, feeding in shallow water during incoming tide; Oesterdam, december 2010.*

5.12 Black-headed Gull

Black-headed Gulls were in summer the first estuarine bird species which left the high water roost to start feeding along the water line. They followed the water line (Figure 3.18) and at low water most were feeding near the low water line. Since we had in summer no counting plots near the low water line, we missed the latter numbers. This also explains the apparent decline of the total number of feeding birds from two hours before low water onwards. It is of interest to note that from low water onwards more and more Black-headed Gulls flew from the low water line to the higher flats. A part of the Black-headed Gulls on the Rattekaai preyed upon *Heteromastus* in this tidal stage, but most birds walked well distributed over the exposed tidal flats in the very shallow water to pick up *Crangon*. The number of birds feeding in the incoming water's edge was limited.

Black-headed Gulls spent in summer 7-8 hours on the tidal flats and used dependent on the tidal stage all tidal flats, but the predation pressure was maximal on the higher flats. The situation was completely different in spring when they ignored the high flats and birds were only seen on the lower flats near the low water line. The duration of their total feeding period was not more than 3-4 hours.

A likely explanation of this large difference is that the density of *Crangon* left on the exposed higher flats during low water was high in summer (Figure 3-10), but (too) low in spring. The samples taken in winter suggest indeed that the few *Crangon* present within the tidal zone are mainly found at the lower shore (see section 3-2). This is not the entire story, however. Greenshank exploited the higher flats in spring (Figure 5-10), where they preyed upon *Crangon*. Either both species selected other size classes and/or Greenshank accepted a lower prey density than Black-headed Gulls.

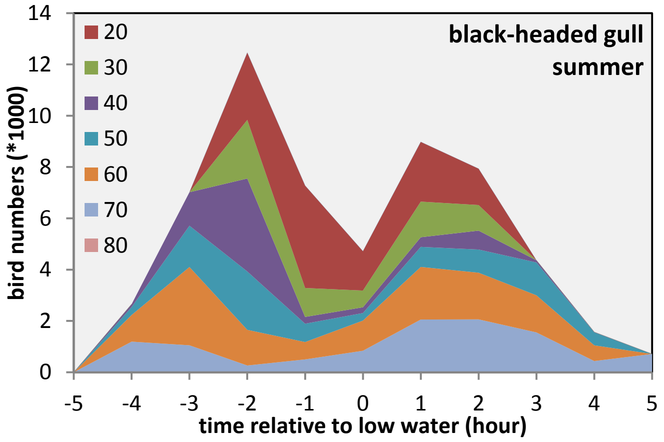
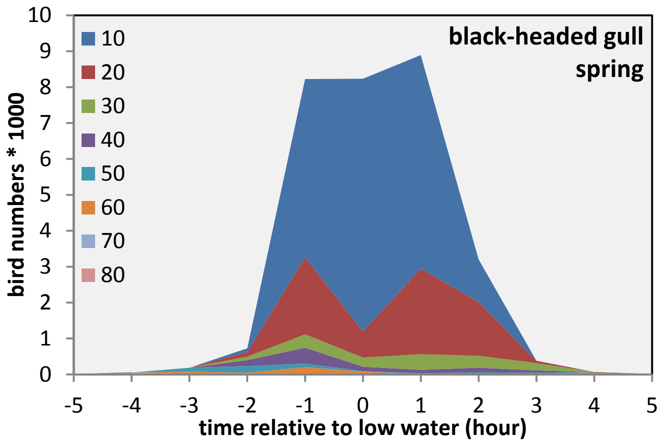
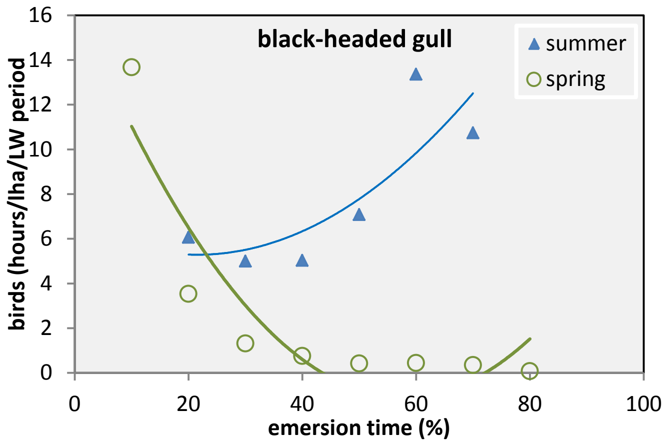


Figure 5-18- Number of feeding Black-headed Gulls on the tidal flats and the total explotation (bird hour/ha) on the feeding area during the course of the low water period in summer and spring, given separately for tidal flats with a different emersion time.





5.13 Herring Gull

The way in which Black-headed Gulls and Herring Gulls exploited the tidal habitat do not differ much in summer and spring. Both species followed the water line during the ebb but during incoming water they flew to the higher flats to feed there; both species were also mainly found on the lower shore in spring (Figure 5-19). Nonetheless, they fed on different prey species. Herring Gulls preyed on large *Carcinus*, although they were seen eating flatfish during low water (sometimes dead ones washed ashore). They ignored the many small *Carcinus* and we have also not seen that they took *Crangon*. Herring Gulls could plunge-dive to capture for *Carcinus* at receding and incoming tide, but at low water they walked long distances to find large crabs. Where green algae were present, the flaps were turned around to detect *Carcinus*. In late summer, a large part of the tidal flats near the Rattekaai was covered by green algae (below which many, large *Carcinus* were present), which must have been the main reason why so many Herring Gulls were concentrated here (Figure 4-2).

The total time spent on the feeding area is estimated at 5-6 hours in winter and 5 hours in spring.

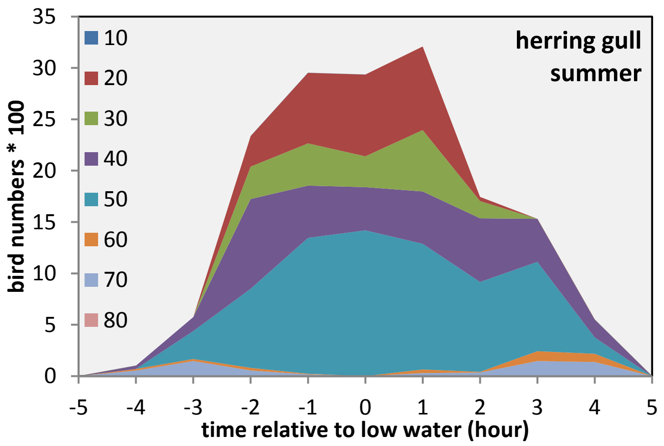
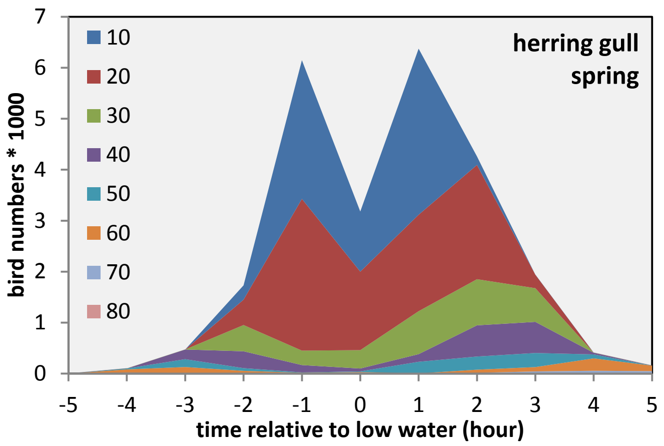
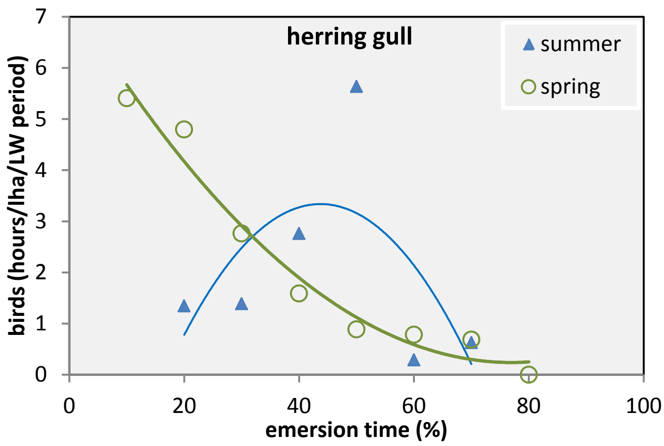


Figure 5-19- *Number of feeding Herring Gulls on the tidal flats and the total explotation (bird hour/ha) on the feeding area during the course of the low water period in summer and spring, given separately for tidal flats with a different emersion time.*





6 Discussion: erosion

What has been the impact of the erosion on the tidal flats on the estuarine bird species? A straightforward answer cannot be given, due to all other changes going on in the Oosterschelde (see below), but the data summarized in this report can be used to give a preliminary indication of the current loss of feeding possibilities for the bird species concerned.

The overall trend is a declining emersion time of the tidal flats (Figure 1-2), but the trend is different for tidal flats being exposed for a short or long time. The surface area being exposed during at least 40% of the time became smaller, whereas there are now much more tidal flats with a short emersion time (<20%) than 25 years ago (Figure 6-1).

