ANT Oosterschelde:

Long-term trends of waders and their dependence on intertidal foraging grounds

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Summary

The Oosterschelde estuary and its extensive tidal flats are of high importance for international wader (*Charadrii*) populations. However, foraging opportunities for waders are now threatened because of long-term effects of a coastal engineering project (the Delta project) that cause net erosion of tidal flats. Between 1990 and 2007, 6 km^2 of intertidal flats was lost. In the coming century another 40 km^2 is expected to disappear, resulting in an almost complete loss of all intertidal flats.

The ANT study ("Autonomous Negative Trend" of the Oosterschelde estuary) aims to deliver the scientific support needed to assess the feasibility and affordability of the different conservation goals of Natura 2000. The main aim is to advise in which locations in the Oosterschelde estuary what kind of measures can be taken in order to meet (part of) the Natura2000 conservation goals for quality and quantity of the habitat of protected shorebird species. To meet this aim we first need to get insight in how the birds use the intertidal areas, and what factors determine their presence. That we do not fully understand the autonomous trends in bird numbers is clear from a discrepancy between expected and observed trends in wader numbers. Although we would expect to see declining wader numbers because of the ongoing erosion of the intertidal, we in fact see steady and even increasing numbers of several species. Of the Natura2000 waders we only see a clear decline in the Oystercatcher (*Haematopus ostralegus*), Spotted Redshank (*Tringa erythropus*), and Kentish plover (*Charadrius alexandrinus*). The present study aims to describe and explain observed trends in bird numbers by exploring relationships between bird numbers and biotic and morphological changes in the intertidal area of the Oosterschelde estuary.

In this study we aimed to answer the following research questions:

1. How did the morphology of intertidal flats develop until present; what were the changes in exposure time and area and are there differences between areas within the estuary?
2. Is the decrease in area of intertidal flats also observed in the lower intertidal zone?
3. How did the abundance of benthic invertebrates, especially those suitable as food for waders, develop over time and are there differences between areas within the estuary?
4. How did numbers of birds dependent on the intertidal for foraging develop in the Oosterschelde and its compartments? Can these trends be attributed to:
    - changes in the morphology of the intertidal flats;
    - changes in the abundance of prey species;
    - population fluctuations and other (external) causes.

We analysed long-term trends in 1) the morphology of intertidal flats, 2) the abundance of benthic prey species, and 3) the abundance of waders dependent on the intertidal for foraging. By studying relationships between the morphology of tidal flats and both the occurrence of birds and prey species, and relationships between abundance of birds and their prey species, we set out to find causal relationships between characteristics of the intertidal foraging grounds and bird presence.

Changes in morphology of the tidal flats were already studied (Jacobse et al. 2008) using elevation maps of three different years (1990, 2001, 2007). They found net erosion rates in the higher intertidal areas. Because sediment eroded from the upper parts of tidal flats was transported into the gullies and onto the lower parts of the intertidal, the area of lower intertidal flats did not decrease yet. We here pose the hypothesis that erosion of tidal flats has not already resulted in mass declines of waders because up until present the main sediment losses concentrated on the higher intertidal zone. The area most profitable for foraging waders in terms of prey abundance may not yet have decreased yet if located mainly in the lower intertidal. We refined the study by Jacobse et al. (2008) in time and space, by analysing elevation data that were collected annually by Rijkswaterstaat along (RTK) transects covering almost all tidal flats of the Oosterschelde estuary, in the period 1987 – 2010. This allowed us to study changes in elevation from year to year, and at smaller spatial scales.

At the same time a comparison between our approach (using transects) and the approach by Jacobse et al. (2008) (using elevation maps) allows for quality check of both methods. This is valuable because there is thought to be a high level of uncertainty in the elevation maps, while our method using transects has other specific issues.

The abundance of prey species was studied using existing time series on benthic macrofauna. Long term changes in abundance of benthic macrofauna as consequence of the erosion of tidal flats were previously studied by Escaravage et al. (2003). We did our own analysis with the same dataset, updated until 2008. We additionally analysed long-term changes in abundance of bivalves, using IMARES data on shellfish survey that, unlike the benthic macrofauna survey, cover the entire intertidal of the Oosterschelde etuary. Although waders have been counted on a monthly basis since 1987/1988 (and even before), this extensive dataset has never before been used to find causal relationships with the biotic and abiotic environment on the scale of the Oosterschelde estuary and its compartments.

For the period 1987 – 2010 and for different tidal flats throughout the estuary our results show that there was an absolute decrease in intertidal area with exposure times > 40%, but no decrease in areas with exposure times < 40%. Although the RTK transect data are more refined in space and time than the elevation maps, the results are more difficult to translate to changes in absolute areas of intertidal. No long-term changes in biomass and abundance of benthic fauna were found, other than an increase of the Pacific oyster stock and cover of intertidal flats and a decrease in cockle stock in the Eastern compartment. No changes in benthos could be related to long-term erosion of tidal flats. Certain species showed a clear relationship with surface elevation of the tidal flats (further referred to as 'elevation' in this document), both negatively and positively. In general, benthic biomass was found to be highest in the lower and mid-intertidal zone, at exposure times below 60%. The distribution of prey species over the tidal zone is thought to be of high importance in explaining the distribution of waders in the tidal zone. Differences between wader species in preferred foraging habitat, but also differences between species in minimum foraging times needed, may have large consequences for their vulnerability to the progressing erosion of tidal flats in the future.

We found some relationships between wader numbers and the abundance of certain prey species, but these relationships are often weak. Causal relationships are difficult to find because of a high degree of variation and uncertainty in foraging preferences and strategies of birds, but also in distribution of benthic biomass. Although bivalves are monitored throughout the entire intertidal of the estuary, other benthic macrofauna is only monitored in some locations that are not always representative for a larger spatial unit. Nevertheless, the decrease in Oystercatcher numbers could clearly be attributed to changes in food availability: replacement of mussel culture from intertidal to subtidal bottom plots, and a decrease in cockles in the Eastern compartment. Furthermore, the densities of mud snails (*Hydrobia ulvae*) and sand masons (*Lanice conchilega*) appear to be determining for several waders.

As erosion of tidal flats progresses, bird species that are dependent on prey species that mainly occur in the upper intertidal, such as the mud snail, are expected to be affected by the effects of erosion of tidal flats before species that are generalists or dependent on prey that is distributed homogeneously throughout the tidal zone or that mainly occurs in the lower intertidal. The most vulnerable species in particularly the Eastern compartment are expected to be the Shelduck, Knot, Oystercatcher and Dunlin. For birds that are dependent on prey species and communities occurring lower in the intertidal, such as the sand mason, the abundance of their main prey species is expected not to be affected until locally the higher intertidal areas are completely eroded. At that point, sedimentation from the higher intertidal will halt and the lower intertidal will also start to decrease in area. Species belonging to this category are mainly the Grey Plover, Dunlin, and Curlew. However, even if the preferred prey species occur in the lower intertidal, availability of prey in higher intertidal areas may still be of key importance for survival of certain waders since foraging time in the lower intertidal may be too limited to gather enough food.

Numbers of waders could not be related to direct effects of erosion of tidal flats (decrease in foraging area and foraging time), yet. Also indirect effects of erosion of tidal flats, through effects on food composition and availability, could not be demonstrated yet. We therefore conclude that wader numbers in general did not decrease because they still have enough foraging are left. Foraging area and foraging time are expected not to be limiting still, but this may change rapidly in the future. Up until present eroded sediments from the higher intertidal have replenished the lower tidal flats with the result that the area of lower intertidal flats has not decreased yet. As soon as the upper intertidal has eroded completely, the mid and lower intertidal area will start to erode as well. Since the mid and lower intertidal harbour a higher biomass of prey species in general, erosion of this part of the tidal zone is expected to lead immediately to decreasing bird numbers. As a result of erosion of tidal flats the tidal flats have become flatter. Therefore the expected future decrease in area of relatively profitable tidal flats may occur at a faster rate than observed until present, and will be augmented by any rise in level. There is, therefore, a realistic chance that we may see a relatively sudden change in the carrying capacity of the Oosterschelde estuary for waders. A change that may be very difficult, or even impossible, to turn around. Oystercatchers do show a decline already, and numbers are expected to decrease further in the near future.

1. Introduction

Waders of the Oosterschelde estuary

The Oosterschelde area is of high importance for international populations of waders (*Charadrii*, e.g. the Oystercatcher, Figure 1). The area is visited by migratory birds in autumn and spring, and many species use the area as a wintering site. For many migratory birds, the intertidal flats of the Oosterschelde estuary act as rich foraging grounds which are used to fatten up before their long voyage southward. For migratory birds passing through in spring, when they return to their northern breeding grounds, the Oosterschelde estuary once again acts as an important stopover area, especially when the birds are delayed due to adverse weather conditions (Nienhuis and Smaal 1994; Van de Kam et al. 1999).

Figure 1. Oystercatchers roosting in the Oosterschelde estuary (courtesy Rob Strucker).

Habitat changes in the South-western Delta

Before the 1960s the entire South-western Delta area of the Netherlands, where Rhine, Meuse and Scheldt enter the North Sea, formed an extensive network of estuaries. Extensive salt marshes and tidal flats presented waders with rich feeding grounds and lots of opportunities for breeding. This changed drastically in a period of several decades after a large flood in 1953 in which many people were killed. In order to increase safety and prevent such a flood from ever happening again, a large coastal engineering project was started, the so-called Deltaplan or Delta Works. The present lakes Grevelingenmeer, Veerse Meer and Haringvliet were closed off from the North Sea through barrier dams. The lakes Grevelingenmeer and Veerse Meer and the Oosterschelde estuary were closed off from riverine inputs as well through compartmentalisation dams (Figure 2). As a result, the formerly saltwater estuarine areas of the Haringvliet, Veerse Meer and Grevelingenmeer turned into freshwater, brackish water and salt water lakes respectively, with a strongly reduced to non-existent tidal amplitude. Areas further upstream (the current Volkerakmeer, Zoommeer, Markiezaat, Hollandsch Diep and Biesbosch) turned from tidal brackish to salt areas into freshwater areas without any tidal movement. The intertidal flats of the Oosterschelde remained because the estuary was not closed off completely from the North Sea, but instead a storm surge barrier was built that is only closed in events with exceptionally high water levels. The Westerschelde estuary maintained its open connection to the North Sea because of the shipping lane to Antwerp. The tidal flats of the Oosterschelde and Westerschelde estuaries are now nearly the only ones to be found in the South-western Delta area (Nienhuis and Smaal 1994).

Figure 2. The South-western Delta area. Barrier dams constructed in the framework of the Delta plan are shown in red.

Erosion of tidal flats

The Oosterschelde estuary is still changing as a result of the infrastructural works of the Delta project. The compartmentalisation dams and the storm surge barrier decreased the tidal water volume going in and out the Oosterschelde, as well as the tidal currents. As a result, the gullies are too wide for the reduced water volume. During storm events, the tidal flats are eroded, whereas tidal currents are too weak to bring back the sediments on the tidal flats. As a consequence the sediments are transported from the higher intertidal zone into the gullies, and the tidal flats are slowly eroding. Until 2001, on average 0.5 km^2 of the intertidal permanently eroded per year. Each year, an estimated total of 1 million m^3 sand is disappearing into the gullies. More than 50% of the entire intertidal of the Oosterschelde estuary is predicted to have disappeared by 2045 (Van Zanten and Adriaanse 2008).

The erosion of tidal flats is expected to affect shorebird populations severely, especially those species which are fully dependent on intertidal flats for foraging. Between 1990 and 2007, 6 km^2 of intertidal flats was lost. In the coming century another 40 km^2 is expected to disappear, resulting in an almost complete loss of all intertidal flats (Jacobse et al. 2008). Furthermore, the morphological changes in the intertidal may cause changes in benthic communities and prey species availability for waders.

Changes in the Oosterschelde estuary since 1986

Erosion of tidal flats is an ongoing process, ever since the storm surge barrier was completed. However, there have been other changes and events since 1986 that are known to, or may have, influenced wader populations in the Oosterschelde estuary. These events are summarised in Figure 3.

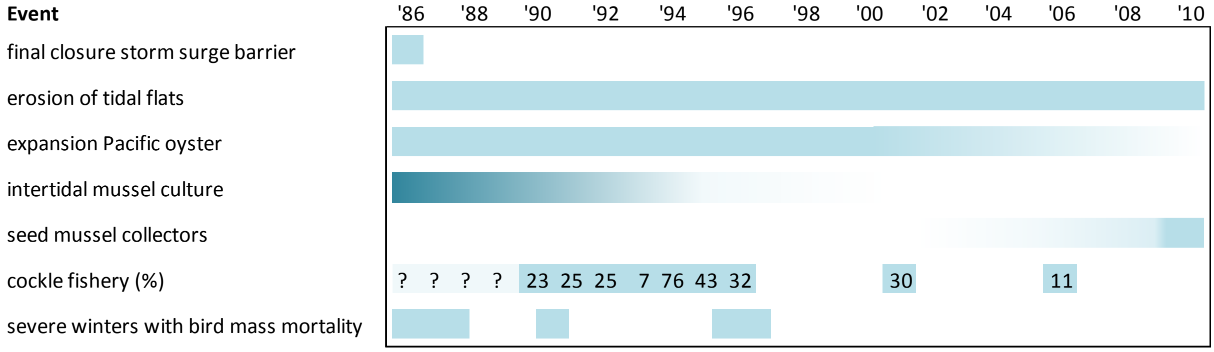

Figure 3. Schematic overview of changes and events in the Oosterschelde estuary that has, or may have, influenced the numbers of waders in the estuary. There have been several episodes of cockle fishery, expressed as the percentage of the total cockle stock fished.

In the Oosterschelde estuary mussels are mainly cultured on bottom plots. Up until the mid-1990s mussels were cultured on plots in both the intertidal and subtidal areas of the Oosterschelde estuary. During low tide, the exposed mussels and associated biota were available for predation by birds. Around 1995, however, management of bottom-cultured mussels changed and the intertidal plots were not used for mussel culture anymore. All mussels were relocated to subtidal bottom plots, where they are unavailable for waders. Around 2000, experiments with seed mussel collectors started to find an alternative and more reliable way for mussel farmers to obtain mussel seed, than by bottom trawling (mainly in the Wadden Sea). Seed was collected by suspending ropes and nets in the water column. In 2010, the total area of the Oosterschelde estuary available for seed mussel collectors was scaled up to 2 km^2 within the framework of a large-scale transition process where mussel farmers are encouraged to change from bottom trawling for seed to seed collection, in order to preserve and protect the Wadden Sea ecosystem (Quirijns 2010). Previously, most of the mussel seed used for culture in the Oosterschelde estuary was fished in the Wadden Sea. The seed mussels growing on these seed collectors are always submerged and are an unlikely food source for waders, but they may affect food availability indirectly by affecting the carrying capacity of the Oosterschelde ecosystem for bivalves and other filter feeders. The carrying capacity also appears to have been affected by the rapid increase in total filter feeder stock due to expansion of the Pacific oyster *Crassostrea gigas* (Troost 2010). Expansion of the Pacific oyster has been going on since initial introduction in 1964, but appears to have stabilised already. The percentage of the intertidal area covered by oyster beds has increased to around 9% in 2005 (Figure 4).

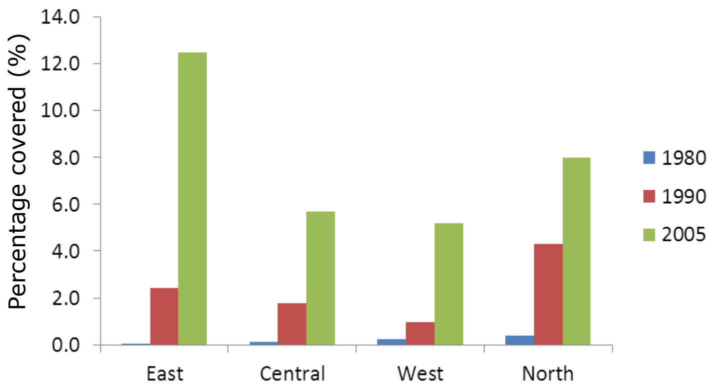

Figure 4. Percentage of the intertidal covered by Pacific oyster beds in four compartments of the Oosterschelde estuary (see Figure 6).

In the Oosterschelde estuary mechanical cockle dredging is only allowed if enough cockles remain available for Oystercatchers; 150 Kg + 10% of cockle meat is reserved per Oystercatcher per year.

Mechanical cockle dredging is only allowed in years when the cockle stock in densities higher than 50 m^{-2} exceeds the food reservation for Oystercatchers (Anonymous 2004). Fishing by rake is also allowed, up to a catch of 1/17 part of the total possible catch in densities over 50 m^{-2}. In the Oosterschelde estuary there have been several episodes of cockle fishery, expressed as the percentage of the total cockle stock fished in Figure 3. Since 2005 the cockle stock has been declining, and cockle fisheries only took place in 2006. In the years before 2005 there were more episodes of cockle fishery, but also in the period 1993 - 2005 a certain part of the cockle stock was reserved for Oystercatchers (Bult et al. 2000).

Finally, there were a few severely cold winters in which part of the Oosterschelde estuary froze locally, making foraging on intertidal flats almost impossible. In the winters of 1985/1986, 1986/1987, 1987/1988, 1990/1991, 1995/1996 and 1996/1997, many birds were killed. For example, in January 1997 more than 4000 dead Oystercatchers were collected in the Oosterschelde estuary (Meininger et al. 1998). Of these winters, those of 1987/1988, 1995/1996 and 1996/1997 are characterised as particularly cold based on the Cold Index by Hellmann. The index is calculated by summing all average temperatures below 0 °C per 24 hours in the period November 1st – March 31st. A cold index between 100 and 160 is characterised as 'cold', above 160 as 'very cold' Figure 5).