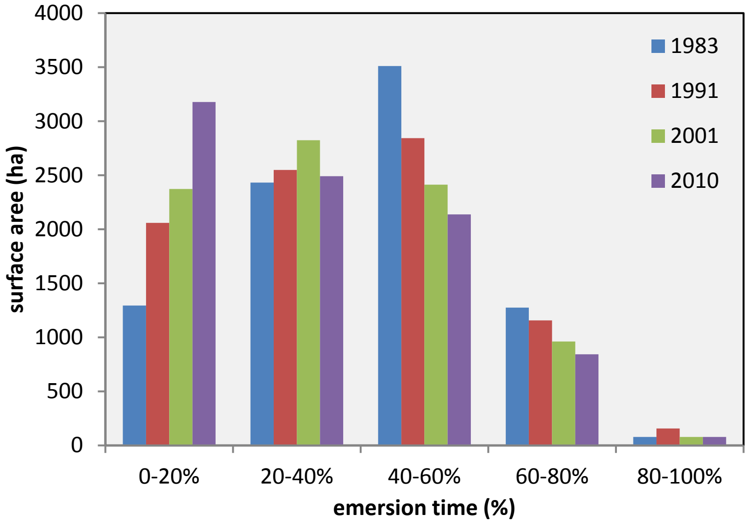
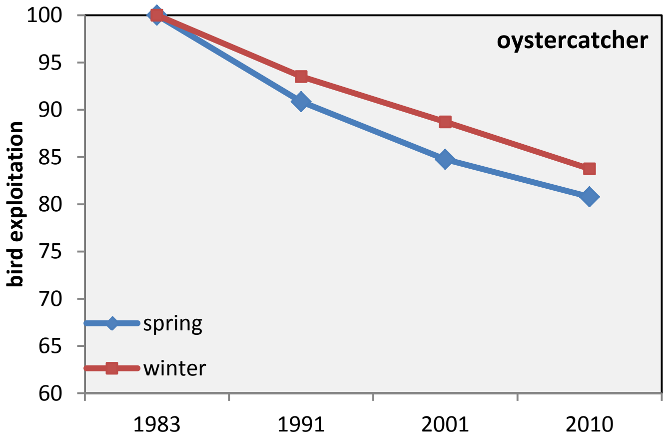


Figure 6-1- *The surface area (ha) of tidal flats in the Oosterschelde in 1983, 1991, 2001 and in 2010 being exposed for <20%, 20-40%, 60-80% and >80% of the time. From: Geurts van Kessel (2004). The surface area in 1983, 1991 and 2001 has been measured; 2010 was forecasted.*

Some birds feed more on the higher parts of the intertidal zone (Grey Plover, Shelduck) and others more on the lower parts (e.g. Curlew). The changed emersion periods, as shown in Figure 6-1, imply that the Grey Plover would have been more affected than the Curlew. To what degree the different species have lost feeding time can be quantified using the data summarized in chapter 5. For each emersion category, we multiplied the bird exploitation (bird hours /ha in winter or spring; chapter 5) by the surface area in the same emersion class in either 1983, 1991, 2001 or 2010 (Figure 6-1). These figures were summed to get the total bird exploitation per season in 1983, 1991, 2001 and 2010. The changes in the total bird exploitation relative to 1983 are shown in Figure 6-2.

Figure 6-2 is based on the assumption that the total bird exploitation per emersion class is invariable. In other words, the graph shows the changes in the bird exploitation as far it can be derived from the gain and loss of tidal flats with different emersion times. The predicted loss is very large in two species feeding on the higher tidal flats (Shelduck and Grey Plover; 30%) and large in Oystercatcher, Bar-tailed Godwit and Knot (20%), but less or (still) absent in the other species (Figure 6-3).

Figure 6-2- *(next page). The predicted change in bird exploitation in the Oosterschelde assuming that the exploitation (bird hours/ha per emersion class), such as measured in 2009-2011 (chapter 5) has been exactly the same in 1983, 1991, 2001 and 2010. Hence the predicted change in bird exploitation as shown in the figure is assumed to be fully due to the change in the surface area being exposed during <20%, 20-40%, 40-60%, 60-80% and >80% of the time (Figure 6-1).*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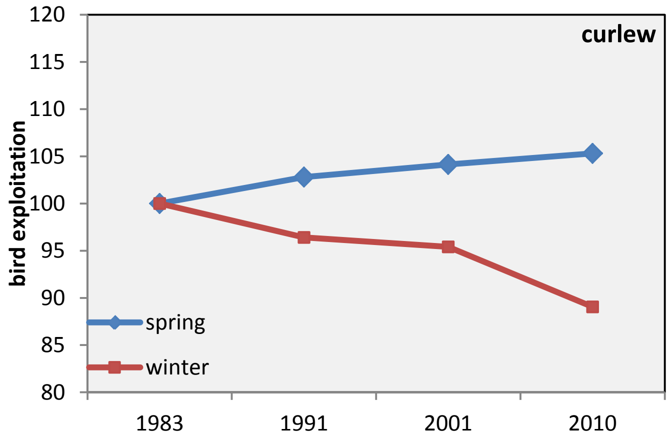
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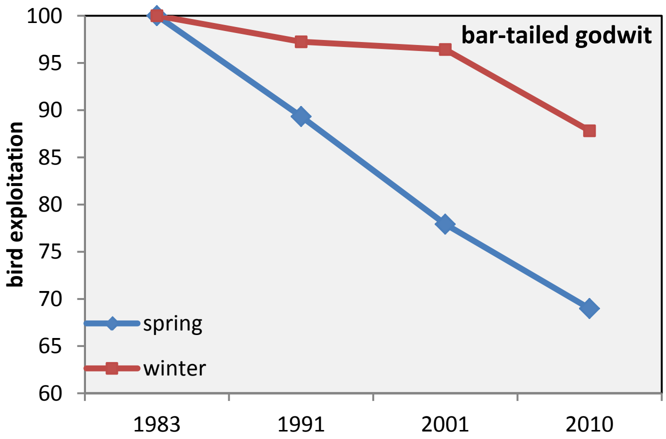
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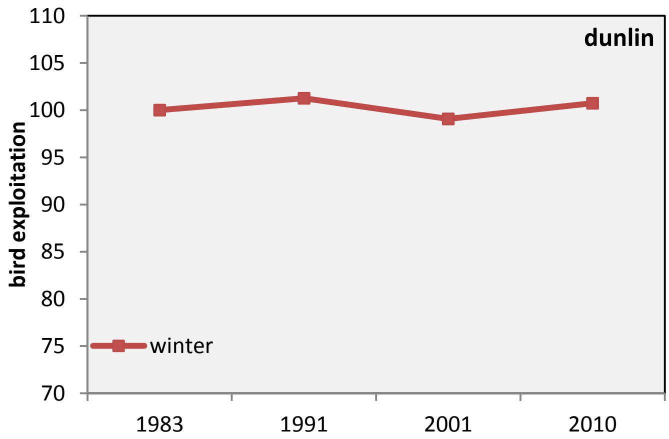
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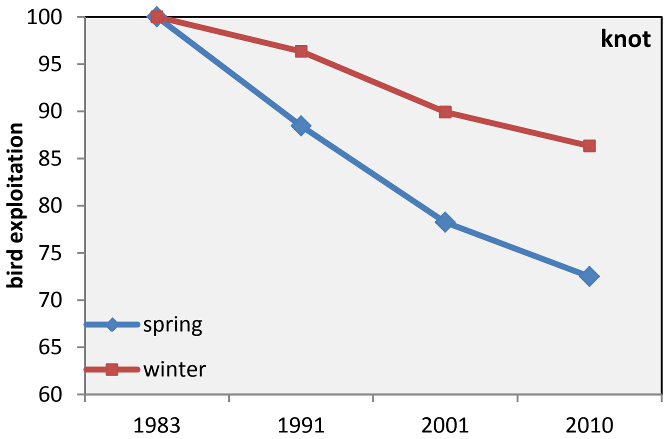
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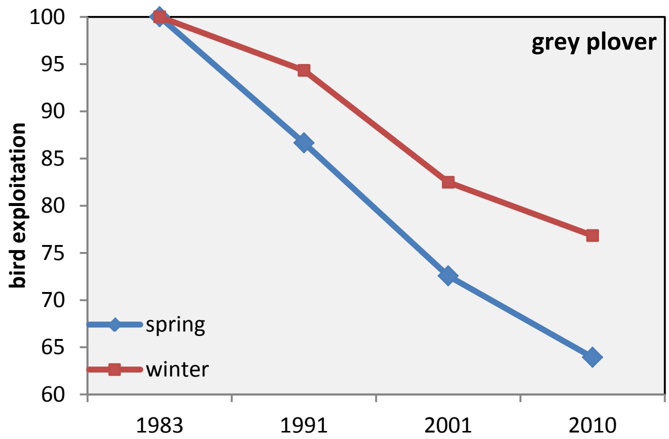
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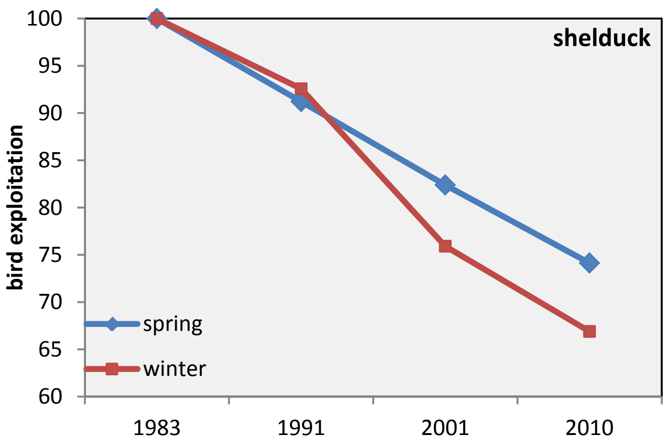
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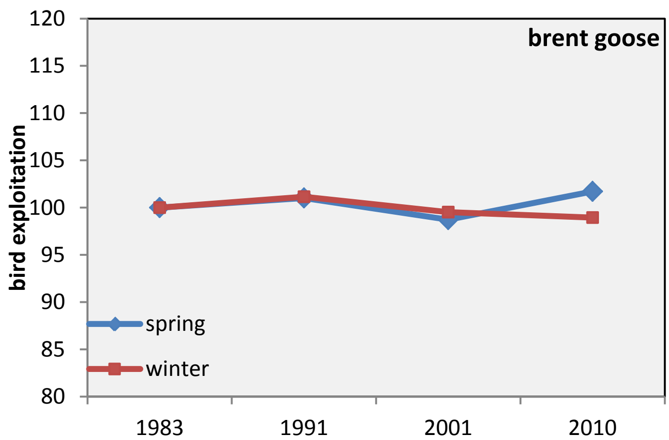
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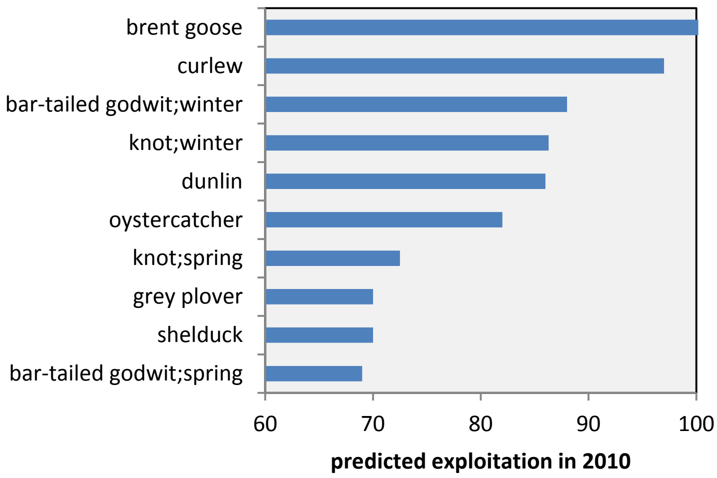

Figure 6-3- *The predicted change in bird exploitation in the Oosterschelde between 1983 (set at 100) and 2010, assuming that the exploitation (bird hours/ha per emersion class), such as measured in 2009-2011 (chapter 5) has been the exactly the same in 1983. Same data as Figure 6.2.*

The trends shown in Figure 6-2 have to be interpreted as a preliminary stress index and not as a prediction how the bird populations should have changed. For one reason, it is unlikely that birds would not have attempted to adjust their exploitation of the tidal zone if they meet such a large change as shown in Figure 6-1. On the other hand, the current erosion limits the possibilities for the birds to feed and this is certainly true for the species feeding on the higher tidal flats. If erosion is already a problem for the feeding birds, one might expect that, other things being equal, the actual population trends would reflect the impact of erosion as shown in Figure 6-3. The monthly bird counts give the opportunity to check this supposition.

Strucker *et al*. (2011) give the population trends for different species in terms of indices. They have taken together the counts carried out in 1987-1991 and in 1992-1996 and calculated the annual index for all recent years. Figure 6-4 shows the population trend of the Oystercatcher and the Curlew.

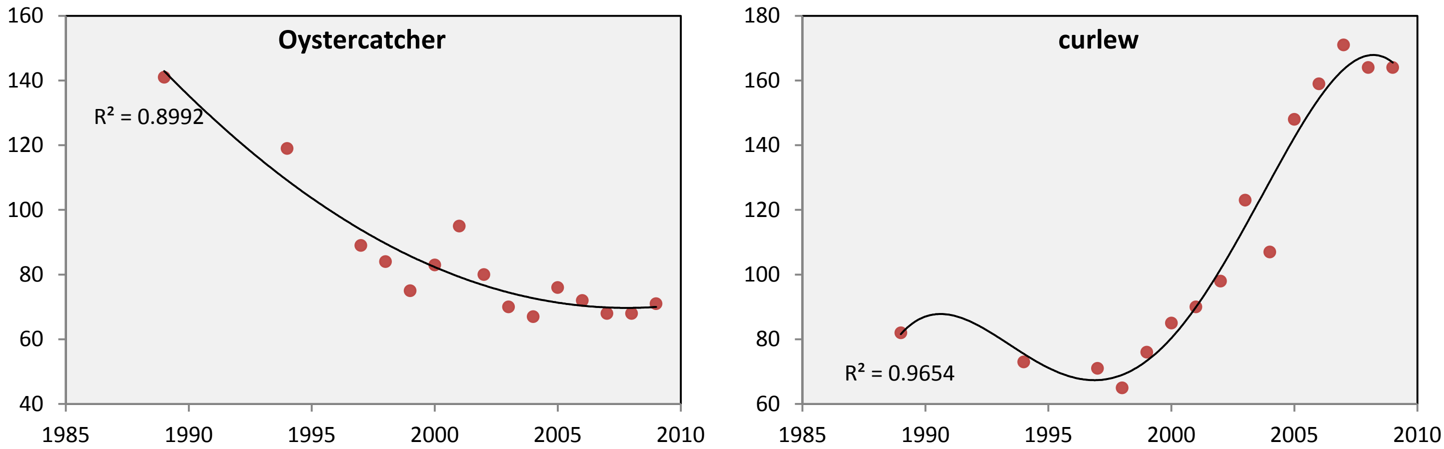

Figure 6-4- *The change in numbers of Oystercatchers (left) and Curlews (right) present in the Oosterschelde, expressed as indices. The indices are based on monthly counts; 1987-1991 and 1992-1996 are taken together. From Strucker* et al. *(2011)*

Using Strucker's data, we calculated the relative change in the counted numbers between 1987-1991 and 2007-2009 (Table 6-1; Figure 6-5).The population of the Oystercatcher has been more than halved, while the Curlew become twice as common. On average, the species showed an increase of 16%.

species	1987/91	2007/09	change
brent goose	113	93	82.3
shelduck	76	88	116.2
oystercatcher	141	69	48.9
grey plover	100	105	105.3
knot;winter	76	119	156.6
knot;spring	72	107	149.1
dunlin	99	118	118.9
bar-tailed godwit; winter	105	92	87.9
bar-tailed godwit; spring	109	100	91.4
curlew	82	166	202.8

***Table 6-1-** The bird numbers (given as indices) in 1987-1991 and 2007-2009. The last column gives the relative number in 2007-2009 with the number in 1987-1991 set at 100. Data from Strucker* et al. *2011.*

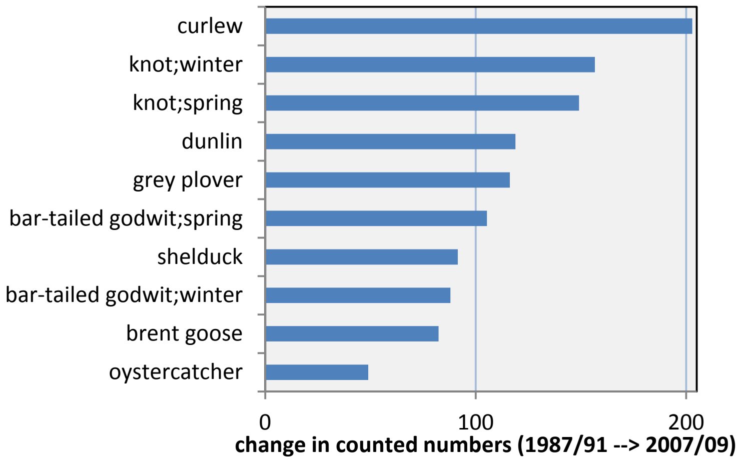

***Figure 6-5-** The actual change in bird numbers in the Oosterschelde between 1987-1991 (set at 100) and 2007-2009. Same data as last column in Table 6-1.*

The predicted change in bird exploitation (from Figure 6-3) and the actual change in numbers (from Figure 6-4) are plotted against each other in Figure 6-6. Evidently, there is no relationship between the population change and the extent to which the predicted exploitation has been declined due to the erosion. Apparently, the feeding conditions in the Oosterschelde birds have changed so much that the negative impact of the erosion has been overruled, and/or the birds have found ways to compensate for reduction in the available surface area and available feeding time.