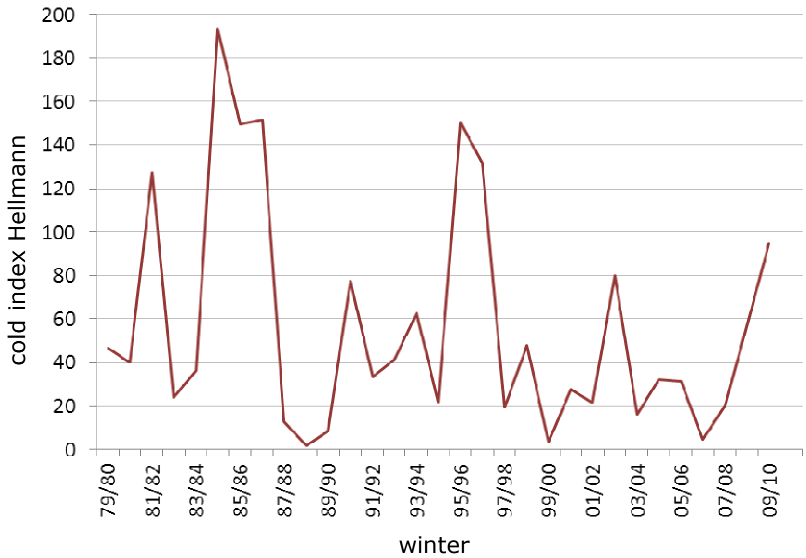

Figure 5. Cold Index of Hellmann, for air temperatures in the Netherlands (based on data KNMI, De Bilt).

Autonomous trend of the Oosterschelde estuary

The ANT study ("Autonomous Negative Trend" of the Oosterschelde estuary) aims to deliver the scientific support needed to assess the feasibility and affordability of the different conservation goals of Natura 2000. The aim is furthermore to advise in which locations in the Oosterschelde estuary measures need to be taken in order to meet (part of) the Natura2000 conservation goals for quality and quantity of the habitat of protected shorebird species. The ANT study also includes an evaluation of which types of measures (e.g. nourishment, oyster reefs for stabilisation of tidal flats) offer the most promising solution in stopping or mitigating the erosion of the tidal flats in the Oosterschelde and at the same time limit the ecological disturbance.

Aim of this study

To be able to advise at which locations conservation measures need to be applied, we first need to get insight in how the birds use the intertidal areas, and what factors determine their presence. Apart from factors acting on a larger spatial scale, such as population fluctuations due to environmental conditions or predation in arctic breeding areas, trends in numbers of birds visiting the Oosterschelde estuary may also be determined by local factors such as food availability and winter temperatures.

That we do not fully understand the autonomous trends in bird numbers is clear from the discrepancy between expected trends and observed trends. Although we would expect to see declining wader numbers because of the ongoing erosion of the intertidal, we in fact see steady and even increasing numbers of several species. Of the Natura2000 waders we only see a decline in the Oystercatcher (*Haematopus ostralegus*), Spotted Redshank (*Tringa erythropus*), and Kentish plover (*Charadrius alexandrinus*). Within the ANT framework, the present study aims to explain observed trends in bird numbers by exploring relationships between bird numbers and biotic and morphological changes in the intertidal area of the Oosterschelde estuary. Although waders have been counted on a monthly basis since 1987/1988 (and even before), this extensive dataset has never been used to find causal relationships with the biotic and abiotic environment on the scale of the Oosterschelde estuary and its compartments.

Additionally, we here pose the hypothesis that erosion of tidal flats has not already resulted in mass declines of waders because up until present the main sediment losses concentrated on the higher intertidal zone; sediment has eroded from the upper parts of tidal flats, and transported into the gullies and onto the lower parts of the intertidal. The area most profitable for foraging waders in terms of prey abundance may not have decreased yet if located mainly in the lower intertidal. Zwarts (2009) observed for several waders that they spend most of their time in the lower and mid-intertidal. In general waders forage in those areas where they can achieve the highest intake rates. However, wader distribution in the intertidal will be a result of the combination of available time and space but also prey abundance and availability and competition between individuals.

In this study we aimed to answer the following research questions:

1. How did the morphology of intertidal flats develop until present; what were the changes in exposure time and area and are there differences between areas within the estuary?
2. Is the decrease in area of intertidal flats also observed in the lower intertidal zone?
3. How did the abundance of benthic invertebrates, especially those suitable as food for waders, develop over time and are there differences between areas within the estuary?
4. How did numbers of birds dependent on the intertidal for foraging develop in the Oosterschelde and its compartments? Can these trends be attributed to:
    - changes in the morphology of the intertidal flats;
    - changes in the abundance of prey species;
    - population fluctuations and other (external) causes.

Approach

We analysed long-term trends in 1) the morphology of intertidal flats, 2) the abundance of benthic prey species, and 3) the abundance of waders dependent on the intertidal for foraging. By studying relationships between the morphology of tidal flats and both the occurrence of birds and prey species, and relationships between abundance of birds and their prey species, we set out to find causal relationships between characteristics of the intertidal foraging grounds and bird presence.

2. Methods

Morphology of intertidal flats

Data collection

Regarding the morphology of the intertidal, exposure time is the most relevant parameter for waders, in addition to sediment composition. Several grid maps are available in GIS from Rijkswaterstaat, for the years 1990 and 2001. In these maps, exposure time is calculated from water depth maps. Water depths were also measured in 2007, but this map was never converted to an exposure time map. In this study, we only used the exposure time maps as a reference. Trends in the intertidal area were studied using an analysis by researchers of Royal Haskoning (Jacobse et al. 2008) of the elevation maps of 1990, 2001 and 2007 by Rijkswaterstaat. The study by Royal Haskoning was commissioned by Rijkswaterstaat through Deltares. For detailed analyses of changes in the intertidal area within exposure time categories we used data on elevation measured bi-annually by Rijkswaterstaat along transects covering almost the entire intertidal area of the Oosterschelde estuary (‘RTK profiles’; Figure 6). The purpose of these measurements is to monitor erosion and sedimentation of tidal flats and salt marshes.

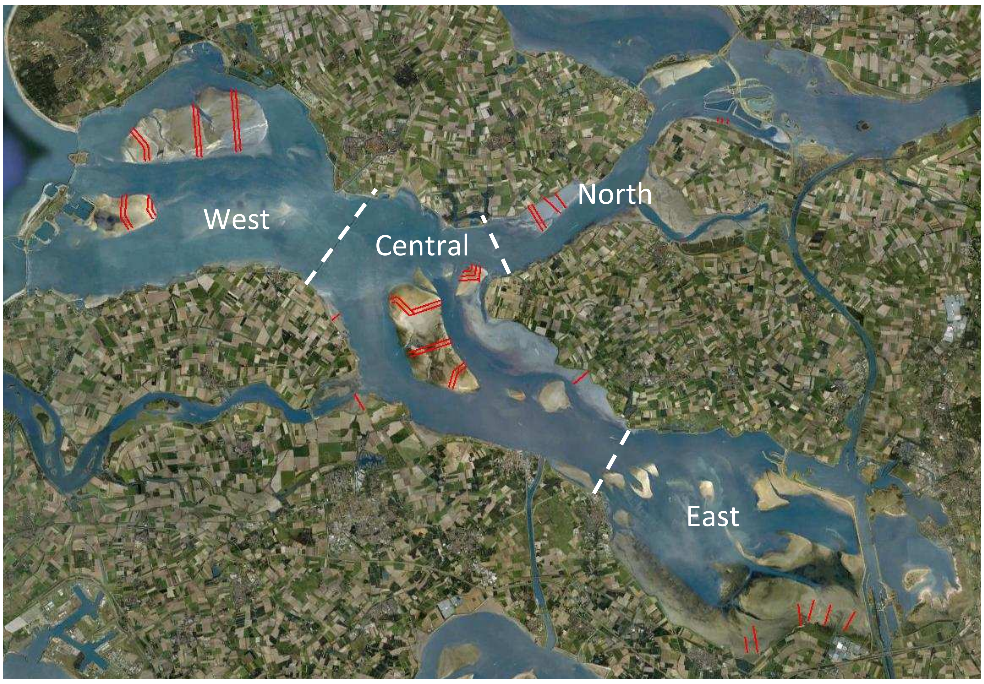

Figure 6. Transects in the intertidal of the Oosterschelde estuary, in the four different compartments, along which elevation measurements are conducted by Rijkswaterstaat since 1987. Only a selection is given of the transects used in this study (in red).

Analysis

Elevations from the transect measurements were converted to exposure times using a polynomial function

$$ET(h) = ah^3 + bh^2 + ch + d \qquad \text{Eq. 1}$$

In which ET is the exposure time (in %), h is the elevation relative to NAP (in cm), and a, b, c, and d are constant parameters (with 10 decimals). Different parameters were applied for three tidal zones: low intertidal (< -100 cm NAP), mid intertidal (-100 to +100 cm NAP) and high intertidal (> +100 NAP). For each of the four compartments the parameters of these polynomial functions were different according to differences in tidal movement of the sea water level. The formulas are based on mean tidal movement at the locations Krammersluizen (northern compartment), Stavenisse (central compartment), Bergse Diepsluis (eastern compartment) and Roompot (western compartment). The different parameters per tidal zone and per compartment are shown in Table 1. An example is given in Figure 7.

Table 1. Parameters used for the different compartments and different tidal zones in equation 1, to calculate exposure times from elevations. For a correct relationship between tidal height and exposure time it is essential to maintain 10 decimals.

Compartment	parameter	Low intertidal	Mid intertidal	High intertidal
Northern	*a*	0.0000001217	0.0000010569	-0.0000065562
	b	0.0025533742	-0.0003261763	0.0019685700
	c	0.9849219310	0.2473972863	0.1309147953
	d	95.6556609952	50.9973527093	46.0485649231
Central	*a*	0.0000029449	0.0000020232	-0.0000004719
	b	0.0040139155	0.0003058951	-0.0014888161
	c	1.2172850781	0.2465300348	0.7391051626
	d	106.3644461721	50.8075021791	14.7647328405
Eastern	*a*	-0.0000057470	-0.0000003803	-0.0000043865
	b	-0.0010416531	-0.0003452022	0.0014580289
	c	0.3246678105	0.2560357688	0.1034903225
	d	60.6141600763	51.2609327732	52.0616841186
Western	*a*	0.0000219556	0.0000071250	0.0000156407
	b	0.0130531021	-0.0002385373	-0.0099601551
	c	2.5515195428	0.2371662850	2.1096266113
	d	164.3428587477	50.2677668008	-48.7033376028

Calculated exposure times were validated by comparing the values of 2001 to exposure times derived from the exposure time GIS grid of 2001 for the exact same locations. Per location we calculated the absolute difference in exposure time between the two methods. The average difference was 2.9% (s.e. 0.2) for the Western compartment, 4.6% (s.e. 0.1) for the Central compartment, 7.5% (s.e. 0.4) for the Northern compartment and 4.1% (s.e. 0.2) for the Eastern compartment. Average differences were 0.5, 0.7, -1.5 and -2.6% respectively.

After having transformed all measured elevations into exposure times, we calculated for which distance of a transect one measuring point was representative, and divided this by the maximum total length of the transect, i.e. the maximum distance ever covered (the length covered generally varied slightly from year to year because of differences in tidal level, and therefore in the emerged area of tidal flat). This yielded relative lengths of the total transect belonging to all data points. The distance of transect for which a measuring point was representative was calculated as half the distance to the previous point along the transect plus half the distance to the next point along the transect. For the first and last points of a transect, half the distance to respectively the next and previous point were taken.
In some cases we removed the outer ends of a transect if data for only very few years were available for this particular section. In most cases these outer ends were located in the lower intertidal.

Differences between years in transect length in these sections are explained by differences in tidal height during low tide, and therefore accessibility.

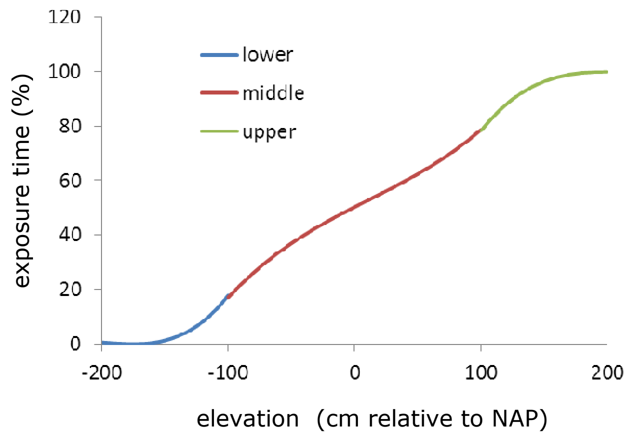

Figure 7. Example of the relationship between elevation and exposure time, calculated using Eq. 1 and the parameters shown in Table 1, for the Western compartment. Three different sets of parameters were used for three zones in the intertidal: the lower, middle and upper intertidal.

Next, per emerge time category (10 equal categories in the range of 0 – 100% exposure time) we summed up all representative relative distances, yielding relative distances per exposure time category (e.g. 15% of the distance falling into the 30-40% exposure time category). These relative distances can also be interpreted as relative areas in the direct surroundings of the transects.

Table 2. Overview of tidal flats per compartment, the number of transects per tidal flat and the period covered (the first and last year of a period in which all transects per tidal flat were measured). Within this period not all years were always covered. The number of years covered is given between brackets. The numbers in the last column refer to Figure 8, where the locations of the different tidal flats are indicated.

Compartment	Tidal flat	N of transects	Period covered	Location in Fig. 8
Northern	Slaak	3	1994 – 2009 (11)	19
	Slikken van Viane	4	1995 – 2008 (9)	21 + 22
	- North	2	1993 – 2008 (15)	21
	- South	2	1989 – 2009 (15)	22
Central	Slikken van de Dortsman	5	1987 – 2009 (17)	13
	Galgeplaat	10	1987 – 2009 (12)	30 + 32
	Kats	1	1993 – 2009 (17)	2
	Zandkreek (South)	1	1994 – 2009 (14)	3
Eastern	Rattekaai	4	1995 – 2009 (13)	6
	Krabbendijke	2	1993 – 2009 (14)	6
	Rattekaai + Krabbendijke	6	1995 – 2009 (12)	6
Western	Roggenplaat	8	1988 – 2009 (14)	26 + 27
	Neeltje Jansplaat	9	1989 – 2009 (10)	28

On most of the tidal flats measured, more than one transect was present (Table 2). Per tidal flat, and per compartment, average relative distances (or areas) were calculated per exposure time category by weighting according to maximum transect length. Only years were used in which all transects on one tidal flat were measured.

Additionally, average exposure times for the total intertidal area of the different compartments were analysed from elevation maps created by Rijkswaterstaat from measurements covering the entire Oosterschelde estuary in 1990, 2001 and 2007. In the study by Jacobse et al. (2008) the total area of different tidal zones was calculated for the different tidal flats of the Oosterschelde estuary (Figure 8).

We used the areas in the intertidal range (-150 to +200 cm relative to NAP) and calculated total areas for the years 1990, 2001 and 2007.

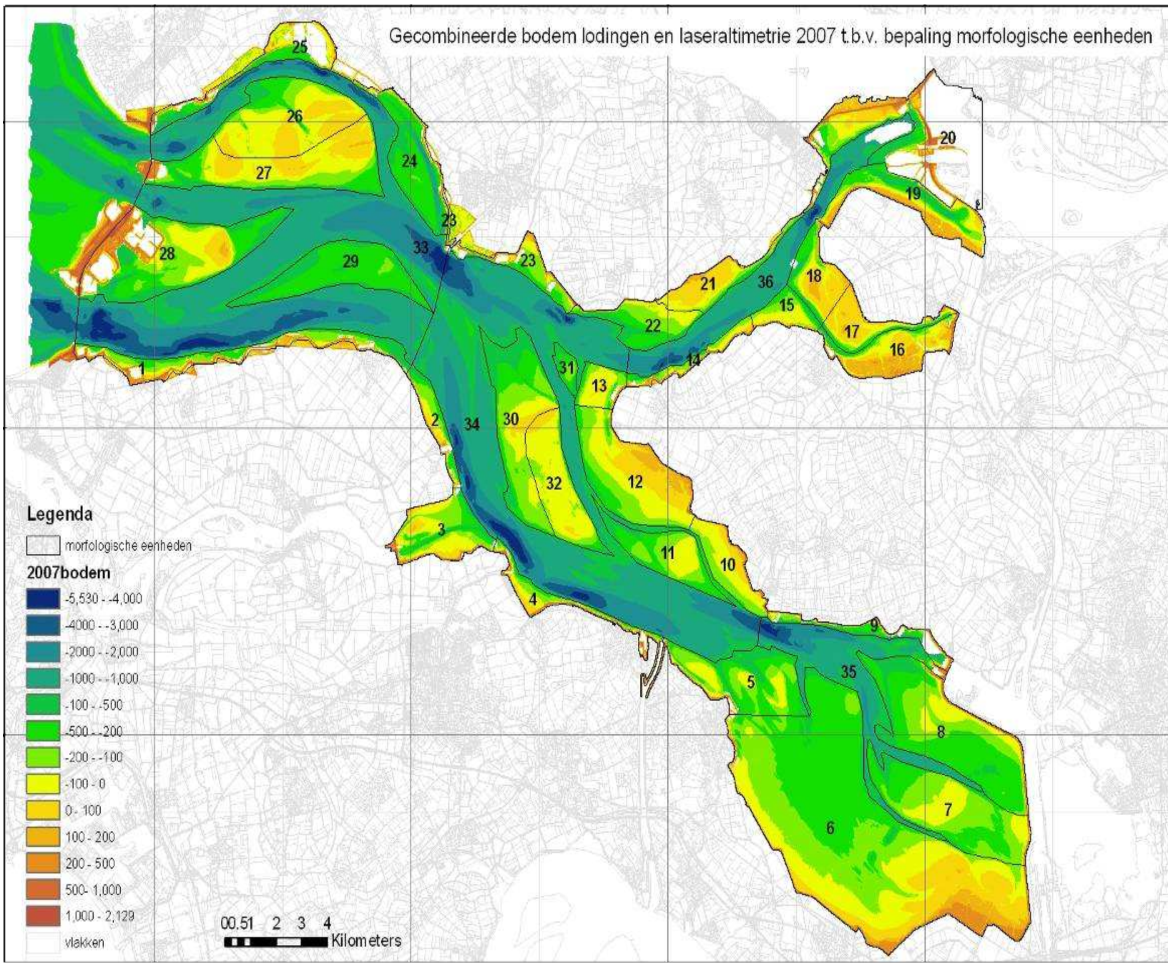

Figure 8. Compartments used in the study by Royal Haskoning (Jacobse et al. 2008).