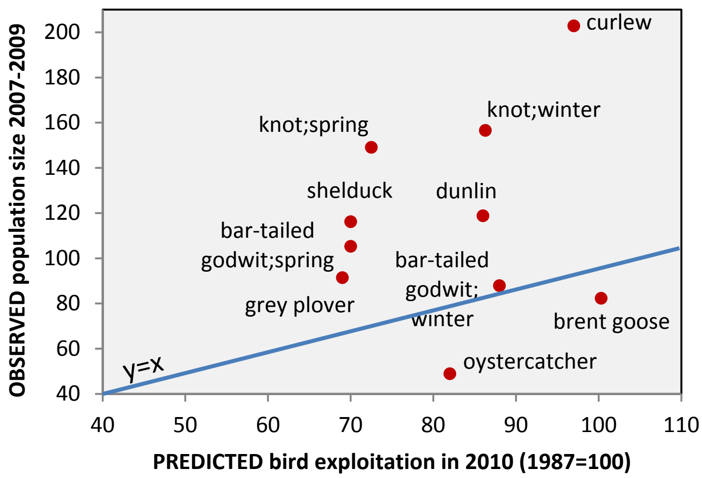

***Figure 6-6-** The actual change in bird numbers (Figure 6-4) as a function the predicted change in bird exploitation (Figure 6-3).*

7 Discussion: food

7.1 Changes in the food supply

Much has changed in the Oosterschelde since the storm-surge barrier has been built, although several of these changes have nothing to do with the barrier itself. Erosion of the tidal flats is but one of these changes having a negative impact on the birds (Figure 6-2). This makes it more difficult to use empirical data (such as population trends of birds) to evaluate the ecological effects of erosion, and use such an analysis to make predictions how bird numbers will change at a further loss of tidal flats. Any evaluation of the impact of the eroding of tidal flats on estuarine birds has to take into account the impact of contaminating factors which have, or may have, contributed to the on-going changes in the feeding conditions of the estuarine bird species.

Seven changes, beside eroding tidal flats, can be mentioned:

- change in the food supply: (1) disappearance of intertidal mussel beds, (2) increased cover of Pacific oyster beds in the tidal zone,
- changing conditions having an impact on the food supply: (3) increased cover by *Ulva* and other macroalgae, (4) higher water temperature, (5) possibly higher water coverage,
- changing conditions having an impact on the exploitation of the food supply: (6) increased human disturbance, (7) increased predation risk.

Disappearance of mussel beds

No intertidal habitat attracts so many birds as a mussel bed, up to 100-200 birds/ha (Zwarts 1991b). Oystercatchers are always the most numerous bird species on mussel beds. They are the only bird species being able to open large *Mytilus* (beside crows and gulls dropping Mussels from the air on a hard substrate). Some birds depend on (stolen) mussels after being opened by Oystercatchers (Common and Herring Gull) or eat the flesh remaining in the shell (e.g. Grey Plover, Turnstone). Other bird species feed on the many other prey found between the mussels, below the *Fucus* and in the tidal pools between the mussel ridges (e.g. *Carcinus*, *Crangon*, goby fish). Moreover, due to the presence of mussels, the surrounding is more silty and enriched, attracting still more birds. A quarter of all birds in the Dutch Wadden Sea was concentrated on the mussel beds in the 1970s, although they covered only 3% of the intertidal flats (Zwarts 1991b). That is why the disappearance of intertidal mussel beds had such a large impact on the entire estuarine ecosystem (Beukema & Cadée 1996).

Many birds in the Oosterschelde used tidal mussel beds, and its direct surroundings, as feeding area (Meire *et al.*1994b; his plots 6, 10 and 22 in his Figures 4 and 5). That is why the disappearance of tidal mussel beds from the Oosterschelde in the early 1990s (van Berchum & Wattel 1997) had the same large negative impact on the waders as in the Wadden Sea.

The disappearance of the *Mytilus* from the tidal flats affected the Oystercatcher the most, since *Mytilus* were, beside *Cerastoderma* the major winter prey for this bird species. Oystercatchers may also feed on burrowing bivalves (*Macoma*, *Scrobicularia*) or worms (*Nereis*, *Arenicola*), but these prey are only taken in the summer months, being in winter unprofitable due to their larger burying depth and rarely accessible (review in Zwarts *et al.* 1996a, 1996c). *Mya* may be an important prey but only when they are two years old (being as first-year too small and as after their second growing season too deeply buried). In the rare circumstances that *Mytilus* as well as *Cerastoderma* (or second-year Mya) are absent, Oystercatchers are forced to feed in winter on the just-mentioned “summer” prey, but their intake rate during feeding (and thus their daily consumption) is too low to survive the winter (Camphuysen *et al.* 1996; Zwarts *et al.* 1996c).The mass winter mortality of Oystercatchers in the Oosterschelde in the mid-1980s was also due to a combined effect: low temperatures and a low food supply (Blomert & Meininger 1998; Duriez *et al*. 2009).

Increased cover by oyster beds

The cover by reef structures of Pacific Oyster *Crassostrea gigas* in the intertidal zone of the Oosterschelde increased from 25 ha in 1980 to 8100 ha in 2003 (Kater & Baars 2004). The species can be a threat for other filter feeding bivalves depending on the same food supply, but also have a positive impact on the ecosystem (Troost 2010). Like mussels, oysters enrich the surroundings, tidal pools come into existence and several species, being important prey for birds, may establish in and around oyster beds. Wijsman *et al.* (2007) found indeed more waders (Oystercatcher, Curlew, Dunlin) feeding on oyster beds than on control sites without oysters. Some of our plots (in the SE corner of Viane-low and SE-corner of Galgeplaat) were partly covered by oysters. These plots were visited by Oystercatchers, Curlews, Redshank and Greenshank, but their density was not much higher than on surrounding tidal flats.

More observations are needed to know to what degree oyster beds replace the former function of mussel beds as attractive feeding site for waders.

Figure 7-1- *Oyster beds may be attractive feeding areas for birds although they do not eat oysters themselves (beside an occasional Oystercatcher). Mussels use (dead) oysters to settle (attracting Oystercatchers).* Carcinus *live between the oysters (being a prey for Curlew and other crab-eating bird species). Tidal pools become in existence between the reefs, offering an easy food supply for birds feeding on* Crangon *and goby fish (such as Spoonbills shown on the photo). The bare patches between the oyster beds may attract more birds, since there is more food (e.g.* Nereis *and other worms) due to a change in the sediment composition (higher fraction of clay and very fine sand; more organic matter).*

Increased cover by *Ulva* and other macroalgae

De Jong (1987) predicted in 1987 that macroalgae would increase in the Oosterschelde due to the changing ecological conditions. The macroalgae have increased so much that they form thick mats and cover, especially in the south-eastern part of the Oosterschelde (van Berchum & Wattel 1997). Since few animals can live beneath these mats, this reduces the food supply for waders (e.g. Rafaelli 2000). The only bird species we have seen feeding on these mats was the Herring Gull, being able to extract large *Carcinus* from beneath these mats.

Figure 7-2- *Green mats covering a large part of the tidal flats near the Rattekaai in August 2009. Beside Black-headed Gulls and Herring Gulls, the area was hardly used by other birds.*

Higher water temperature

The sea water temperature in the Oosterschelde during the summer has increased by 1.5 °C, from 17.6°C to 19.1 °C on average, in less than 30 years (Geurts van Kessel 2004). The increase of the sea water temperature along the Dutch coast is partly due the climate change (Van Aken 2008), but the warming up of the sea water in the Oosterschelde is larger than elsewhere due to the reduced exchange of water between North Sea and the Oosterschelde since the construction of the storm-surge barrier.

The winter temperature determines the annual variation in the biomass of the macrobenthos to a large degree (*e.g*. Beukema & Dekker 2005, Beukema *et al*. 2009). During a severe winter there is mass mortality, but after such a winter the recruitment is more successful. The recruits survive better after a severe winter, because *Crangon*, being a major predator on these juveniles, appear later on the tidal flats after severe winters.

Crangon and *Carcinus* grow up in the tidal zone, but retreat into deep water as soon as the sea water temperature goes down in autumn. Both species reappear on the tidal flats in spring, although not yet on the high shore and in the most shallow water. The higher sea water temperatures in the Oosterschelde must have extended the period during which *Crangon*, but also *Carcinus* remain present on the tidal flats. In any case, we saw birds still eating them in December and also found both prey species on the tidal flats of the Dortsman at air temperatures around 0 °C.

The current higher sea water temperatures (and associated larger numbers of *Crangon* in spring in the lower part of the tidal zone) limit the possibilities for Cerastorderma to settle on the lower part of the flats. This must be the reason for the observed upward shift of *Cerastoderma* in their distribution along the tidal gradient in the Oosterschelde (Kater *et al.* 2006). The growth rate of *Cerastoderma* declines with a shorter immersion time (as shown by Kristiansen (1957) and many others since then), thus *Cerastoderma* occurs now in the Oosterschelde in a limited, and –regarding their production– also not optimal, range of the tidal zone. As a consequence, the food supply of Oystercatchers is reduced.

Increased water coverage?

80% of the Dortsman was covered by shallow water at low tide (Figure 3-11). Although not deeper than 12 mm, on average, it was sufficient for juvenile *Crangon* to live. Also, other tidal flats in the Oosterschelde remain covered by water during their exposure. Is a water coverage of 80% higher than on tidal flats elsewhere? Measurements in the Wadden Sea reveal that the water coverage amounts to nearly 80% in sediment with a clay content of 2% declining to 40% in muddy sediment (clay content 10%). The explanation is that soil relief declines with the clay content of the substrate: sandflats have ripples and mudflats stay flat since the sediment flows smoothly (Zwarts 1988; reproduced as Figure 1.5 in van de Kam *et al.* 2004). The clay content of the sediment on the Dortsman is less than 1%, and thus fits well in the just described relationships between height of the ripples, water coverage and sediment composition.

Although quantitative data are lacking, the soil microrelief might have increased on the tidal flats in the Oosterschelde since the construction of the storm-surge barrier (Dick de Jong, pers. comm.) as a consequence of which the tidal flats remain wetter during the low water period than in the past. If true, this might have contributed to the current mass presence of *Carcinus* and *Crangon* on the tidal flats, offering the estuarine bird species in the Oosterschelde such an important food supply during a large part of the year.

Increased human disturbance

Schekkerman *et al.* (1994) and Prop (1999) speculated already that the eastern part of the Oosterschelde was disturbed so often by people that waders avoid these feeding areas. The waders present in late summer are concentrated in the western part of the Oosterschelde where there is no, or hardly any, human disturbance on the feeding areas.

The numbers of tourists in Zeeland have increased during the last dozens of years, while the "tourist season" has been extended from July-August to April-October. But does this imply that there are also more people walking over the mudflats? That is certainly the case in areas where people are allowed to come and which became extremely easily accessible (e.g. Speelmansplaten, Plaat van Oude Tonge), but areas such as Galgeplaat, Roggenplaat, Rattekaai became free of disturbance since they are closed off (Peter Meininger & Dick de Jong, pers. comm.).

The impact of disturbance should not be underestimated. The large tidal flats of the Dortsman, for instance, are hardly used as feeding area in summer. Unfortunately, people tend to walk on the Dortsman at receding and incoming tides, thus at the moment when the birds, in an undisturbed situation, would be concentrated here.

Increased predation risk

Peregrine Falcons have been almost absent from NW Europe due to persecution and the use of pesticides. The species has recovered since the 1970s. Peregrine Falcons were rarely observed in the Oosterschelde during waders counts in the 1970s and 1980s, but since then the numbers have increased to about 10-16 birds since 2003 (Figure 7-3). What did waders do to minimize the risk to be taken? Was there a change in the use of tidal roosts and/or feeding areas? This is still unknown. We also do not know anything about the hunting areas of the falcons. Are the vast, wide-open tidal flats more safe than the areas near to the shore? Van Hout (2000) concludes from his extensive study on raptor predation on waders that these predators through the fear they create have a tremendous influence on the structure and dynamics of shorebird populations and communities, and this is probably not different in the Oosterschelde.

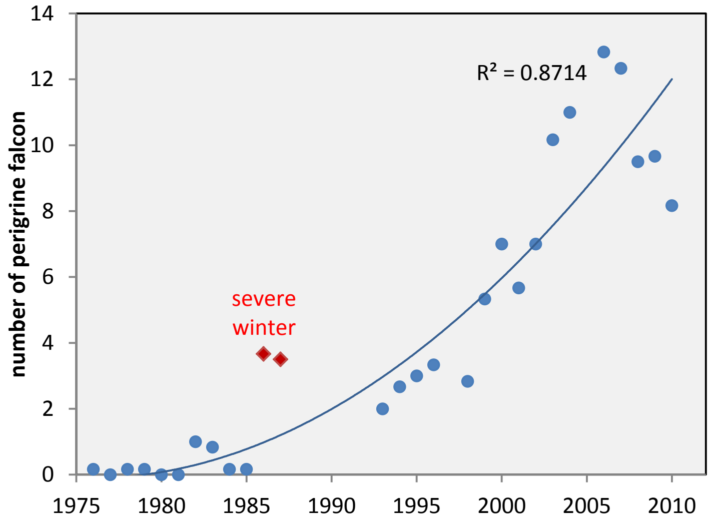

Figure 7-3- *Number of Peregrine Falcons counted in the Oosterschelde, averaged for the monthly wader counts carried out during the winter half year (October – March). The curvilinear regression line is based on all data, except two severe winters.*

Sources: Meininger & van Haperen 1988, Meininger et al. *1984, 1995, 1996, 1997, 1998; Berrevoets* et al, *1999, 2000, 2001, 2002, 2003, 2005, Strucker* et al. *2005, 2007, 2009, 2010, 2011.*

7.2 Changing numbers of waders

Waders and other estuarine bird species have been counted in the Oosterschelde since 1966 and even each month since 1975. All these results have been published in a long series of (annual) reports: Saeijs & Baptist (1977), Meininger *et al.* (1984 - 1998), Berrevoets *et al.* (1999 - 2005) and Strucker *et al.* (2005 - 2011). Together, an impressive, and unique ecological data set. It is out of scope of this report to discuss the observed annual changes and long-term trends in the bird population of the Oosterschelde, but it is worthwhile to pay attention to the decline of the Oystercatcher and the increase of the other species, since it clearly illustrates the on-going changes in the tidal habitat of the Oosterschelde.

Oystercatcher

Oystercatchers reached their peak numbers (70.000-110.000) in January-February before 1985 (Meininger *et al*. 1984, 1994). After the construction of the barrier and secondary dams, the peak numbers declined to 90.000 but this peak number was already reached in October. The counts carried out since then showed a further decline of the numbers to 40.000-50.000 in recent years, while these peak numbers are reached already in August-September (Figure 7-4).

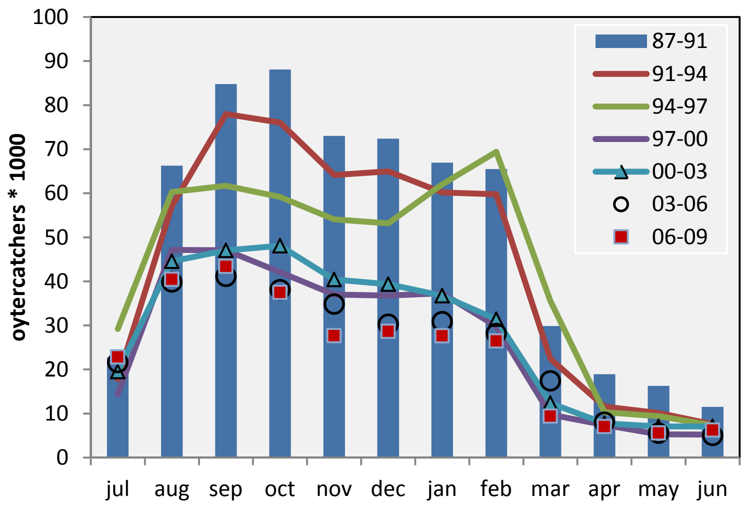

Figure 7-4- *Number of Oystercatchers per month in the Oosterschelde, averaged over periods of three years between 1986/87 and 2008/09.*

Sources: Meininger & van Haperen 1988, Meininger et al. *1984, 1995, 1996, 1996, 1998; Berrevoets* et al.*, 1999, 2000, 2001, 2002, 2003, 2005, Strucker* et al. *2005, 2007, 2009, 2010.*

Obviously, the decline of the Oystercatchers differed per month. Using all data, the average annual declines between 1986/87 and 2008/09 amounted to: 0.46% in July, 1.9% in August, 2.6% in September and 2.9% in October and November.

The disappearance of *Mytilus* in the tidal zone and the relatively low biomass of *Cerastoderma* has severely reduced the winter food supply. The Oystercatchers in summer and, also to a lesser degree, in early autumn still have the opportunity to feed on other prey being still harvestable in these months, but hardly later in the season. This may be a likely explanation why the winter numbers of the Oystercatchers have declined so much more than earlier in the season.

Curlew

In contrast to Oystercatchers, Curlews have increased the last 20 years in the Oosterschelde, but the seasonal trends have not changed (Figure 7-4). Like in the past, the peak numbers are reached in September. For all months the annual increase of the population amounted to 2.1%, on average. This suggests that there was no seasonal shift in their food supply. There is also no reason to assume, for instance, that their main prey, *Carcinus* have become more available during the winter than in the summer.

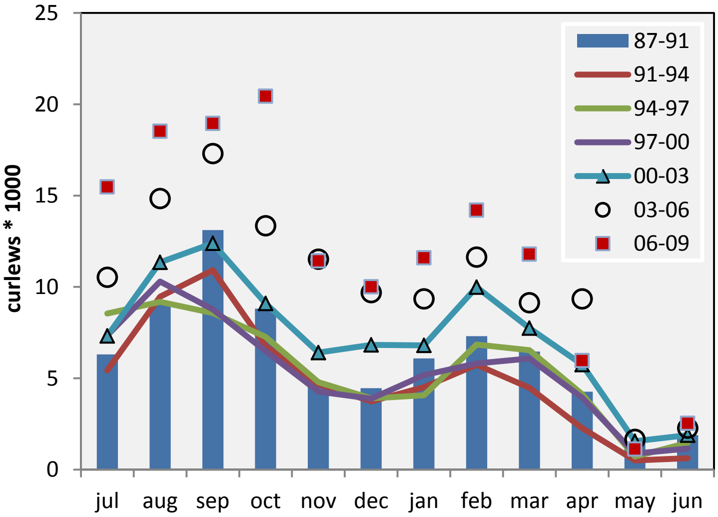

Figure 7-5- *Number of Curlews per month in the Oosterschelde, averaged over periods of three year between 1986/87 and 2008/09.*

Sources: Meininger & van Haperen 1988, Meininger et al. *1984, 1995, 1996, 1996, 1998; Berrevoets* et al.*, 1999, 2000, 2001, 2002, 2003, 2005, Strucker* et al. *2005, 2007, 2009, 2010*

Figure 7-6- *Life is easy for Curlews in the Oosterschelde in summer due to the mass presence of* Carcinus *on the intertidal flats. That is why the birds can take a long rest during their feeding period and stop feeding early during incoming tide.*

8 Discussion: feeding

Will there be fewer waders in the Oosterschelde at an ongoing erosion of the tidal flats? The question is simple, but to answer the question it is necessary to take into account nearly all important aspects of the feeding ecology of the bird species concerned. The direct effect of erosion is a shorter feeding time, so to start, it is crucial to know how long the birds have to feed.