Benthic fauna

Data collection

Data on abundance and biomass of the dominant bivalves preyed upon by waders (edible cockle *Cerastoderma edule*, blue mussel *Mytilus edulis* and Baltic tellin *Macoma balthica*) were available from the annual shellfish survey carried out by IMARES, commissioned by the Ministry of Economic Affairs, Agriculture and Innovation. The shellfish survey in the Oosterschelde estuary started in 1990 and is carried out each year in spring. Methods are described in detail by Kesteloo et al. (2010). Cockles are categorised according to their age in 0-year old, 1-year old, 2-year old and 3-year old or more. Until 2000, Baltic tellins have been counted as one group only, but since 2001 were also measured and categorised into <5 mm, 5 – 15 mm and >15 mm length. It should be noted that spat of both species is mostly only counted when 1-year old, since cockle spat settles during and after the spring survey, and spat of both species is generally still too small to be retained by the sieves (mesh size 5 mm). The category Baltic tellins of <5 mm therefore represents an underestimation of numbers and biomass present in that year.

Within the monitoring programme MWTL, the benthic fauna of the Oosterschelde estuary has been monitored since 1990. Sampling is carried out each spring and autumn by the Monitor Taskforce of NIOO-CEME (Netherlands Institute of Ecology – Centre for Estuarine and Marine Ecology), commissioned by the Ministry of Infrastructure and Environment.

In the intertidal, three areas are sampled (Roggeplaat, Viane and Rattekaai) and in each area 10 stations are located. Methods are given by Escaravage et al. (2003).

Additionally, we used data on benthic fauna sampled in the INTERECOS campaign in 1989 at locations Roggenplaat en the Western compartment, Galgeplaat in the Central compartment and Krabbenkreek in the Northern compartment (Meire et al. 1994b; Seys et al. 1994), and in a resampling of the Roggenplaat in 2008 (De Mesel et al. 2009), to relate benthic biomass to exposure time. For all sampling stations the exact coordinates were known, and these were used to determine elevations from the elevation maps of Rijkswaterstaat for the years 1990 and 2007. For the sampling campaign in 1989, elevations of 1990 were used. For the resampling campaign in 2008, elevations of 2007 were used.

Analysis

Trends in abundance and biomass of benthic prey species were analysed visually using scatter plots and statistically through linear regression. For shellfish we made selections of certain size categories, dependent on which bird species we studied. Oystercatchers are known to feed mainly on mussels and cockles that are larger than 8 mm (Zwarts and Wanink 1993). Knots primarily feed on Baltic tellins smaller than 16 mm, and also cockles smaller than 12 mm (Zwarts and Wanink 1993). To study a relationship between shellfish prey species and their bird predators we therefore combined cockles of 1 year and older and Baltic tellins larger than 15 mm as prey species for Oystercatchers, and cockles of 0-year and 1-year and Baltic tellins of 5 - 15 mm as prey species for Knots. For both bird species we also investigated relationships with the total of cockles, Baltic tellins, and the sum of both.

We furthermore selected the most abundant prey species, and species which are known to be utilised as staple food by birds, from the benthic fauna dataset for further analysis. Trends in total benthic biomass were investigated for the entire Oosterschelde estuary and its compartments. We also made an analysis for biomass and abundance of abundant polychaetes, molluscs and crustaceans. Trends were studied visually through scatter plots with linear trend lines, and statistically using linear regression.

Furthermore, total benthic biomass and biomass of different benthic species that may serve as prey for waders were related to exposure time. Elevations for the different sampling locations were transformed into exposure times as described above for 'morphology of intertidal flats', with equation 1 and parameters for the Western compartment (Table 1). The sampling locations were categorised according to four categories of exposure time: 0 – 20%, 20 – 40%, 40 – 60% and 60 – 80%. Only one sampling location was located in the exposure time class of 80 – 100% and was therefore eliminated from the analysis.

Waders

Data collection

Numbers of waders are counted monthly in the saltwater parts of the South-western Delta, including the Oosterschelde estuary, since 1978/1979. Since 1990 this is part of a biological monitoring programme of the salt water bodies in the Netherlands (MWTL: "Monitoring van de Waterstaatkundige Toestand des Lands"), since 1990 commissioned by Rijkswaterstaat (presently Rijkswaterstaat Waterdienst, part of the Ministry of Transport, Public Works and Water Management). The results are reported annually (e.g. Strucker et al. 2010). In the analyses presented here, the basic dataset was used.

Shorebird numbers are counted once per month, during a series of high tides. During high tide, the birds are concentrated on high tide roosts, where they are relatively easy to count. The entire shore of the Oosterschelde estuary is split up into smaller areas, that cover all high tide roosts (Figure 9). The large intertidal flats of Roggenplaat and Neeltje Jans are counted from a boat. Missing values in the dataset are replaced by modelled values through imputing (Underhill & Prys-Jones 1994 in Strucker et al. 2008a). We used the dataset from 1987/1988, when the closure of the Oosterschelde estuary was completed. From this year on, all data have been checked, validated, and missing data imputed.

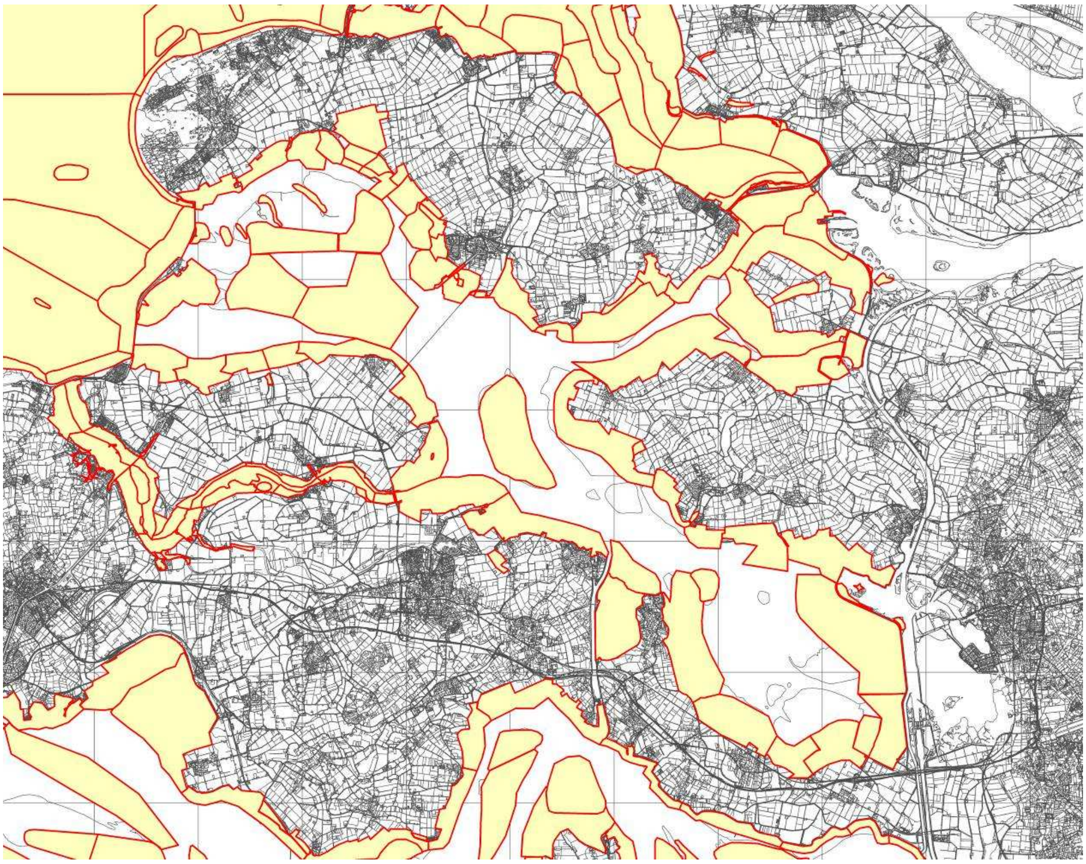

Figure 9. Counting cells in the South-western Delta area: Oosterschelde estuary and surrounding water bodies.

The total number of birds that depend on intertidal foraging grounds in the Oosterschelde estuary (as listed in Table 3) were related to the total area of intertidal flats for the four compartments. This yielded a 'density' per compartment, with the assumption that the birds are spread evenly over the entire intertidal. This was done for the three years for which bottom-height maps covering the entire estuary were available: 1990, 2001 and 2007. For each of these years, the total number of birds was averaged over a period of three seasons: 1989/1990 – 1991/1992, 2000/2001 – 2002/2003, and 2006/2007 – 2008/2009.

Selection of species

In this study we considered the waders protected under Natura 2000. These waders are to a large extent dependent on the tidal flats for foraging and can be directly affected by a change in quantity (area) and quality (e.g. food) of the tidal flats (Table 3). Species that are less dependent on the intertidal flats for foraging, such as the Golden Plover (*Pluvialis apricaria*) and Lapwing (*Vanellus vanellus*), were not considered. The Kentish Plover is dependent on the intertidal flats for foraging, but this species was not included in the analyses because its declining numbers can almost be entirely attributed to a continuously declining breeding population (Meininger and Arts 1997; Strucker et al. 2008b).

Special attention was given to waders that show a different trend in the Oosterschelde estuary compared to other intertidal areas (Westerschelde estuary and Dutch Wadden Sea). For these species, it is likely that the observed trend is caused by developments within the Oosterschelde. In contrast, where trends in the Oosterschelde estuary follow trends observed in the Westerschelde estuary and Wadden Sea, the cause should probably be looked for on a larger spatial scale, such as for instance circumstances in the breeding grounds. Waders that show a different trend in the four compartments of the Oosterschelde

Table 3. Overview of birds considered in this study. A population estimate is given (East-Atlantic flyway Delany and Scott 2006; Aarts et al. 2008), as well as the target population size in the Oosterschelde estuary (Natura2000). Trends of the studied shorebird species in the Oosterschelde estuary (OS), Westerschelde estuary (WS) and Dutch Wadden Sea (WSea) until 2008/2009 were derived from www.sovon.nl (Network Ecological Monitoring (SOVON, RWS, CBS)).

Species	English name	Dutch name	Highest numbers in Oosterschelde estuary	Food	Population Estimate	Oosterschelde Natura2000	OS[1]	OS since '98/'99	WS[2]	WSea[2]
Tadorna tadorna	Shelduck	Bergeend	November – April (peak in winter)	Small benthos (*Hydrobia*), diatoms	300,000	2,900	+	0	+	+
Haematopus ostralegus	Oystercatcher	Scholekster	August - February	Mainly bivalves (*Cerastoderma* > 8 mm)	1,020,000	24,000	-	-	0	-
Recurvirostra avosetta	Avocet	Kluut	April – June	Crustaceans, polychaetes	73,000	510	+	+	+	0
Charadrius hiaticula	Ringed Plover	Bontbekplevier	May, August - October	Small polychaetes and amphipods	200,000	280	0	0	-	+
Pluvialis squatarola	Grey Plover	Zilverplevier	August - May	Polychaetes (*Nereis*, *Arenicola*)	247,000	4,400	0	+	0	+
Calidris canutus	Knot	Kanoet	October - February	Mainly bivalves (*Macoma, Cerastoderma* < 10 mm)	340,000 *canutus* 450,000 *islandica*	7,700	+	+	0	0
Calidris alba	Sanderling	Drieteenstrandloper	April – May, August - October	Small polychaetes and amphipods	123,000	260	+	+	+	+
Calidris alpina	Dunlin	Bonte strandloper	October - May	Small polychaetes and amphipods	1,330,000	14,100	+	+	+	+
Limosa lapponica	Bar-tailed Godwit	Rosse Grutto	August – May	Large benthos: *Arenicola*, crabs	120,000 *lapponica* 520,000 *taymyrensis*	4,200	0	0	-	+
Numenius arquata	Curlew	Wulp	July – April (peak in autumn)	Large benthos: *Arenicola*, *Mya*, crabs	420,000	6,400	+	+	+	+
Tringa erythropus	Spotted Redshank	Zwarte Ruiter	July – October	Polychaetes, crustaceans, small fish	100,000	310	-	-	0	0
Tringa totanus	Redshank	Tureluur	July - November	Polychaetes, crustaceans, small fish	250,000 *totanus* 65,000 *robusta*	1,600	+	+	0	0
Tringa nebularia	Greenshank	Groenpootruiter	July - September	Polychaetes, crustaceans, small fish	310,000	150	0	-	+	+
Arenaria interpres	Turnstone	Steenloper	August - May	Crustaceans, polychaetes	94,000 *Canada* 83,000 *N Europe*	580	+	+	-	0

estuary also received extra attention. Here, the cause may be found on an even smaller scale than the Oosterschelde as a whole. Such trends may be related to local trends in food. We analysed the following 9 species in detail: Shelduck *Tadorna tadorna*, Oystercatcher *Haematopus ostralegus*, Ringed Plover *Charadrius hiaticula*, Grey Plover *Pluvialis squatarola*, Knot *Calidris canutus*, Dunlin *Calidris alpina*, Bar-tailed Godwit *Limosa lapponica*, Curlew *Numenius arquata* and Spotted Redshank *Tringa erythropus*.

Analysis

Trends in numbers of waders are characterised by being non-linear. Often stable periods are alternated with sudden increases and/or decreases, which makes detecting significant trends very difficult. The program "Trendspotter" was especially designed to detect flexible trends (Visser 2004). Trendspotter gives an average trend with confidence intervals. These intervals are used to determine the significance of a trend.

3. Results

Morphology of intertidal flats

Changes in intertidal area and exposure time

The total intertidal area of the Oosterschelde estuary has decreased with an estimated net 6.7 km^2 between 1990 and 2007. Of the area above NAP (≈ MTL) about 3.2 km^2 has been lost, of the area below NAP about 3.5 km^2 (Jacobse et al. 2008). Figure 10 shows changes in intertidal area for different tidal flats within the four compartments. A decrease in total intertidal area can be clearly observed for Slikken van Viane – South in the Northern compartment, Galgeplaat in the Central compartment, and Verdronken land van Zuid-Beveland in the Eastern compartment. The intertidal area of the Eastern compartment is eroding the fastest (as also concluded by Jacobse et al. 2008). However, care should be taken in interpreting results for the Eastern compartment, as will be discussed later.

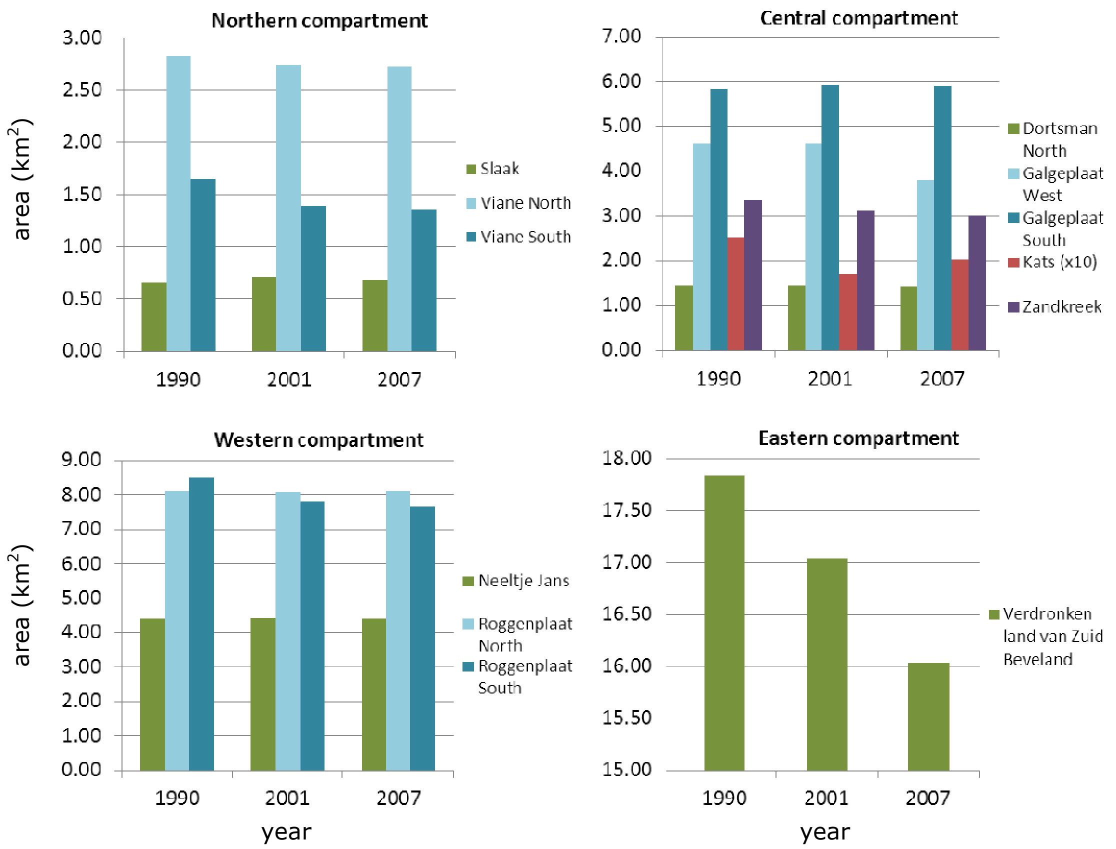

Figure 10. Changes in the total area of tidal flats in the Oosterschelde estuary in the tidal range of -150 to +200 cm relative to NAP, based on measured values in 1990, 2001 and 2007. Results are given per compartment. In the cases of Slikken van Viane, Galgeplaat and Roggenplaat data were available for sub-areas, which are given here.