8.1 Feeding time, food requirements, intake rate

The time spent on the feeding area (T) is determined by their daily food requirements (FR) and the rate at which they are able to collect their food (intake rate or IR). The function is simple: T = FR/IR. Thus, to answer the question about the feeding time, one has to know the daily food requirements and the intake rate.

Feeding time

A comparison between 13 wader species on the Banc d'Arguin (Mauritania) revealed that the daily time spent on the feeding area varied between 13 hours/day in the Little Stint (a wader of only 21 g) and 5 hours/day in the Curlew (the largest wader with a body weight of 750 gram) (Zwarts *et al.* 1990). A negative relation between feeding time and body weight was found in other wader studies, but also in woodland birds and seabirds and thus appears to be a common phenomenon (references in Zwarts *et al.* 1990). For the waders on the Banc d'Arguin the feeding time was described as an exponential function of body weight with an exponent -0.22.

Food requirements

The daily food requirements can be predicted from formulae that estimate energy expenditure. The energy expenditure of a resting bird (its basal metabolism) is closely related to its body weight. The relationship is linear when weight and energy requirements are plotted on a double log scale. The basal metabolism (kJ per day) can be calculated from the body weight (W): 437 x $W^{0.73}$: The energy expenditure of free-living birds is 2-3 times higher than the basal metabolism and can be estimated at: 1092 x $W^{0.73}$. 80% of the consumed energy is actually digested when birds feed on worms and the soft parts of bivalves. The energy content of this type of food varies little and amounts to 23 kJ per g meat (not including water (80%) and inorganic material (4%)). The required daily consumption (g dry flesh) is 59 x $W^{0.73}$. Thus, a Dunlin (50 g) needs 6.7 g dry meat per day, an Oystercatcher (500 g) 35.8 g and a Curlew (750 g) 48.2 g.

Birds have to increase their daily food requirements when it is cold. Above a certain temperature the bird doesn't need to spend any energy keeping warm, but below this temperature the energy requirements increase steeply. For a turnstone (100 g) the cost of living increases by 5% relative to its basal metabolism for every 1° C the air temperature drops below 20° C. For larger waders as the Oystercatcher (500 g), the air temperature must drop below 10° C before the costs of thermoregulation increases by 3.5% for every 1° C that the temperature drops below 10° C (Kersten & Piersma 1987).

Birds also have to increase their daily food requirements when they fat up. Grey Plovers having spent the winter in West Africa arrive early May in the Oosterschelde. They are able to increase their body weight within some weeks from 200 g to 300 g and even more (Meininger & van Swelm 1989). With these body reserves they are able to fly another 4000 km to their arctic breeding grounds. The daily increase in body weight in individual waders fattening up varies between 1 and 4% relative to their fat-free body weight. To fat up, birds have to consume more than they need at a constant body weight. On average, waders have to increase their daily consumption by 25% for every 1% increase in body weight (Zwarts *et al.* 1990).

Concluding, the daily food requirements may be estimated for each bird species, but varies seasonally, being at a maximum twice as high during cold weather and when the birds increase their body weight.

Intake rate

The daily food requirements are a function of body weight to the power ¾, while the time spent on the feeding area is a function of body weight to the power -1/4. This implies that the intake rate on the feeding area as function of body weight should have an exponent 1, thus being proportional to body weight rather than metabolic requirements (Zwarts *et al.* 1990).

An Oystercatcher has to consume 36 g dry flesh to keep its body weight constant but this may increase to 50 g a day in winter. If the bird forages 10 hours a day, its intake rate arrives at 1 mg/s (or 1.4 mg/s at a daily consumption of 50 g). The intake rate by Oystercatchers has been measured in 253 studies (Zwarts *et al.* 1996a). The average intake rate when feeding is 2 mg/s. The highest intake rates were found in birds preying upon large *Cerastoderma* or large *Mytilus*. The lowest intake rate ever measured was 0.5 mg/s in Oystercatchers feeding on very small *Cerastoderma* (8 mm or 3.3. mg) in the Oosterschelde during the autumn of 1986 (Meire 1996). The Oystercatcher is the only wader species for which we know how the intake rate varies with prey species, prey size, prey density and season.

Processing rate

When birds have only a limited time to search for prey, they must increase their intake rate to attain their food requirements. However, the food has also to be digested and this set an upper limit to the food intake. Oystercatchers cannot store more than 80 gram fresh flesh (or 12 g dry flesh) and the rate of food digestion, known as the processing rate, is not higher than 4.4 mg fresh meat or 0.66 mg dry flesh per second (Kersten & Visser 1996). At an average intake rate of 2 mg/s and foraging without any rest, the bird is full after 2 hours and either has to take a break or, if it continues to feed, food cannot be taken faster than the processing rate of 0.66 mg/s. The implication is that an Oystercatcher cannot consume more than 25 g of dry food during a low water period of 6 hours and thus, even at an extremely rich food supply, cannot meet their daily energy requirements in a single low water period (Zwarts *et al.* 1996b).

How often is the intake rate of estuarine birds limited by food availability and how often by the speed at which the birds can process the food? In summer there is so much food available for Oystercatchers that they can always reach a high intake rate, through which consumption is limited by the bird's processing speed. But in winter, food is often so scarce that the intake rate is limited by food availability. The birds cannot eat faster than their limited food allows.

The limitation in the food intake due to the processing rate is the crux of the model developed by Rappoldt *et al.* (2003) to simulate the food intake and distribution of Oystercatchers over the tidal flats, taking into account the available feeding time such as determined by the tide. The model produces a stress index for the winter. The model was used to do specific prediction for the Oystercatcher population in the Oosterschelde (Rappoldt *et al.* 2004, 2006).

How to achieve a higher consumption?

Grey Plovers gaining weight in May or waders staying in the Oosterschelde during a frost period need more food. There are three ways to get more food. (1) they can increase their intake rate when feeding; (2) they can spend more time feeding during their stay on the feeding area; (3) they can prolong their daily feeding period.

Waders on the Banc d'Arguin increased their daily consumption by 30% when they started to gain weight, but the species differed in the way this was achieved. Dunlins extended their feeding period, but Whimbrels got more food by an increased intake rate and not by foraging more hours a day (Zwarts *et al.* 1990). Such detailed information is still lacking for the Oosterschelde. Figure 8-1 takes together the information given in chapter 5. As found elsewhere, large wader species spent less time foraging than small waders.

The feeding period varied in winter between 6 hours per low water period in Curlews and 9 hours in Knot (Figure 8-1). The relationship between body weight and feeding time in winter was weak, since Oystercatchers spent nearly as much time feeding on the tidal flats as the much smaller Grey Plover and Dunlin. This is an indication that Oystercatchers had to work hard to achieve their food requirements. The available studies (Zwarts *et al*. 1996a) show that Oystercatchers usually feed 5 -6 hours during a low water period; longer feeding periods have been observed, but are rare (Figure 8-2).

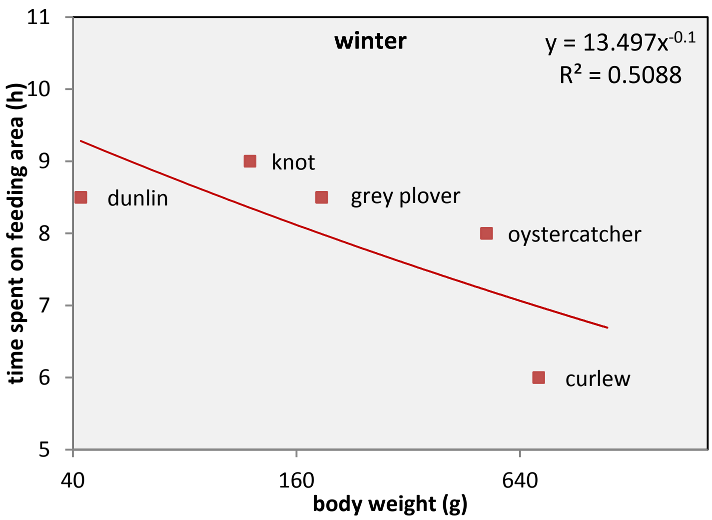

Figure 8-1- *The time spent on the feeding area in winter. The graph is based on data presented in Chapter 5.*

The feeding time in spring is known for more species in spring (Figure 8-3). Again, there is a negative relationship between feeding time and body weight. Unfortunately, no data are available for Dunlin and Knot, but we may safely assume that the feeding time of Knot and Dunlin was at a maximum as long as Greenshank (10 h), but most likely even shorter. The regression line is calculated, assuming that both waders spent 9.5 h on the feeding area. The regression line would hardly change when the three non-migrating species would be omitted; the equation would change into: $23.093x^{0.197}$ (R^2=0.70).

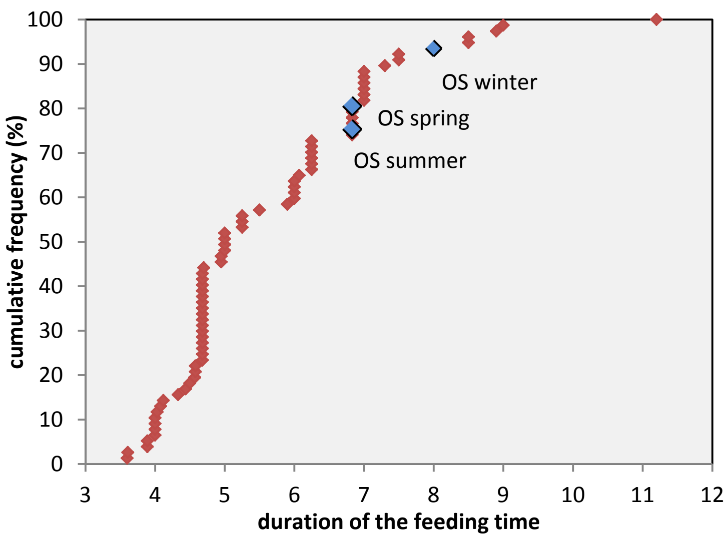

Figure 8-2- *A cumulative frequency distribution of the time spent by Oystercatchers on the feeding area during a tidal cycle. The blue symbols refer to the feeding time in the Oosterschelde (this study). The other data are taken from the appendix given in Zwarts* et al. *(1990a); a selection is made for 74 studies on free-living, non-breeding birds feeding on tidal flats.*

Do waders feed longer during cold weather or when preparing to migrate back to the northern breeding areas? Curlews spent 5 hours on the feeding area in summer, 5.5 hours in spring and 6 hours in winter. Oystercatchers in spring do not gain weight, so there is no reason to expect a longer feeding time. Indeed, their feeding time was in spring as long as in summer, 7 hours. During the winter it was 8 hours. A comparison cannot be made for other waders due to lack of data for the summer period.

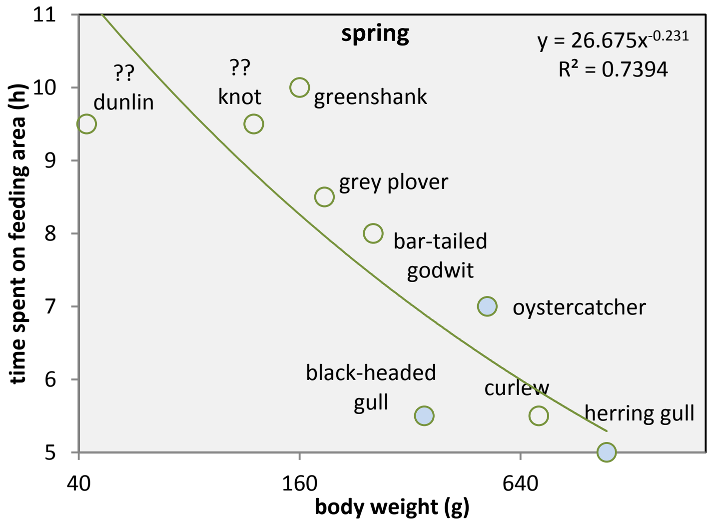

Figure 8-3- *The time spent on the feeding area in spring. The graph is based on data presented in Chapter 5. The duration of the feeding time was not measured, but estimated in Knot and Dunlin. All birds are gaining weight, except Black-headed Gull, Oystercatcher and Herring Gull ((indicated with blue symbols). The regression is calculated over all nine species.*

In conclusion, the time spent on the tidal flats to forage varies between species, being longer in the smaller waders. The birds feed longer during the winter and when they gain weight in spring. A prolonged feeding time of one hour is insufficient, however, to achieve the expected additional food intake of 30-50%. A higher intake rate might be possible, but seems unlikely. Most likely, the birds further enhance their food intake by feeding more at night. We spent some nights in the hide on the mudflats in December and saw birds feeding, but did no nocturnal observation in summer (although we know from studies elsewhere that waders do not feed at night during the summer; see below).

8.2 When and where to feed

Birds need a certain amount of food and also have a limited amount of time available to forage. Estuarine birds feed on the exposed tidal flats, but can also feed on the higher parts of the tidal zone and at high water. Moreover, they can feed at night. From a theoretical point of view, birds would decide to select their feeding times in such a way that they can meet their energy requirement in as less time as possible. In other words, optimal foraging birds rank their intake rate which they can achieve in different circumstances and feed only in suboptimal habitat when the food consumption in the optimal habitat is insufficient to attain their daily food requirements.

Night

Feeding waders are less successful when they feed at night (for a review see van de Kam *et al.* 2004). It takes them more time to detect a prey and also more time to handle a captured prey. Cockle-eating Oystercatchers cannot detect their prey at night by sight and have to touch the surface continuously to locate a prey. The intake rate of Curlews feeding on *Nereis* is at night twice as low as by day. It takes them more time to find a prey and if they have captured a prey, many are broken and can only be eaten piecemeal.

Tidal flats at night are ranking low regarding their intake rate. Oystercatchers and Curlews do not feed at night in NW Europe during the summer, but in winter many feed at night, because they have to.

Inland grassland

Birds can also feed at high water, but only a few species do so. Curlews and Oystercatchers feed on earthworms in grassland during the winter. All available studies show that the intake rate of Oystercatchers feeding on earthworms is low compared to their estuarine prey (reviewed by Zwarts *et al.* 1996a). Thus, grasslands rank low regarding their intake rate. Curlews and Oystercatchers only feed on inland grassland at high water between November – February. Large numbers may be seen inland when strong northwest winds push the sea water 50-100 cm higher, causing large areas of the tidal flats to remain submerged at low tide, and thus not available for feeding.

Also Bar-tailed Godwits can be seen feeding on inland grasslands, usually nearby the coast. This occurs very rarely in winter, but often in May, when they feed on leatherjackets (Meininger unpubl.). Bar-tailed Godwits can stay the entire daylight period on inland grasslands, but only do so when they achieve a high intake rate while feeding on leatherjackets (Blomert & Zwarts unpubl.).

High tidal zone

Oystercatchers hardly feed high in the intertidal zone, and if they do their intake rate is low (Ens *et al.* 1996). The higher flats are also of no interest for Curlews. The large prey eaten by these large birds tend to occur low in the tidal zone. In contrast, small, but for Dunlin, Knot and Redshank important, prey often reach their highest densities high on the tidal flats. When Knot feed on *Hydrobia* they can start to feed as soon as the first mud is exposed. That is the same for Dunlin and Redshank feeding on *Corophium volutator.*

This implies that the significance of the higher tidal flats differs per species. But the exploitation of the higher flats by a single bird species can vary locally and temporally. When Knot feed on *Macoma* or *Hydrobia*, they exploit different parts of the intertidal zone. Even when a bird species feeds on the same prey, the exploitation of high and low flats can vary. Cockle beds are usually found on tidal flats being exposed half of the time, but cockle beds can occur higher, but also lower along the tidal gradient. That is also why the distribution of cockle-eating Oystercatchers over the higher and lower parts of the tidal zone is not always the same. Given all this natural variation, bird counts have to be carried out in different seasons and different sites before an average exploitation as a function of emersion can be given for the Oosterschelde. The massive data set collected in the Wadden Sea show that the bird predation is low in sites being exposed for more than half of the time (Figure 8-4). Figure 8-4 is based on bird counts carried out between two hours before to two hours after low water. The peak shifts to the right when the average bird density is calculated over the total emersion period: the maximal density (21 birds/ha) is reached on tidal flats exposed for 48%, declining to 14 birds per ha on flats exposed for 60%.