The distribution of the intertidal over the whole range of exposure times differs markedly between the different compartments (Figure 11). Whereas the majority of the intertidal area in the Eastern compartment lies below 50% exposure time (≈ NAP), the intertidal of the Northern compartment is represented by a large area that is exposed longer than 60% of the time. The Western compartment shows an optimum around 50%. Considering this distribution only, the Central and Western compartments may be considered as intermediary between the two opposite extremes of the Northern and Eastern compartments.

Figure 11 also shows that in the Eastern compartment the intertidal area within the exposure time range of 40 – 60% decreased, and the area within exposure time range 0 – 40% increased. The other compartments do not show obvious changes at this scale.

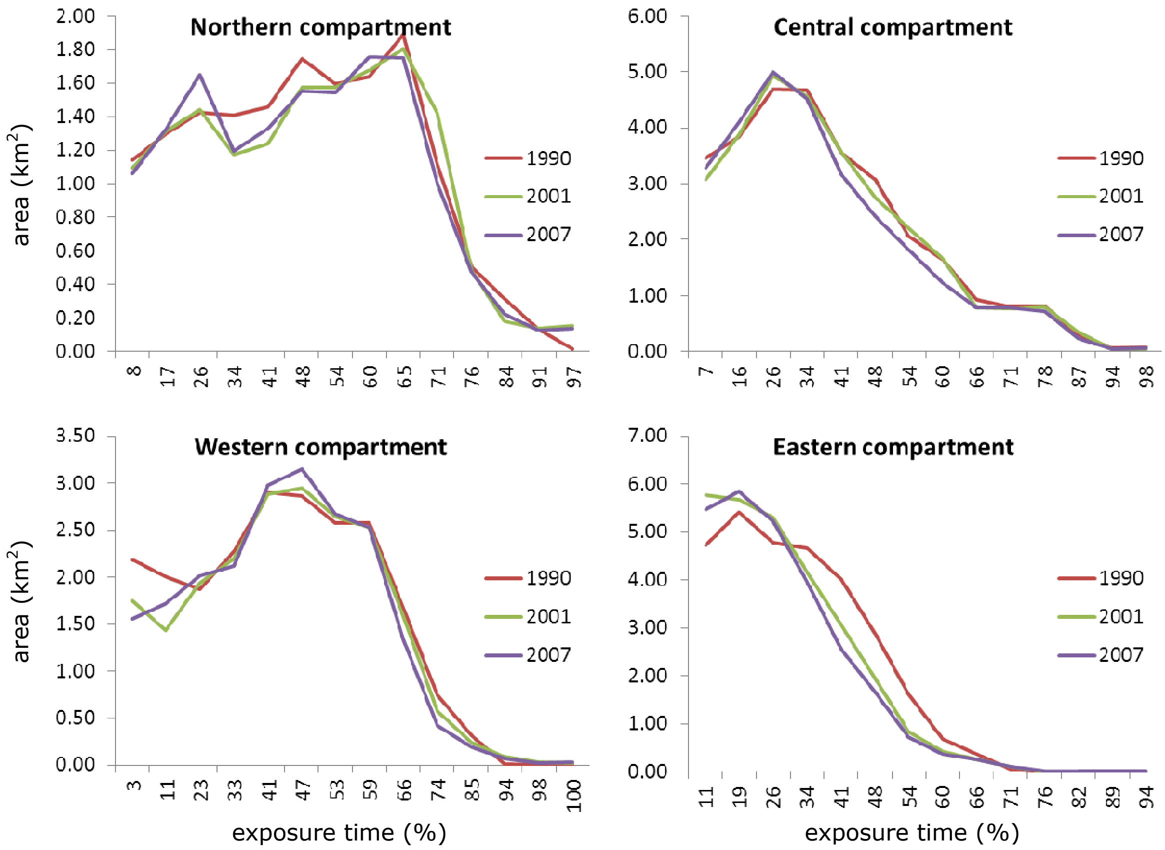

Figure 11. Development of the distribution of the total area of tidal flats within the different compartments over the range of exposure times from 0% to 100% (data from the elevation maps of 1990, 2001 and 2007; area per elevation classes calculated by Royal Haskoning (Jacobse et al. 2008), calculated to exposure times per compartment in this study).

Apart from differences in distribution of the intertidal area over exposure time categories, the different compartments also show large differences in the total area of intertidal flats. The largest intertidal area is found in the Central and Eastern compartments (almost 30 km^2), and the smallest in the Northern compartment with 50% less (15 km^2) (Table 4). Because of the large differences in distribution over the lower and higher intertidal, the comparison is completely different when only the area below or above NAP is considered. The area above NAP is comparable between the Northern, Central and Western compartments, but more than 50% smaller in the Eastern compartment.

The area below NAP is the highest in the Eastern compartment, closely followed by the Central compartment, and then the Western compartment with roughly 45% less and the Northern compartment with roughly 65% less.

Table 4. The intertidal area in the different compartments in 1990, 2001 and 2007: the total area, the area below NAP (corresponds with <50% exposure time) and the area above NAP (>50% exposure time).

Compartment	Intertidal area	1990	2001	2007
Northern	**total**	15.7	15.3	15.1
	<NAP	8.5	7.8	8.1
	>NAP	7.2	7.4	7.0
Central	**total**	30.0	29.4	28.2
	<NAP	23.3	22.8	22.5
	>NAP	6.7	6.7	5.7
Western	**total**	22.0	20.9	20.8
	<NAP	14.1	13.1	13.5
	>NAP	7.9	7.7	7.3
Eastern	**total**	29.2	27.5	26.2
	<NAP	26.5	25.9	24.7
	>NAP	2.7	1.6	1.5

For birds, not only foraging area is important, but also foraging time and prey abundance. To assess differences between compartments in an optimum of combined foraging area and foraging time, the intertidal area times exposure time are related to elevation in

Figure 12.

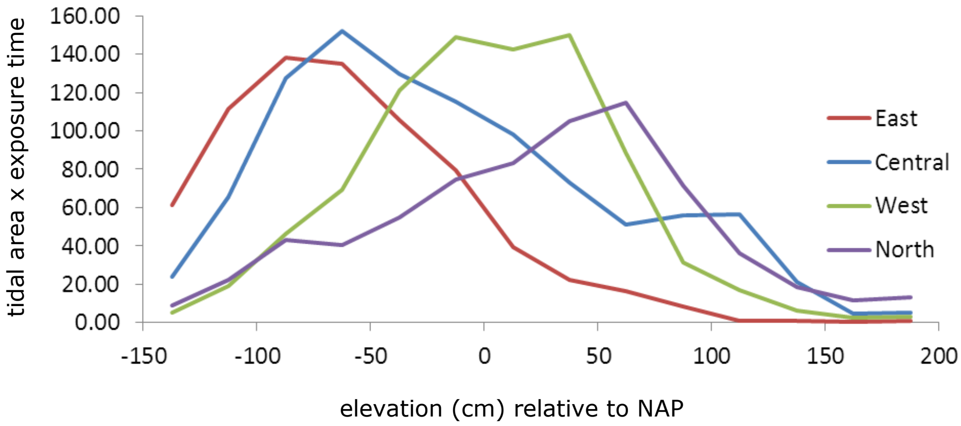

Figure 12. Optimum in the combination of foraging area and foraging time (tidal area x exposure time) in the different compartments in 2007, related to elevation.

The total food availability for waders can be expressed as the product of surface area, exposure time and benthic biomass (Meire et al. 1994a). Our dataset did not allow for a calculation of this index, but we did calculate the product of surface area and exposure time as a measure for availability of foraging area (thus excluding benthic biomass). The highest availability of foraging area is found at lower intertidal levels in the Eastern compartment than in the Northern compartment. The Central compartment is comparable with the Eastern compartment and the Western compartment is in between. In general it can be said that the highest availability of foraging area are found below NAP in the Eastern and Central compartments and above NAP in the Northern and Western compartments.

Shifts in exposure time distribution

The relative area (or distance) within exposure time classes along RTK transects (see Figure 6), averaged for entire tidal flats, showed significant changes over time. After averaging all transects per compartment, we in general found increasing relative areas in exposure time classes lower than 40% and decreases in classes higher than 50% (Table 5). In the Eastern compartment we found the least changes in time, only an increase within the exposure time class of 30 – 40%. The exposure time classes of <10% and >90% gave the least reliable results because of changes from year to year in covered transect length, which was reflected in sometimes large differences in the extreme ends of the transects that are generally found in the upper and lower intertidal. The largest differences were removed prior to the analysis, but some differences still remain.

Table 5. Significant changes in the relative area of tidal flats within a certain emerge time class (10 classes in the range of 0 – 100%), averaged for the different compartments (linear regression $p < 0.05$). Where certain exposure time classes were not present, this is shown with n.a.(= not available).

Compartment	<10%	10-20%	20-30%	30-40%	40-50%	50-60%	60-70%	70-80%	80-90%	>90%
Northern			+	+		-				+
Central						-	-			-
Eastern				+						
Western			+	+		+	-	-	-	

Also when looked at on a smaller spatial scale, that of tidal flats, we generally observed decreasing relative areas in the higher intertidal (exposure times > 40-50%) and increasing relative areas in the lower intertidal (exposure times < 40-50%) (Table 6). No significant changes were observed at location Rattekaai (4 transects).

Table 6. Significant changes in the relative area of tidal flats within a certain emerge time class (10 classes in the range of 0 – 100%), averaged for the different compartments (linear regression $p < 0.05$). Where certain exposure time classes were not present, this is shown with n.a.(= not available).

Compartment	Tidal flat	<10%	10-20%	20-30%	30-40%	40-50%	50-60%	60-70%	70-80%	80-90%	>90%
Northern	Slaak			+		+	-		+	-	
	Slikken van Viane		+	+	+	-				-	+
Central	Galgeplaat	+					+	-			
	Slikken vd Dortsman		+	+	+	-	-	-			
	Kats		+				-				-
	Zandkreek		+	+			+	-			-
Eastern	Rattekaai										
	Krabbendijke				+	-			+		-
Western	Roggenplaat			+	+	+	+	-	-		
	Neeltje Jansplaat			+		-	+			-	

Since the number of years covered by all transects at locations Slikken van Viane and Rattekaai was limited we split these tidal flats into two sub-areas: Slikken van Viane North and South, and Rattekaai East and West. This increased the number of years available for Slikken van Viane from 9 to 15 for the sub-areas. At location Rattekaai the number of years increased from 13 to 18 for the sub-area West. Splitting the areas into sub-areas made no difference for the location Rattekaai, however.

Still no significant changes were detected. At location Slikken van Viane, splitting the area up into two sub-areas resulted in the same pattern as observed for the total area Slikken van Viane. The most conspicuous changes in areas within the exposure time classes were observed at the tidal flats of Slaak, Slikken van Viane South, Slikken van de Dortsman and Roggenplaat (Figure 13). In the Eastern compartment changes were less pronounced.

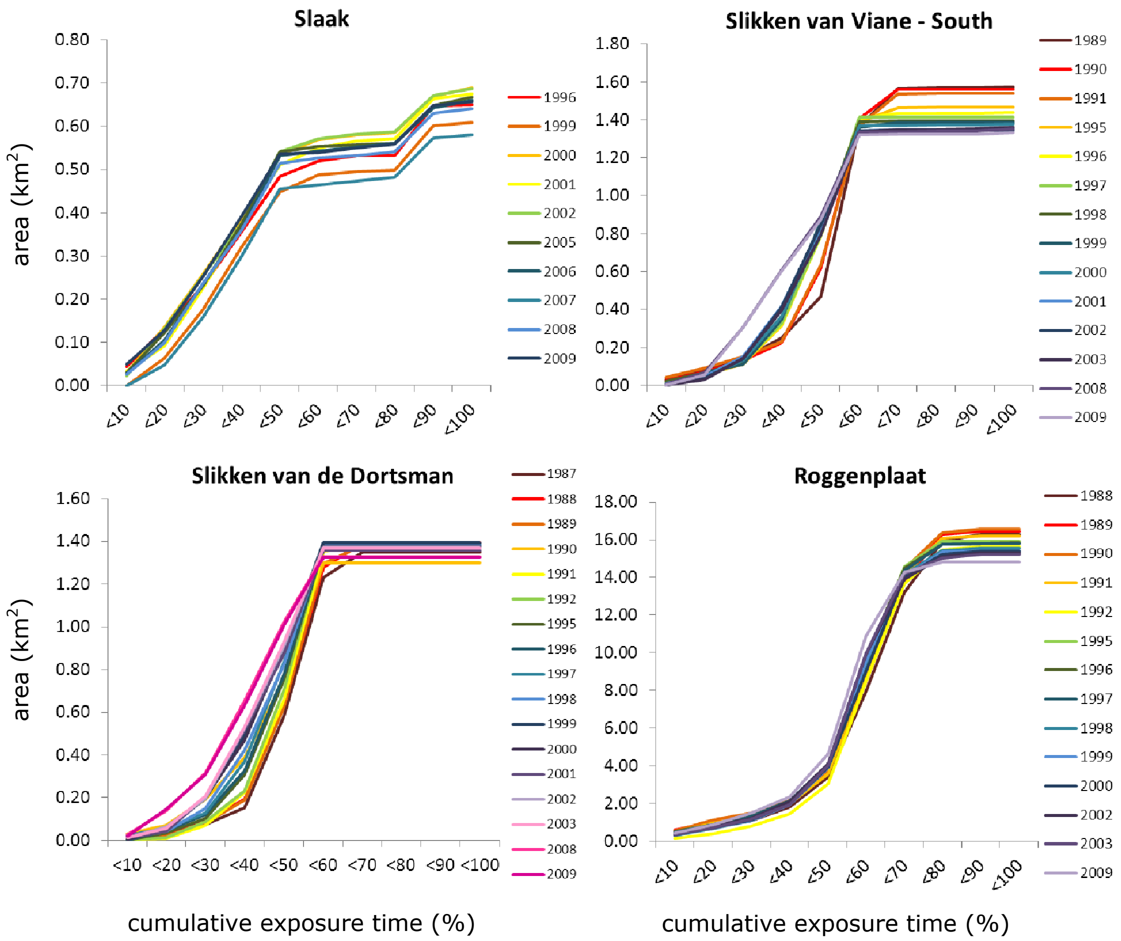

Figure 13. Areas within exposure time classes were calculated for cumulative exposure time classes (x-axis) to show interannual changes. Only tidal flats that showed the most conspicuous changes are shown here (Slaak, Slikken van Viane – South, Slikken van de Dortsman and Roggenplaat).

Benthic fauna

Total abundance and total biomass of the benthic macrofauna (MWTL dataset) showed large year to year variations (Figure 14). The observed fluctuations in total abundance is mainly explained by the fluctuations in one species, the mud snail *Hydrobia ulvae*. This species represents 64% of the total abundance. Other species that contribute to the total abundance are Oligochaeta (7,7%), *Pygospio elegans* (4,5%), *Aphelochaeta marina* (4%), and *Scoloplos armiger* (3%). The fluctuations in total biomass are mainly explained by the fluctuations in the cockle *Cerastoderma edule*, which represents 54% of the total biomass. Other species that contribute to the biomass are the mud snail (14%), *Arenicola marina* (9%), and *Mya arenaria* (5%). Both the total density and total biomass of benthic fauna sampled within the MWTL programme were largely comparable between the three compartments. The decrease in biomass in the Eastern compartment, and increase in biomass in the Western compartment, are largely due to *C. edule*.

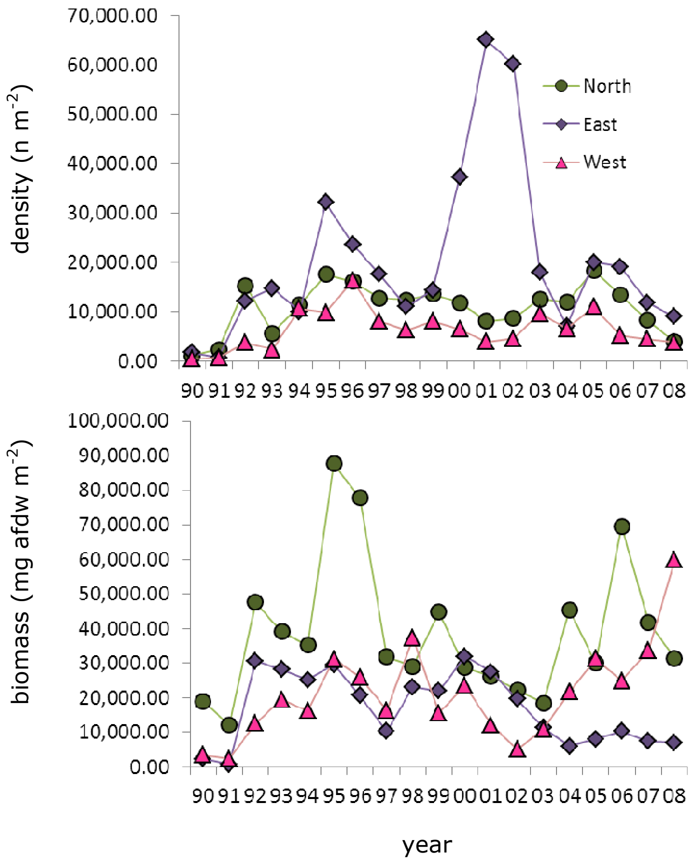

Figure 14. Development of benthic macrofauna of the tidal flats of the Oosterschelde estuary in autumn. Density (upper) and biomass (lower) are given for the total of all species of benthic macrofauna (data MWTL).

Molluscs

Cockles, the main food source for the Oystercatcher, showed no trend in the Oosterschelde estuary as a whole (see also Meesters et al. 2009). In the Eastern compartment, however, the biomass of cockles suddenly decreased to a lower level after 1996 (Figure 15). This sudden decrease was not observed in the other compartments.

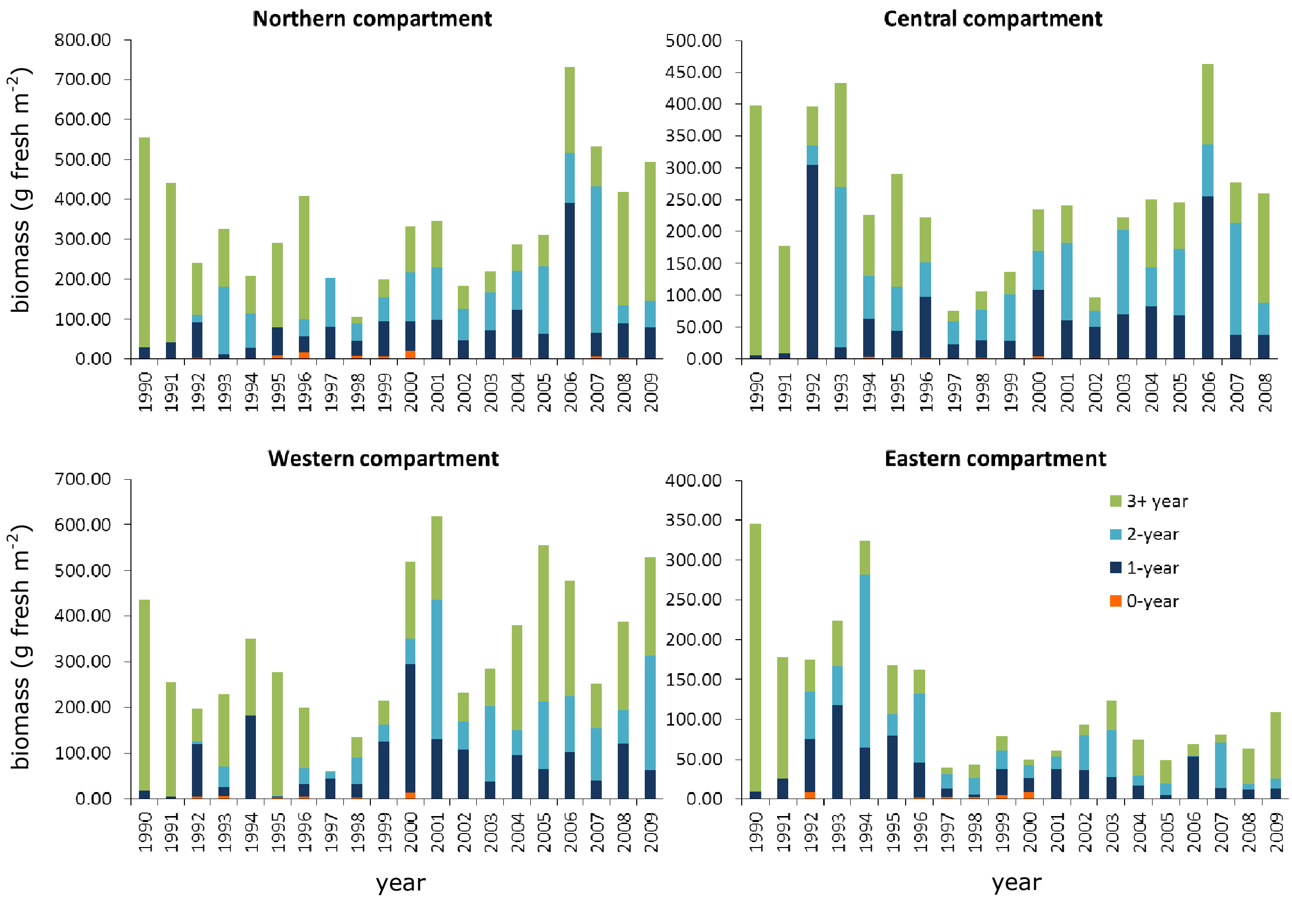

Figure 15. Development of cockle biomass (g fresh weight m^{-2}) in the four compartments of the Oosterschelde estuary. Cockles are divided in four age classes: 0-year (red), 1-year (dark blue), 2-year (light blue) and 3-year and older (green) (data IMARES, WOt surveys).

No trend was observed in biomass of Baltic tellins in the entire Oosterschelde estuary (Figure 16) and its compartments over the entire monitoring period. From 2001 onwards, Baltic tellins are divided into three size classes: <5 mm, 5 – 15 mm and > 15 mm. The smallest size class is hardly ever found because samples are sieved over a 5 mm mesh. This size class has no quantitative value but can be used as a qualitative indication. Striking in the time series of *M. balthica* is the absence of high peaks in abundance since 2000. Recruitment may be failing in the Oosterschelde estuary, as it also does in the Wadden Sea in relation to climate change (Philippart et al. 2003).

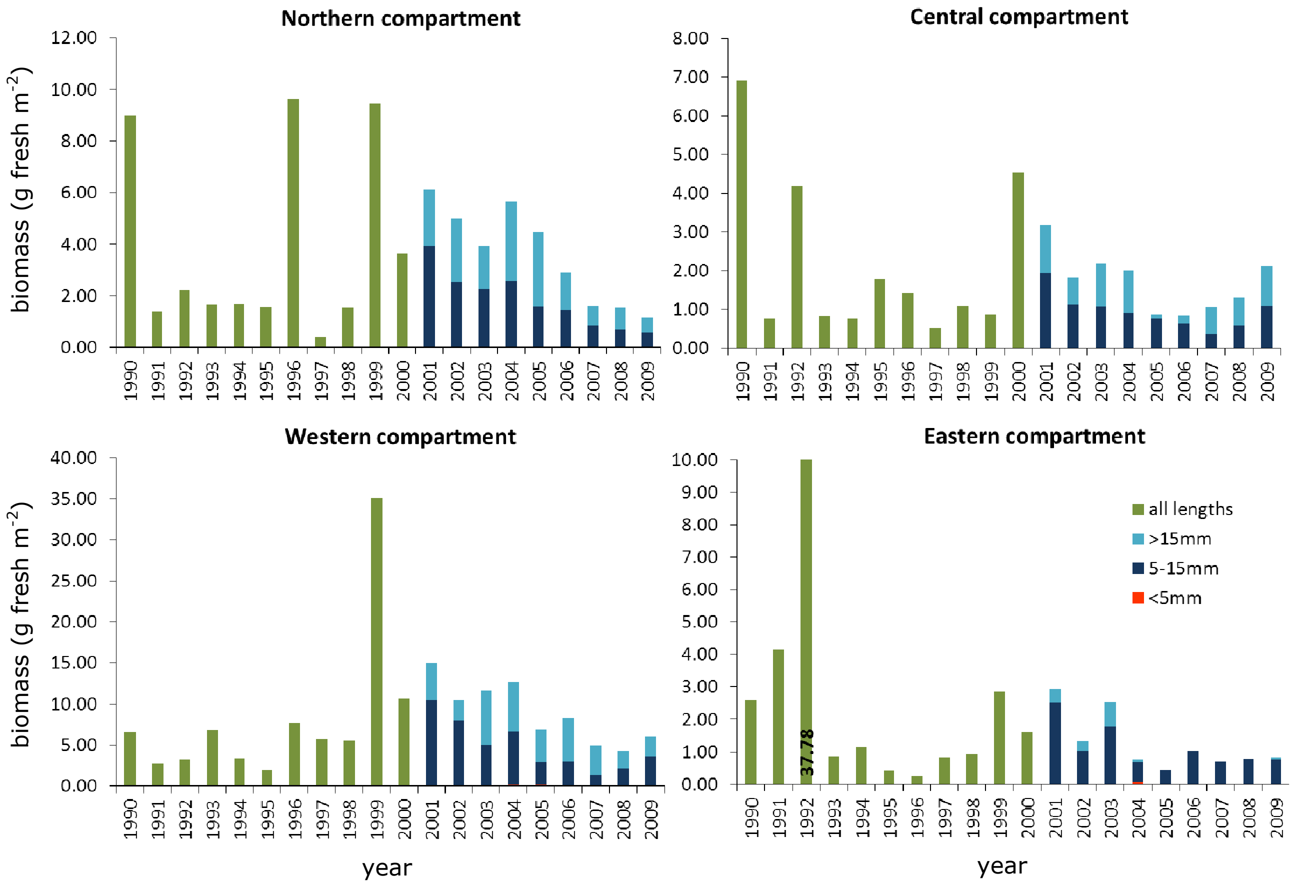

Figure 16. Development of Baltic tellin biomass (g fresh weight m^{-2}) in the four compartments of the Oosterschelde estuary. From 2001, Baltic tellins are divided in size classes: < 5 mm (red), 5 – 15 mm (dark blue) and > 5 mm (light blue) (data IMARES, WOt surveys).

Mussels disappeared almost completely from the intertidal of the Oosterschelde estuary in the mid-1990s (Figure 17), mainly due to an alteration in management of cultured stocks. All intertidal mussel culture was replaced to subtidal bottom culture plots. Natural intertidal mussel beds had already disappeared from the Oosterschelde estuary before the stock assessments started in 1994. Figure 17 also shows data for the period 1985 – 1994. These were derived from the INTERECOS campaign in 1985, 1988 and 1989 (Coosen et al. 1994). For the years 1990 – 1993 the intertidal mussel stock was estimated roughly from mussels collected as by-catch in the annual cockle survey (Kater and Kesteloo 2003).

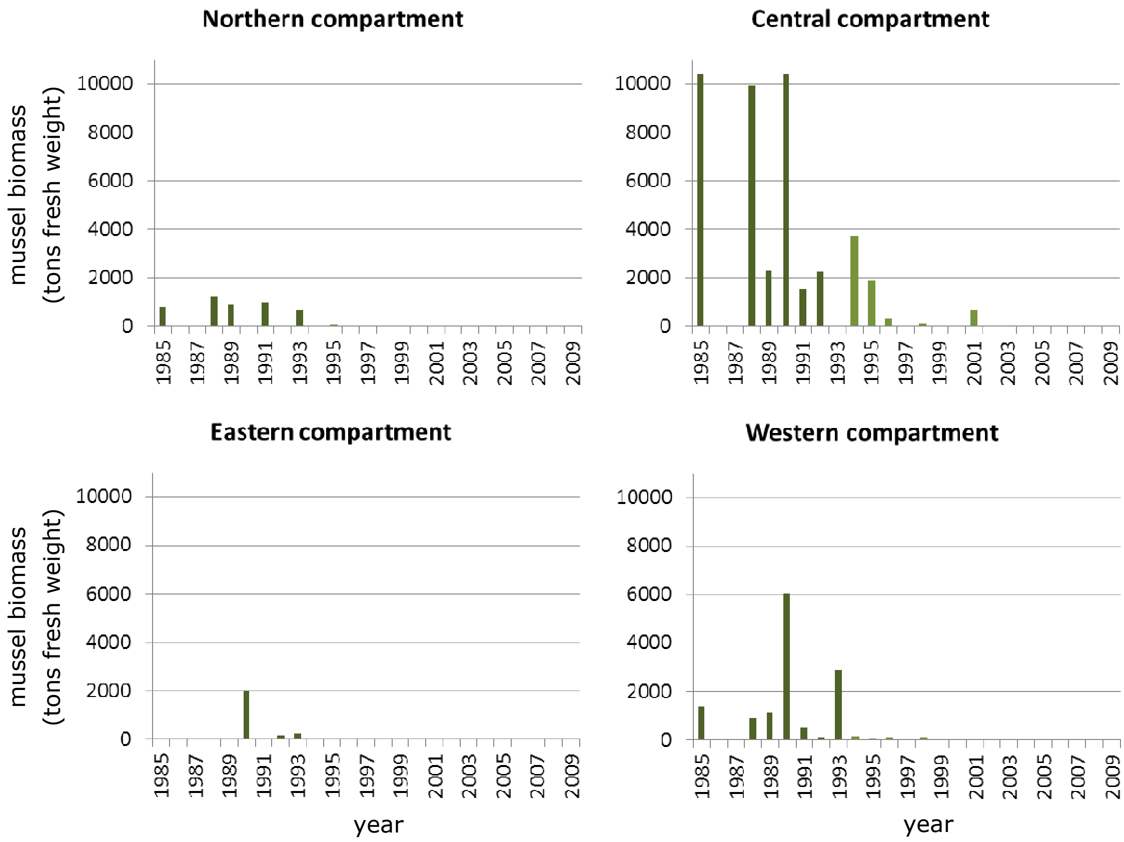

Figure 17. Development of mussel biomass (tons fresh weight m^{-2}) in the different compartments of the Oosterschelde estuary monitored during the annual mussel survey since 1994. Data for the period until 1994 were derived from the INTERECOS campaign (1985, 1988 and 1989) and estimated roughly from the cockle survey (1990 – 1993; IMARES).

Other common bivalves, *Mya arenaria* and *Scrobicularia plana*, did not show clear trends in the three compartments that were sampled in the MWTL programme (Figure 18). The high variability in densities of these large species are probably explained by the sampling technique being not well suited to larger species that occur in lower densities. The mud snail occurs in high densities, especially in the Northern and Eastern compartments. No clear trend was observed. Densities (and biomass) reached a maximum in the Eastern compartment in the period 2000 – 2002 (Figure 18).

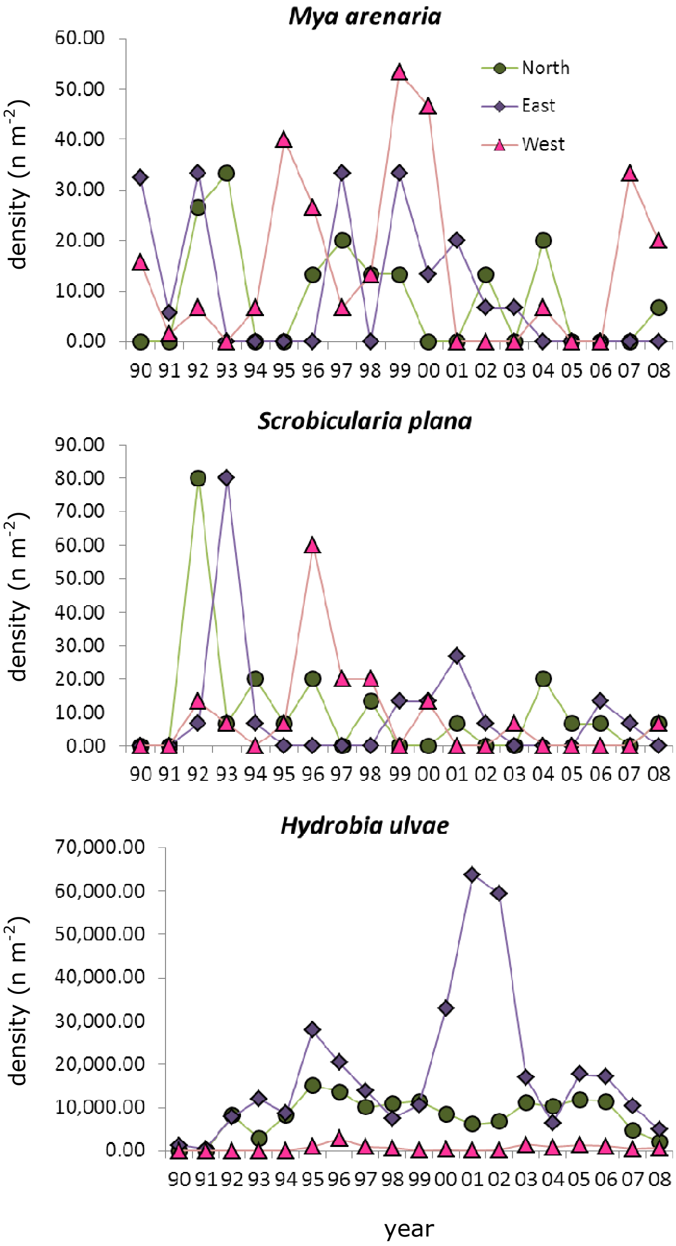

Figure 18. Development of the density of three dominant species of molluscs: mud snail *H. ulvae*, *Mya arenaria* and *Scrobicularia plana* (MWTL data).

Worms

The total of eleven species of dominant polychaetes showed relatively high densities and biomass in the Western compartment, especially in the period 1994 – 2000 (Figure 19). Since the mid-1990s densities and especially biomass have decreased in the Western compartment. In the other two compartments density and biomass are comparable and no clear trends were observed. The total of all oligochaetes showed larger fluctuations from year to year and between compartments. Density and biomass showed a sudden decline to a lower level in the Eastern compartment in 2000. In the same period the density and biomass of oligochaetes appeared to increase in the Northern compartment. Density and biomass seem to decrease since the mid-1990s in the Western compartment, parallel to the observed decrease in common polychaetes.

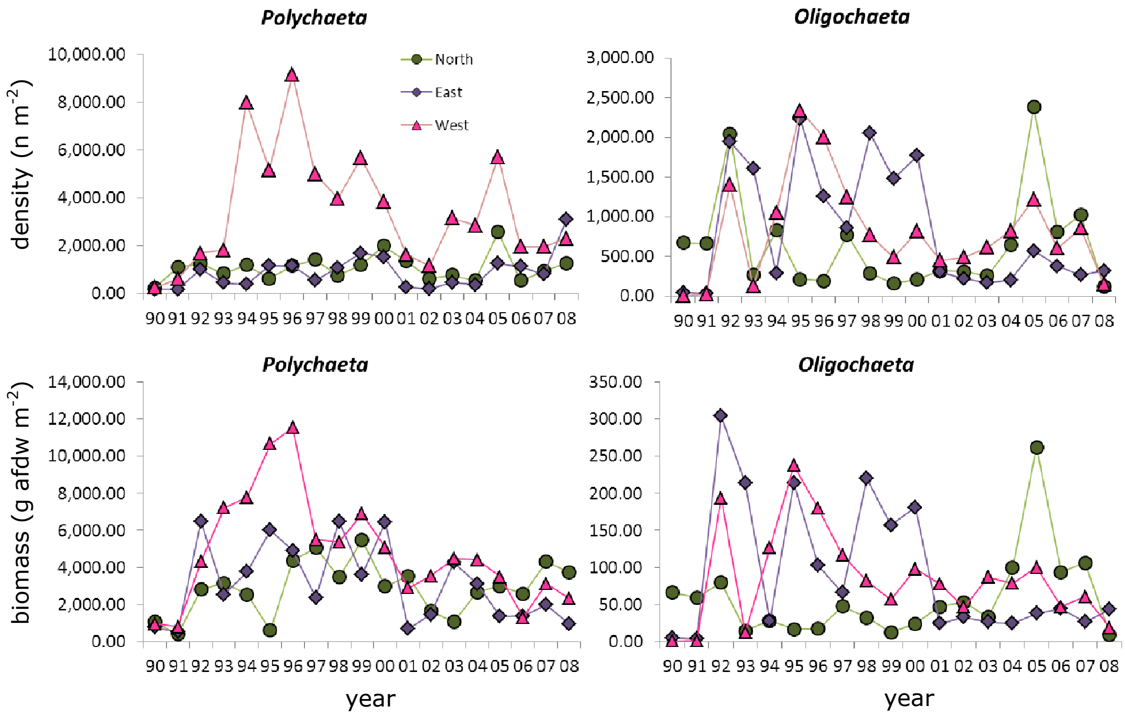

Figure 19. Development of the density and biomass of the most common polychaetes and the total of all oligochaetes. The most common polychaetes include *Aphelochaeta marioni*, *Arenicola marina*, *Capitella capitata*, *Heteromastus filiformis*, *Lanice conchilega*, *Nephtys hombergii*, *Nereis diversicolor*, *Pygospio elegans*, *Scoloplos armiger*, *Spiophanes bombyx*, and *Urothoe poseidonis*).