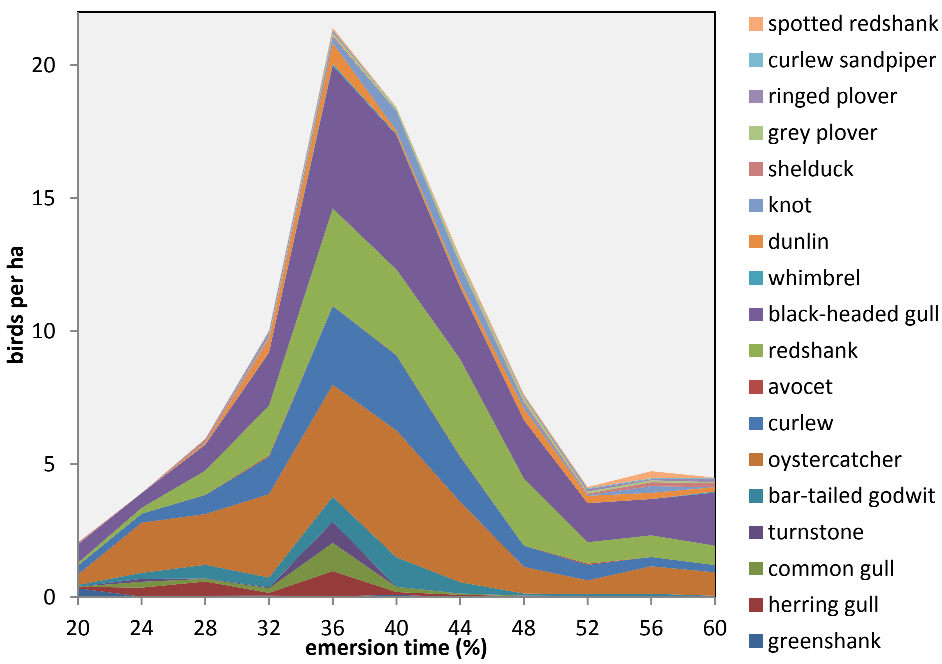

Figure 8-4- *The bird density at low water (between two hours before and after low water) in the Dutch Wadden Sea as function of emersion time. The species are ranked according to their average occurrence relative to the emersion time (from spotted redshank on the higher flats to greenshank on the lower flats). A selection is made of counts from 15 July -15 September. The average bird density is based on 1557 plots of (mostly) 0.1 ha, where on average 50 counts have been carried out. From: Blomert (2002).*

Birds move over the tidal flats during incoming and receding tide, making it more difficult to indicate the ecological significance of tidal flats as a function of the emersion time. It is obvious that birds have to move when they forage along the edge of the incoming tide. But why do they leave areas being exposed for some time during receding tide? Oystercatchers feeding on Cockles search for bivalves with slightly open valves, where they can stab their bill between. If cockles are closed, it takes an Oystercatcher much more time to open the prey. Cockles close their valves when they cannot filter anymore food from the overlying water. This is the explanation why Oystercatchers feeding on Cockles follow the receding water and feed in the shallow water during incoming tide. Another example is Redshank feeding on *Corophium*, When the mudflats are exposed, many *Corophium* comes out of their burrow to feed but after some time they retreat in their burrow and even close their burrow with some mud. The intake rate of Redshank reflects this change in the fraction of *Corophium* being active at the surface (Figure 8-5).

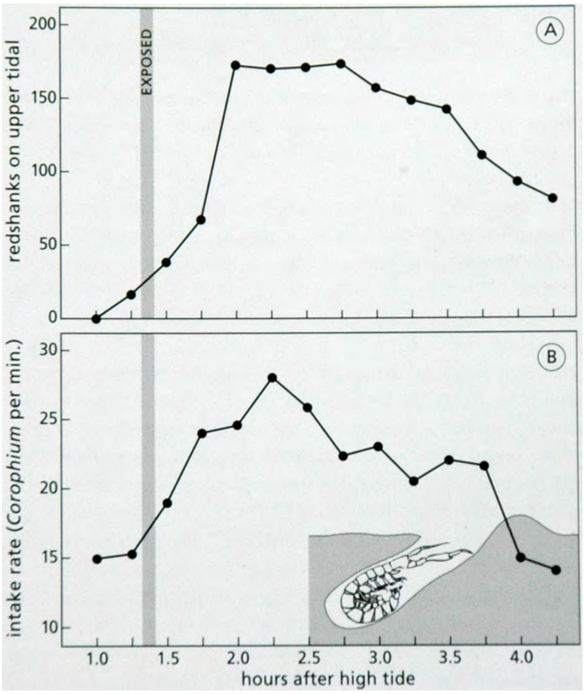

Figure 8-5- *(A) As the tide recedes, Redshank start to feed on* Corophium. *1.5 hour later most birds move to lower parts of the mudflat.*

*(B) The feeding rate (*Corophium *per minute) is low when the flats are still submerged, highest when the flats are exposed but wet, and decreases thereafter as the sediment dries. From: van de Kam* et al. *(2004).*

8.3 Ecological function of tidal flats with long emersion time

The bird counts summarized in Chapter 5 clearly show that the tidal flats being exposed for 70 or 80% are of no interest for most bird species, except for (1) Grey Plover, (2) Shelduck and Knot in winter and (3) Black-headed Gulls in summer.

The bird densities shown in Chapter 5 refer to feeding birds and can be interpreted as a measure of bird exploitation. That is only true, however, when the intake rate would be equal for sites for which the emersion time differs. That is certainly not the case for larger species such as Curlew and Oystercatcher. Most Curlews and Oystercatchers stay on the roost when the first mudflats become available, but the few birds which start to feed are highly unsuccessful. When this is taken into account, the tidal flats with a long emersion time become even less important than revealed from the density counts.

Nonetheless, the significance of the higher flats should not be underestimated. The bird population are not limited when life is easy, but during critical periods in the annual cycle, when food is scarce and/or food requirements are high. Apparent marginal feeding areas can in these circumstances play a crucial role since they enable the bird to prolong their feeding period if necessary. This situation will occur more and more often at the on-going erosion of the tidal flats in the Oosterschelde.

9 Summary and conclusions

9.1 Summary

Estuarine birds move over the tidal flats of the Oosterschelde during incoming and receding tide. Bird counts were carried out during the course of the emersion period in order to quantify the bird exploitation within the tidal cycle. These data were collected for sites pegged out along the entire tidal gradient. Some bird species feed more on the higher, other on the lower parts of the intertidal zone. The current erosion of the tidal flats causes a loss of tidal flats with a long emersion time, whereas the lowly-situated tidal flats have been extended. The collected data were used to indicate the loss of (potential) feeding possibilities (loss of feeding area combined with loss of feeding time) due to the erosion: the predicted loss until now varies between the bird species, being maximal in Grey Plover, Shelduck and Knot (decline of 30%). The loss is 20% in Oystercatchers and still less in species feeding predominantly on the lower shore, such as the Curlew.

Due to the ongoing erosion of the tidal flats, the emersion time will further decline and thus also the time available for feeding. Smaller bird species need to spend more time on the feeding area than larger ones. A large bird as a Curlew forage during a tidal cycle for a period of 5 hour, but a small wader as the Dunlin needs 7-8 hours. Birds forage, on average, one hour longer in winter (when they need more food due to the higher costs of living, while their intake rate when feeding is low due to the poor food supply) and when they prepare to migrate (and need more food to fat up). From this one can conclude that at further eroding of the tidal flats the first victims will be: (1) small bird species, (2) wintering birds and (3) birds fattening up.

Despite the erosion of the tidal flats and loss of feeding possibilities, the estuarine bird species are not yet in decline. The only and obvious exception is the Oystercatcher. The report has searched for an explanation of this puzzling result. Apparently, the impact of the current erosion of the tidal flats has been overruled by other changes in the tidal habitat of the Oosterschelde.

Oystercatchers lost a major winter prey due to the disappearance of mussel beds and also other bird species feeding on and around mussel beds must have lost an important feeding site. This loss is probably compensated, at least for a part, by the increased surface covered by oyster beds. Many bird species in the Oosterschelde feed at present on shorecrabs and shrimps in summer and possibly also in autumn. These prey are also taken by estuarine bird species on the lower shore during the cold winter months and in May (when the sea water is still cold),. That these prey are taken during (nearly) the entire year is probably a recent development, due to the higher sea water temperature. It would be a likely (but still untested) explanation for the remarkable increase of a crab-eating bird species as the Curlew.

The general conclusion is that changes in the food supply explains the greater part of the population trends. The negative impact of an increase in (1) coverage of algae mats, (2) human disturbance, (3) prey risk by raptors did not prevent an upsurge of most of the bird species. So far, this apparently compensates for the loss of feeding grounds due to the present erosion.

9.2 Gaps in our knowledge

The density at which birds feed on the tidal flats varies between less than 1 bird per ha to more than 100 birds per ha. This variation can be explained, for a large part, by variation in the available food supply. The evident loss of feeding area did not lead, at least so far, to a decline of the bird species migrating through, or wintering in, the Oosterschelde. Variation in the annual food supply appears to explain the fluctuations in bird numbers present, at least in some species (see companion report of Troost & Ysenbaert 2011).

Such data can explain the decline of the Oystercatcher but not the long-term increase in the other bird species.

A simple model might be helpful to integrate what we know. To prevent spurious relationships, some actual field data are still badly needed. Hardly anything is known about one of the most basic relationships: which prey species are actually taken by the different bird species during the course of the year, - preferably measured over more than one year. This is the most serious gap in our knowledge.

The preliminary data collected in this study reveal that the majority of the bird species feed on shorecrabs and shrimps (at least in summer 2009; still no data of more summers!). Quantitative data regarding the distribution of these prey over the tidal flats are lacking. The seasonal variation is still unknown too.

The bird density has been measured in summer, winter and spring. The data from the summer were collected while most waders had not yet arrived in the Oosterschelde and several observations days were lost due to human disturbance. A similar series of measurements in September-October would therefore be worthwhile.

Even if the measurements done in July-August, November-December and May, would be complemented with measurements in September-October, the seasonal variation in the exploitation remains still poorly known. A simple way to monitor this seasonal variation is to carry out monthly bird counts along the Oesterdam in the 38 plots being already pegged out between the high and low water line.

More observations are needed to know to what degree oyster beds replace the former function of mussel beds as attractive feeding site for waders. Possibly, the feeding density of birds depends on the coverage by oyster, so this should be quantified in plots where systematic bird counts could be carried out, preferably in the same way as done in this study.

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