Separate polychaetes species did not show clear trends, but there are some striking differences in abundance between compartments (Figure 20). The sand mason *Lanice conchilega* is not encountered at all in the MWTL dataset in the Eastern compartment, but is observed in the Northern compartment and occurs in high abundances in the Western compartment. Many polychaete worms show high peaks in density in the Western compartment, but less so in the other two compartments. This is very pronounced for *Aphelochaeta marioni*, *Nereis diversicolor* and *Scoloplos armiger*. *Heteromastus filiformis* also showed a high peak in density in the Northern compartment at the beginning of the time series. Also in terms of biomass polychaete worms are generally more abundant in the Western compartment.

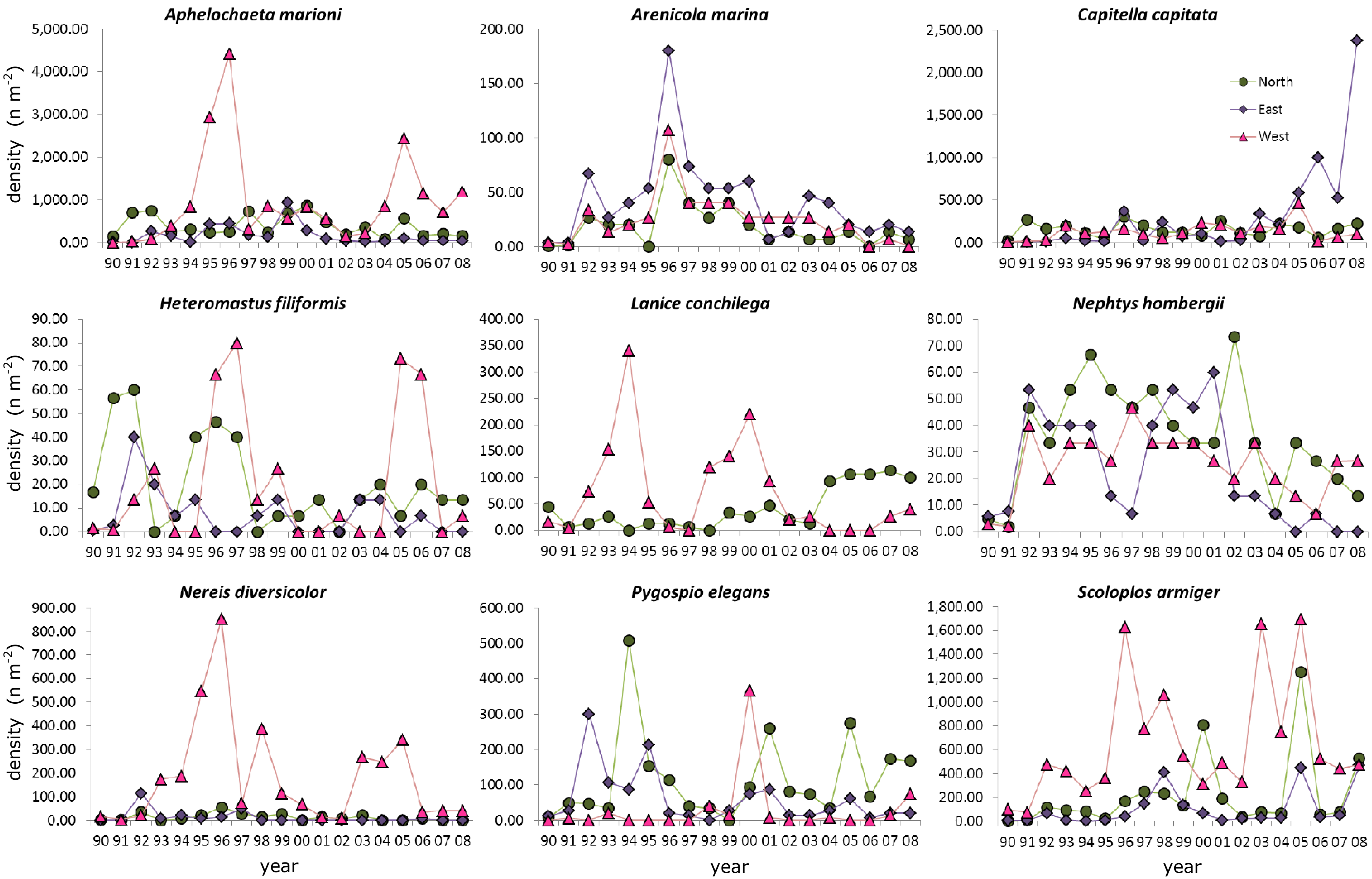

Figure 20. Development of the abundance of the dominant polychaetes *Aphelochaeta marioni*, *Arenicola marina*, *Capitella capitata*, *Heteromastus filiformis*, *Lanice conchilega*, *Nephtys hombergii*, *Nereis diversicolor*, *Pygospio elegans*, and *Scoloplos armiger* in autumn.

Crustaceans

Development of the abundance of three dominant crustacean prey species, *Corophium arenarium*, *Crangon crangon*, and *Gammarus* sp. are characterised by high variation and high peaks in abundance (Figure 21). *Bathyporeia* sp. occurs in high abundance in the Western compartment, but only in low densities in the Northern and Eastern compartments. No long-term trends were observed.

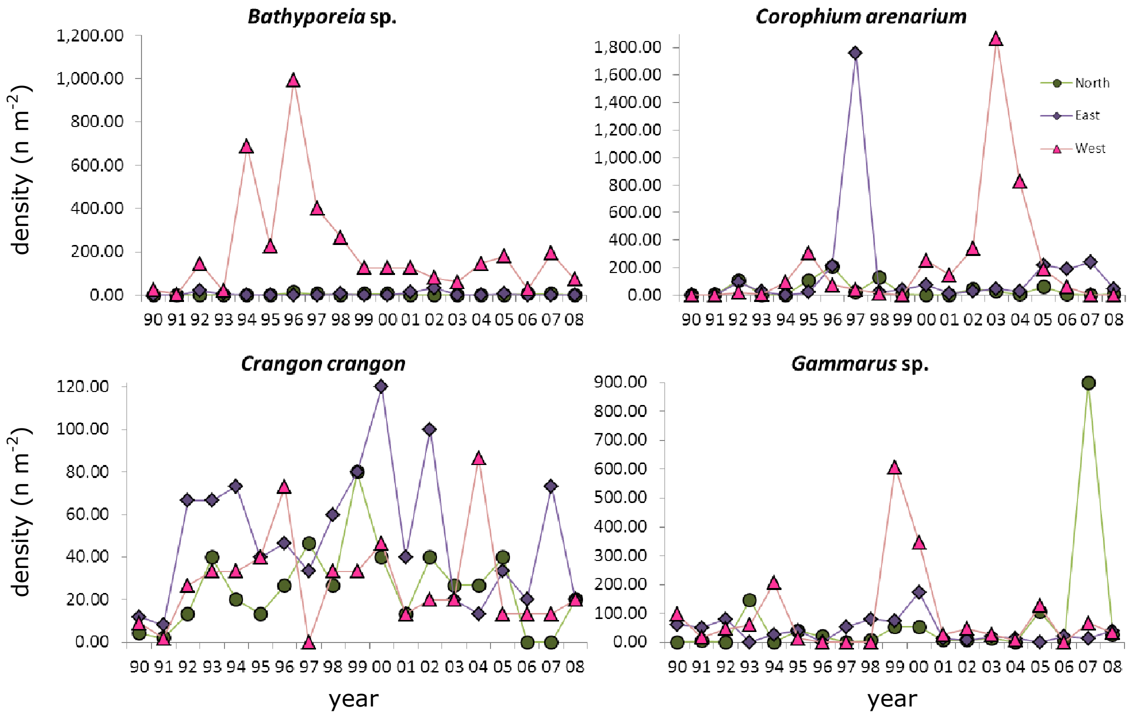

Figure 21. Development of the abundance of the dominant crustaceans *Bathyporeia* sp., *Corophium arenarium*, *Crangon crangon*, and *Gammarus* sp..

Benthic biomass in relation to exposure time

The location Roggenplaat in the Western compartment was sampled for benthic fauna in 1989 within the framework of the INTERECOS campaign. In 2008 the same location was resampled. In both years, more or less at the beginning and end of our study period, total benthic biomass was highest at exposure times lower than 60% (Figure 22). In 2008 only the location Roggenplaat was resampled. In 1989, also the locations Krabbenkreek (Northern compartment) and Galgeplaat (Central compartment) were sampled. This allowed for an investigation of the relationship between exposure time and benthic biomass. Figure 23 shows that the locations Galgeplaat and Roggenplaat showed a similar pattern with

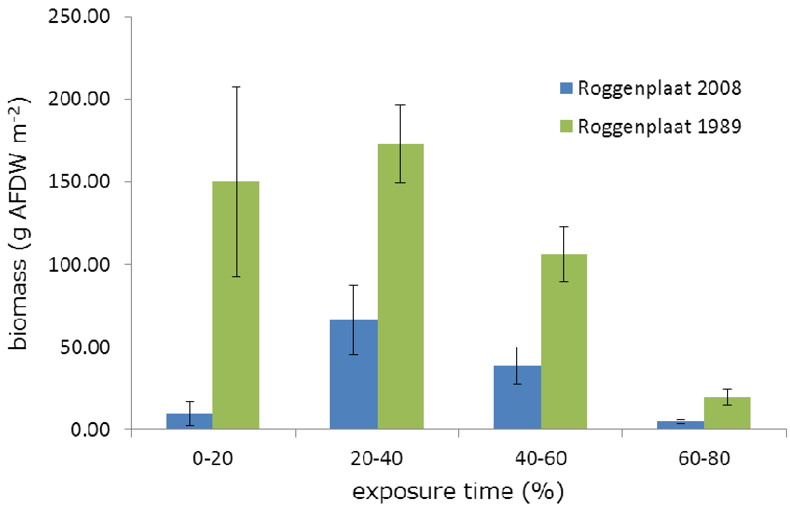

Figure 22. Total benthic biomass on the location Roggenplaat in four different categories of exposure time, for the years 1989 (INTERECOS dataset) and 2008 (resampling, De Mesel et al. 2009). Averages with standard errors are given.

higher benthic biomass below 60% and a maximum biomass at 20-40% exposure time. Location Krabbenkreek showed a different pattern, with a maximum benthic biomass low in the intertidal, at 0 – 20% exposure time. This is entirely due to a large biomass of *Mytilus edulis* as can be seen in Figure 24. Without *M. edulis* biomass, total benthic biomass at Krabbenkreek is the lowest at an exposure time of 0 - 20%, and similar for the exposure time classes between 20 and 80%.

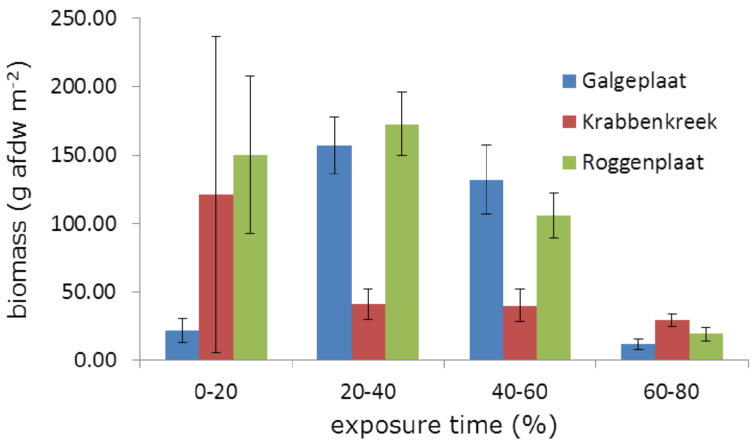

Figure 23. Total benthic biomass on the locations Galgeplaat (Central), Krabbenkreek (North) and Roggenplaat (West) in four different categories of exposure time, for the year 1989 (INTERECOS dataset). Averages with standard errors are given.

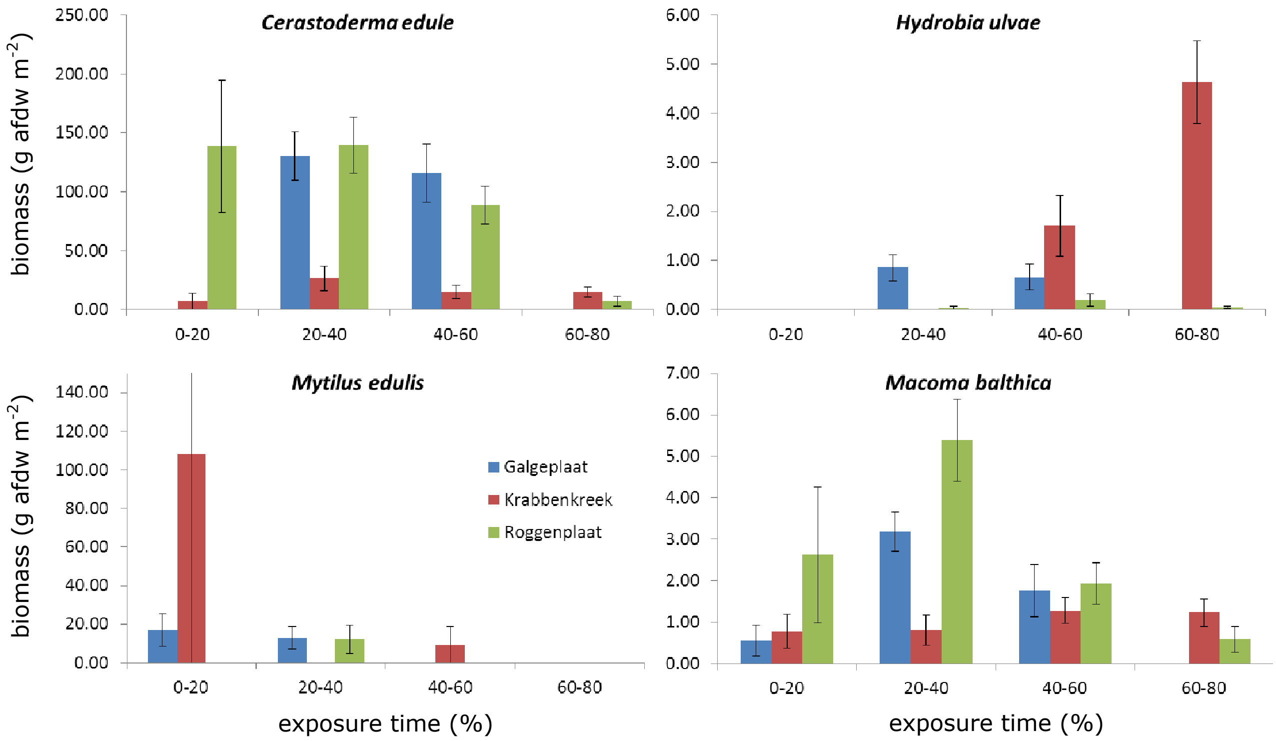

Figure 24. Biomass of common molluscan species (*C. edule*, *H. ulvae*, *M. edulis* and *M. balthica*) on the locations Galgeplaat (Central), Krabbenkreek (North) and Roggenplaat (West) in four different categories of exposure time (1989, INTERECOS dataset). Averages with standard errors are given.

Looking at the distribution of different benthic species it becomes clear that there are large differences. While some species mainly occur in the lower intertidal, others are found mainly in the higher intertidal. Also, the different locations sometimes show different distribution patterns. Out of four common molluscan species, the mud snail showed a different distribution at the different locations (Figure 24). At location Krabbenkreek in the Northern compartment biomass increased with increasing exposure time, corresponding with the observation by Escaravage et al. (2003) for the MWTL dataset. At Roggenplaat and Galgeplaat, however, highest biomass was found between 20 and 60% exposure time. The bivalves *C. edule* and *M. balthica* are mainly found between 20 and 60%, with remarkably high biomass at location Roggenplaat at the lowest exposure time of 0 – 20%. Cockles *C. edule* were found by Kater et al. (2006) to occur in highest densities at exposure times between 40 and 60%. Mussels *M. edulis* were mainly found lower in the intertidal, which is expected to be related to nearby culturing activities. Nowadays, cultured mussels are almost exclusively found on subtidal culture plots, and a small part may be washed onto the intertidal flats where they are found mainly in the lower areas.

Of the common polychaete species, *Scoloplos armiger* showed an increase in biomass towards the higher intertidal at all locations (Figure 25). This was also observed for *Nereis* sp., at location Krabbenkreek and more pronounced at location Galgeplaat, but not at location Roggenplaat. *Lanice conchilega* was mainly found at exposure times shorter than 40%, and was completely absent at location Krabbenkreek. *Nephtys* sp. and *Aphelochaeta marioni* were mainly found at exposure times shorter than 60%, and *Arenicola marina* showed a more homogeneous distribution with the lowest biomass found at exposure times shorter than 20%.

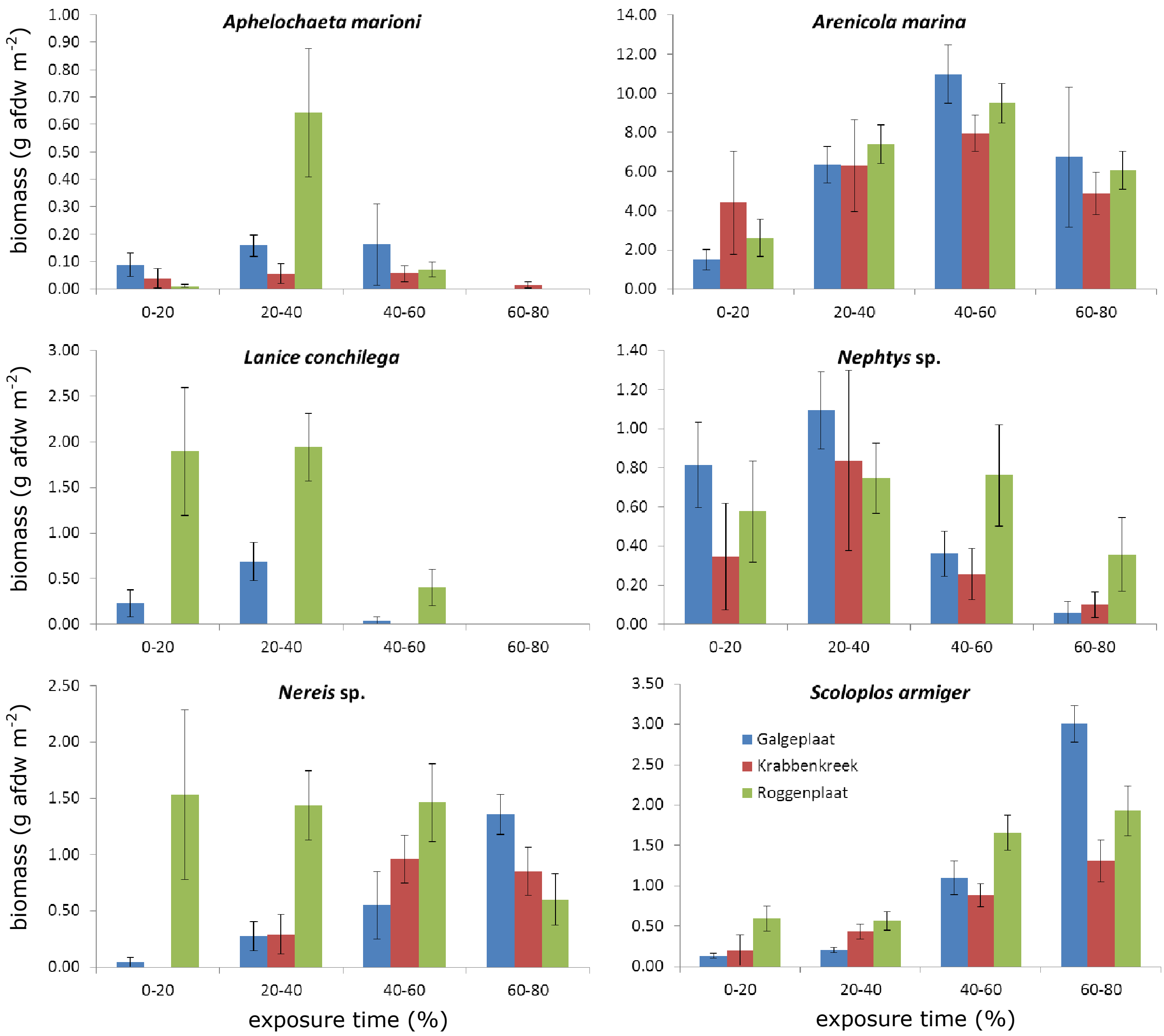

Figure 25. Biomass of six common polychaetes on the locations Galgeplaat (Central), Krabbenkreek (North) and Roggenplaat (West) in four different categories of exposure time (1989, INTERECOS dataset). Averages with standard errors are given.

The crustaceans *Bathyporeia* sp. and *Corophium* sp. showed a clear increase in biomass towards the higher intertidal; highest biomass was found at exposure times longer than 40% (Figure 26). *Crangon crangon*, in contrast, was mainly found at shorter exposure times, and biomass appears to be negatively related to exposure time. This is a species that mainly lives in gullies, and migrates onto the tidal flats for foraging with the tides (Hiddink et al. 2002). *Gammarus* sp. showed no clear distribution pattern but was absent at exposure times of 60 – 80% and completely absent at location Krabbenkreek. The high variability in biomass of *Crangon crangon* and *Gammarus* sp. in especially the lower intertidal is probably explained by the fact that sampling techniques used are not well suited to sample organisms that are highly motile and migrate over larger distances.

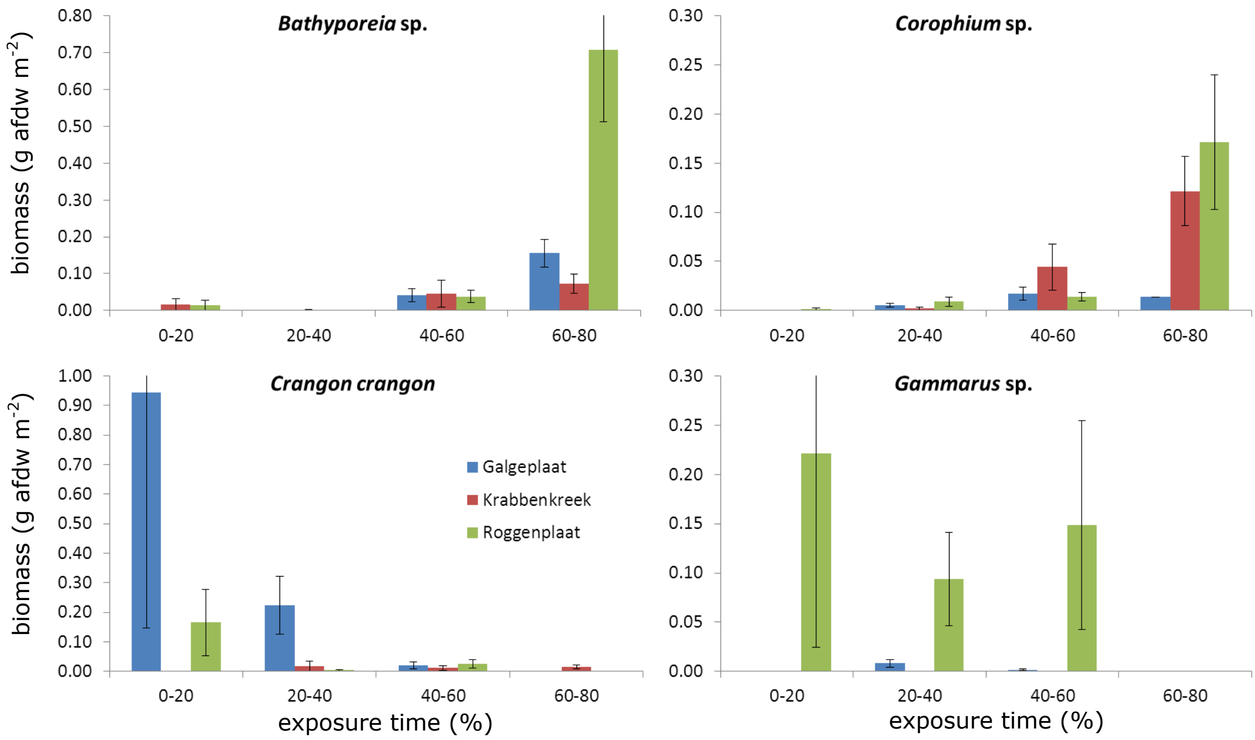

Figure 26. Biomass of four common crustaceans on the locations Galgeplaat (Central), Krabbenkreek (North) and Roggenplaat (West) in four different categories of exposure time (1989, INTERECOS dataset). Averages with standard errors are given.

Waders

Distribution within the Oosterschelde estuary

In 2001 and 2007, the calculated density of birds on the tidal flats of the Northern compartment was high compared to the other compartments (Figure 27). The 'density' of birds showed an increase over time in the Northern and Central compartments but remained stable in the Eastern and Western compartments.

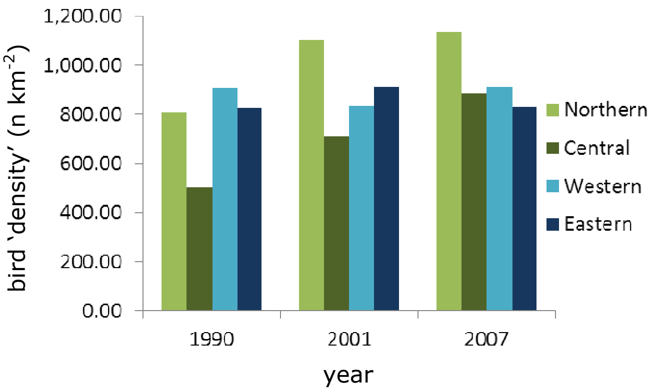

Figure 27. The total number of birds in the four compartments, divided by the total area of intertidal flats (A) and by the total area of lower intertidal (< NAP; B), resulting in a rough estimate of density (assuming a homogenous distribution) for the years 1990, 2001 and 2007.

The increase in bird density observed for the Northern and Central compartments is mainly caused by changes in bird numbers, since the area of intertidal flats did not change much. Looking at bird densities in the different seasons gives an insight in how the relative importance in terms of bird abundance of specific compartments changed over time (Figure 28). Increasing bird densities (mainly caused by increasing bird numbers) were particularly pronounced during the summer season (June – July) in all compartments except for the Eastern compartment. In autumn (August – November), densities changed most pronouncedly in the Central compartment, where an increase was observed. In winter months (December – February) an increase was observed in the Northern and Central compartments, and in spring (March – May) densities mainly increased over the entire period in the Central and Western compartments. Of an increasingly high relative importance, based on these calculated densities, are the Western compartment in summer, and the Northern compartment in winter. Densities in the Eastern compartment remained stable in all seasons. The relative importance of the different compartments showed no apparent shifts within seasons.

General trends

For some of the studied shorebird species, trends observed in the Oosterschelde estuary differed clearly from the trends observed in the Westerschelde estuary and/or Dutch Wadden Sea (summarised in Table 3). Within the Oosterschelde estuary, some species showed large differences between the different compartments, while other showed similar trends in all compartments. Trend information for the entire counting period until 2008/2009 for the different water bodies was derived from the Network Ecological Monitoring (SOVON, RWS, CBS; www.sovon.nl). Trend information for the compartments of the Oosterschelde estuary resulted from our own Trendspotter analyses for the period 1987/1988 – 2009/2010. Differences are summarised here and discussed in more detail for 9 selected species in the next section.

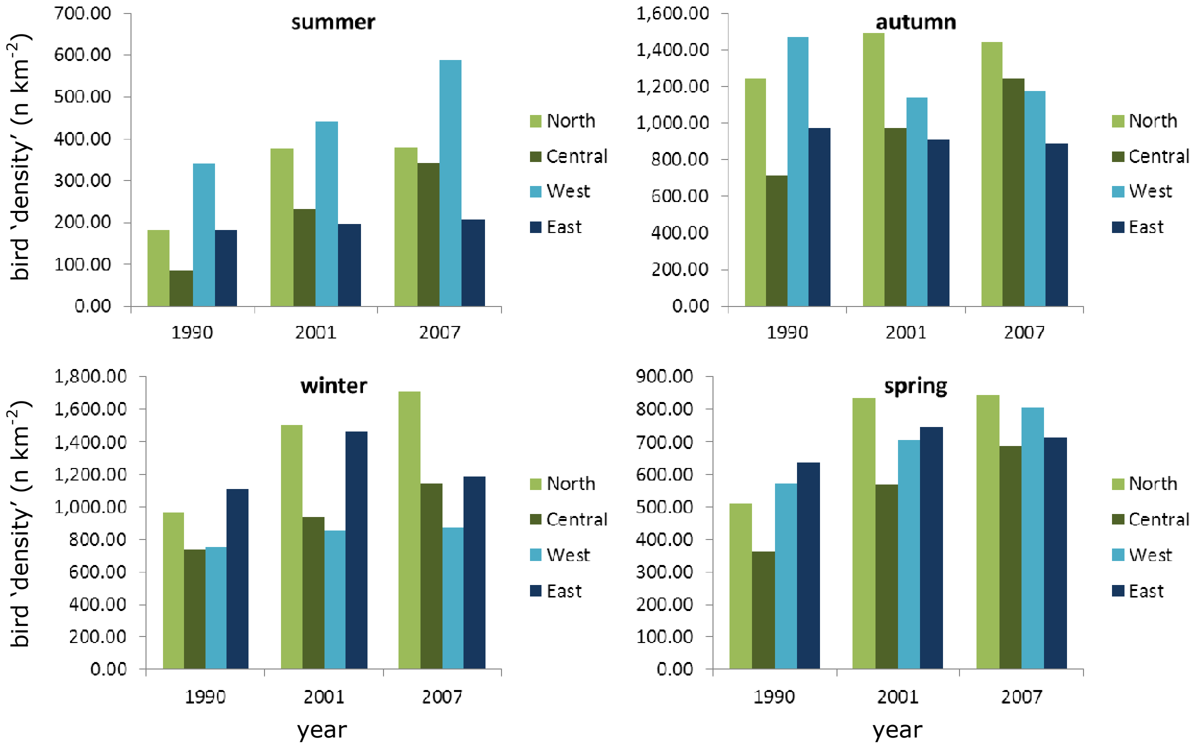

Figure 28. The total number of birds in the four compartments, divided by the total area of intertidal flats in the different seasons, resulting in a rough estimate of density (assuming a homogenous distribution) for the years 1990, 2001 and 2007.

Trends in the Oosterschelde estuary clearly differed from trends observed in the Westerschelde estuary and/or Wadden Sea for the following bird species: Oystercatcher, Avocet, Ringed Plover, Grey Plover, Knot, Bar-tailed Godwit, Spotted Redshank, Redshank, Greenshank and Turnstone (Table 3). The Oystercatcher shows a negative trend in the Oosterschelde estuary, similar to the trend in the Dutch Wadden Sea. Numbers in the Westerschelde estuary are, in contrast, stable since 1999/2000. For the Avocet, both the Oosterschelde estuary and Westerschelde estuary showed a positive trend (in the Oosterschelde largely due to increasing numbers of breeding birds, pers. comm. P.L. Meininger), but numbers are stable in the Wadden Sea. The trends in numbers of Ringed Plover and Bar-tailed Godwit differ between all three coastal waters, with no clear trend in the Oosterschelde estuary. The Grey Plover shows large fluctuations and no apparent trend in the Oosterschelde and Westerschelde estuaries, but an increasing trend in the Dutch Wadden Sea. In the Oosterschelde estuary numbers are increasing over the last decade, following a decrease after the cold winters of the mid-1990s. However, over the entire period 1987/1988 – 2009/2010 the numbers are stable. The Knot shows an increase in the Oosterschelde estuary, whereas elsewhere in the Netherlands numbers show no apparent trend. In the last few years numbers also seem to be increasing in the Westerschelde estuary. The Spotted Redshank and Redshank show no apparent trend in the Dutch Wadden Sea. The Spotted Redshank shows a decrease in the Oosterschelde and Westerschelde estuaries and the Redshank shows an increase in the Oosterschelde estuary whereas numbers remain stable in the Westerschelde estuary. The Greenshank shows an increase in Westerschelde estuary and Dutch Wadden Sea. The increase in the Westerschelde mainly occurred during the period until 2001/2002 after which numbers stabilised at a slightly lower level. In the Oosterschelde estuary no apparent trend was detected over the entire period. SOVON analyses until 2008/2009 show a negative trend in the Oosterschelde estuary over the last decade, but numbers increased again in 2009/2010. It should also be noted that the Greenshank is only present during a few months, and counted numbers are highly dependent on the period of monitoring (e.g. exactly during the migration peak or 2 weeks after; pers. comm. R. Strucker). The Turnstone shows different trends in all areas, with a positive trend in the Oosterschelde estuary, no trend in the Wadden Sea and a decline in the Westerschelde estuary.

Shelduck, Sanderling, Dunlin and Curlew showed a trend in the Oosterschelde estuary that was comparable to the trends in Westerschelde estuary and Dutch Wadden Sea (Table 3). Shelduck showed an increase in all areas, but the increase appears to have stabilised around the level of around 1990 in the Oosterschelde estuary. Numbers in the Westerschelde estuary showed a strong increase. Within the Dutch Wadden Sea, numbers are stable in the Eastern part. For Sanderling, numbers increased in all water bodies and all compartments. The increase in numbers was also observed in surrounding countries although not as pronounced as in the Netherlands (Aarts et al. 2008). Dunlin and Curlew increased in all water bodies. Curlew showed a stronger increase in the Oosterschelde than in the Westerschelde estuary.

Within the Oosterschelde estuary, Shelduck, Oystercatcher, Bar-tailed Godwit and Spotted Redshank showed clear differences between compartments.

In the following section, trends are described in more detail for the following nine species: species that showed a different trend in the Oosterschelde estuary: Oystercatcher, Ringed Plover, Grey Plover, Knot, Bar-tailed Godwit, and Spotted Redshank; Shelduck showed a similar trend in the Oosterschelde estuary as compared to the other estuaries but within the Oosterschelde estuary the species showed differences in developments over time between compartments. Curlew are the largest wader and show a remarkable increase. Dunlin was also included because this is the smallest wader and may therefore (based on hypotheses by Zwarts (2009) that still need to be tested) be among the first species to disappear because of decreased foraging times and the disappearance of higher intertidal flats. Trends for all species in the Oosterschelde estuary and its compartments can be found in Appendix A.

Trends explained for 9 selected species

Shelduck

The Shelduck feeds on small shellfish and mud shrimp (Leopold et al. 2004). It is a common breeding bird in the Netherlands, but there is also a substantial population of wintering Shelducks. During severe winters, large numbers migrate further south, resulting in either lower numbers in the Oosterschelde estuary, or higher numbers due to influx from the Wadden Sea. Numbers of Shelduck showed an increase in the Oosterschelde estuary, Westerschelde estuary and Western Dutch Wadden Sea over the past 20 years. In the Eastern part of the Dutch Wadden Sea, numbers were stable. In the Oosterschelde estuary, the increase in numbers of Shelduck was followed by a decrease since 2002/2003. This decrease was the most pronounced in the Eastern (since 2002/2003) and Western (since 2005/2006) compartments (Figure 29). In the Northern compartment no trend was detected and in the Central compartment numbers may still be increasing slightly or have stabilised.

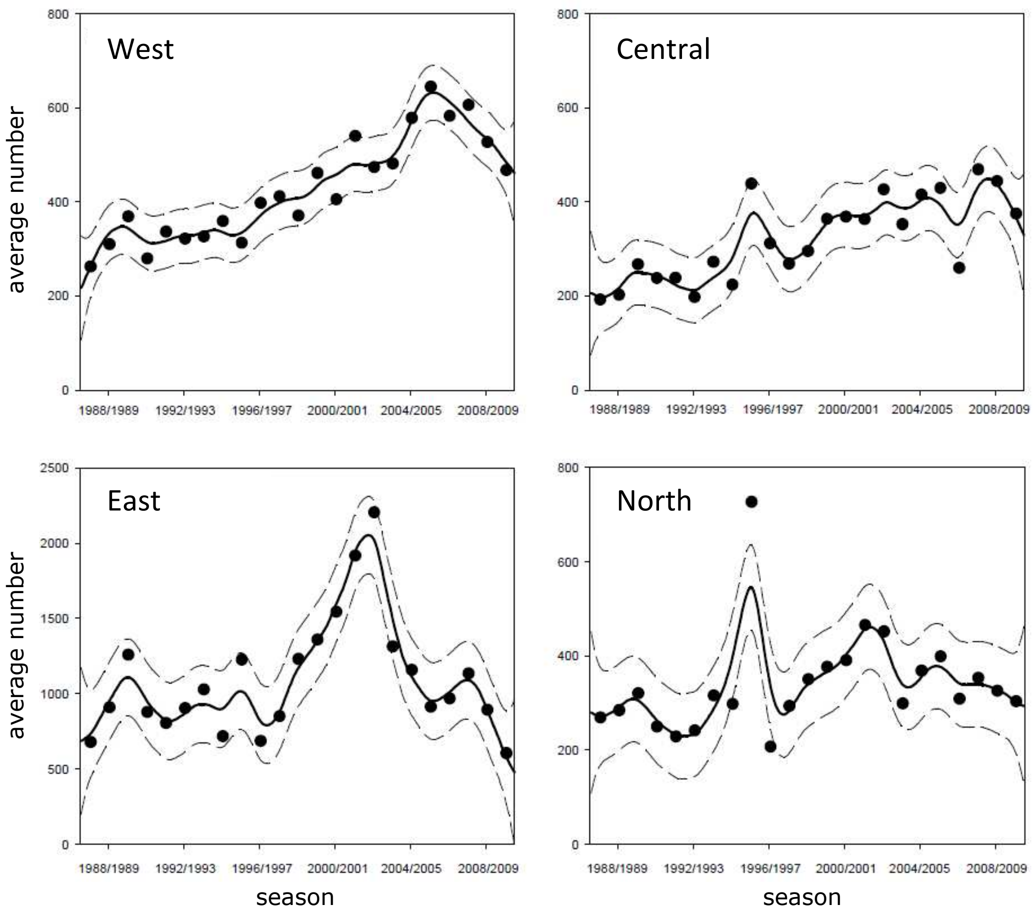

Figure 29. Trends in numbers of Shelduck in the four compartments of the Oosterschelde estuary (Trendspotter, with 95% confidence intervals).

Highest numbers in the Oosterschelde estuary are reached in winter, November – March. This seasonal pattern is observed for all compartments except for the Western compartment where numbers are relatively high in summer and no large differences in numbers exist between seasons. This is probably caused by relatively large numbers of breeding and over-summering Shelducks in the Western compartment, specifically in the "Prunje" area. This is a wetland that may also provide food for Shelducks. In comparison, in the Westerschelde estuary the highest numbers are reached in the summer months, June to August, when Shelducks are moulting (Strucker et al. 2007). The Westerschelde is a moulting area for a substantial number of Shelduck; no moulting Shelducks are found in the Oosterschelde.

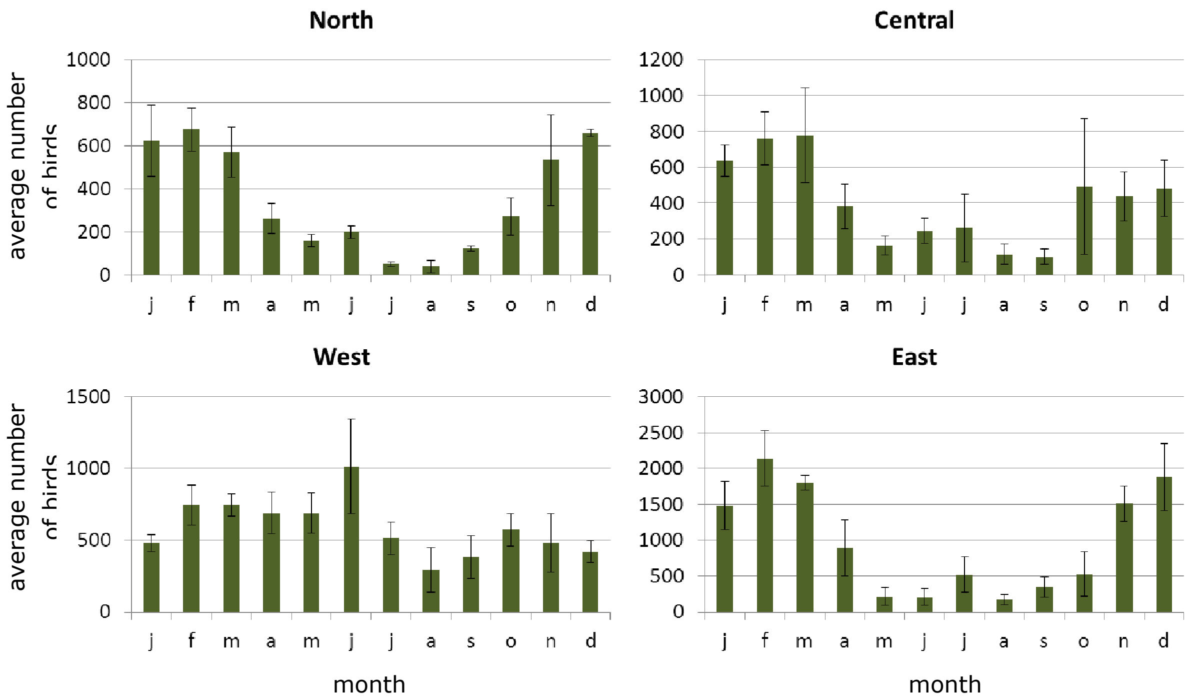

Figure 30. Seasonal occurrence of Shelduck in the Oosterschelde estuary. Per month the average number of the seasons 2005/2006 – 2008/2009 is given.

Numbers of Shelduck are the highest in the Eastern compartment, where they showed a distinct peak in numbers around 2002 (Figure 31). This peak coincided with a relatively high density of the mud snail (Figure 31). The relationship between mud snail density and Shelduck numbers was significant for the Eastern compartment (linear regression: $p < 0.05$, $F = 52.92$, $R^2 = 0.78$)(Figure 32), and also for the Western compartment ($p < 0.05$, $F = 9.69$, $R^2 = 0.39$) and the total Oosterschelde estuary ($p < 0.05$, $F = 38.14$, $R^2 = 0.72$). No relationship was found for the Northern compartment, and for the Central compartment no data on mud snails were available. In the analyses, the severe winters of 1995/1996 and 1996/1997 were excluded because of the strong effect of extremely cold winters on numbers of Shelduck. For example, the severe winter of 1995/1996 caused a strong influx, resulting in relatively high numbers (Meininger et al. 1997).

No relationships were found with density or biomass of potential other prey species (*Corophium arenarium*, oligochaetes and *Gammarus* sp.).

Regarding the dependence of Shelduck on mud snails in the Eastern compartment, the fact that mud snails mainly occur in the higher intertidal, and the relatively small area of higher intertidal in the Eastern compartment, a further decrease in area of higher intertidal flats may directly result in a further decrease of Shelduck numbers.

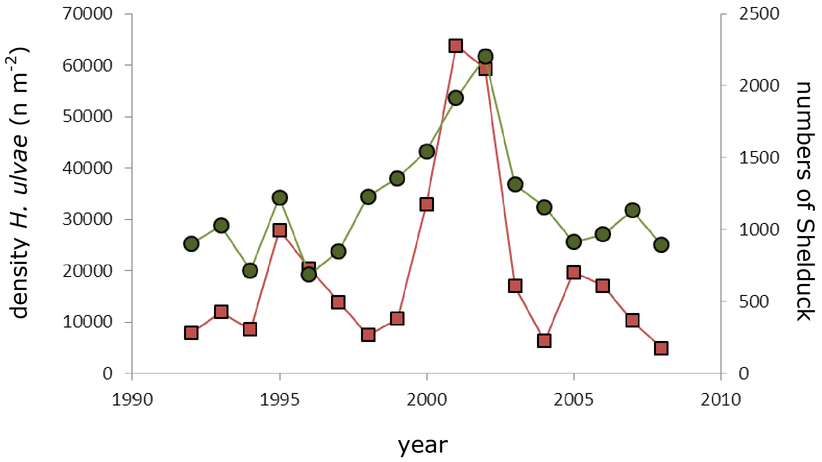

Figure 31. Development of numbers of Shelduck (green) and the density of the mud snail *H. ulvae* (red) in the Eastern compartment.

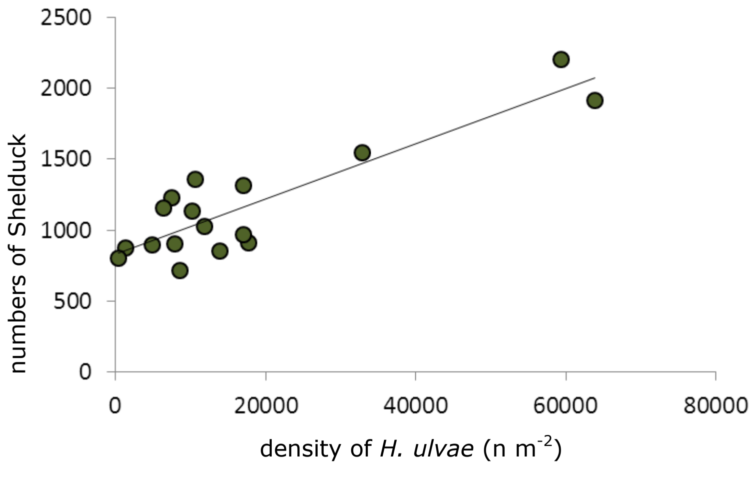

Figure 32. Relationship between the density of mud snails and numbers of Shelduck in the Eastern compartment (linear regression: $p < 0.05$, $F = 37.31$, $R^2 = 0.69$).

Oystercatcher

Most of the Oystercatchers that visit the Oosterschelde estuary in autumn and winter, leave for their breeding grounds in March – April. A smaller part of the birds stays over summer. These are mainly non-breeding birds and sub-adults. The seasonal pattern for the Oosterschelde estuary (Figure 33) is very similar for the different compartments (not shown), although numbers are lower in the Eastern compartment (around 5000 in winter) and Western compartment (around 8000 in winter) than in the other two compartments (around 12000 in winter). In addition, it should be noted that although numbers are comparable between the Northern and Central compartment the total number relative to the intertidal area is higher in the Northern compartment than in the Central compartment and the Western and Eastern compartments.

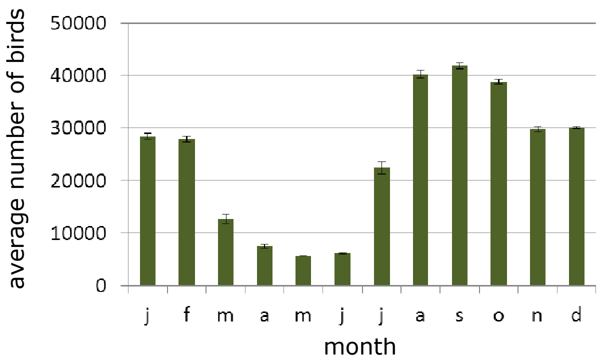

Figure 33. Seasonal occurrence of Oystercatchers in the Oosterschelde estuary. Per month the average number of the seasons 2005/2006 – 2008/2009 is given.

The Oystercatcher is one of the most abundant waders in Dutch estuaries, but numbers are declining, as is the general trend in North West Europe. There are, however, some differences between water bodies in the Netherlands and between compartments within the Oosterschelde estuary. The negative trend in the Oosterschelde estuary differs from the Westerschelde estuary where numbers are stable since 1999/2000. In the Wadden Sea, numbers are declining as well. Within the Oosterschelde estuary the decline was most pronounced in the Central and Eastern compartments while no trend was observed in the Northern compartment. In the Central and Eastern compartments there was a sudden shift to lower numbers around 1996 (Figure 34). The Oystercatcher is a specialist feeder on bivalve shellfish such as the mussel *Mytilus edulis* and the cockle *Cerastoderma edule* (references in Meire et al. 1994a; Leopold et al. 2004), but it has also been observed to feed on large numbers of lugworm, *Arenicola marina* (Zwarts 2009).

The decrease in the Eastern compartment coincided with a decrease in biomass of its main prey species: the cockle. When presented with a high abundance of prey species, migratory Oystercatchers are known to return to the same location in high numbers in the autumn and winter of the next year (Rappoldt et al. 2004). With low food abundance, fewer individuals will return the next year. Furthermore, the availability of cockles is expected to be more limiting in the winter months, when other food sources are lean, gone or difficultly available. We therefore related Oystercatcher numbers (monthly average November - February) to the abundance of cockles in the preceding spring (May) for the Eastern compartment. This yielded a significant relationship (

Figure 35; linear regression: $p < 0.05$, $R^2 = 0.73$, $F = 45.72$). For the entire Oosterschelde estuary we related Oystercatcher numbers to the estimated cockle biomass in autumn, at densities higher than 50 cockles m^{-2}. Each year an estimate of autumn biomass is made using Gompertz growth curves (Kesteloo et al. 2010). This is then diminished with actual fished cockle biomass, which is exclusively concentrated at densities higher than 50 m^{-2}.

The relationship between Oystercatcher numbers in winter and estimated cockle biomass at densities higher than 50 m^{-2} in the preceding autumn was significant (linear regression: $p < 0.05$, $F = 723.2$, $R^2 = 0.97$).

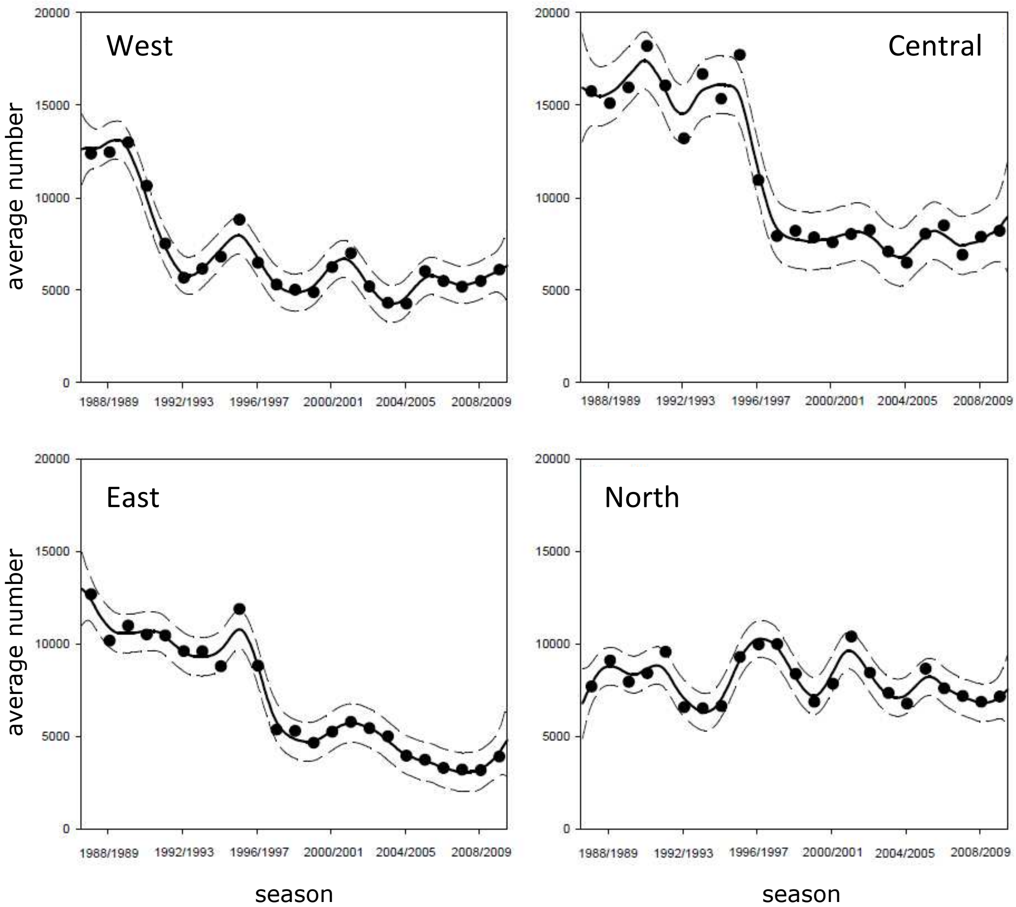

Figure 34. Trends in numbers of Oystercatcher in the four compartments of the Oosterschelde estuary (Trendspotter, with 95% confidence intervals).

In the Central compartment, where cockle biomass showed no apparent trend and intertidal mussels were the most abundant, winter numbers (Nov-Feb) of Oystercatcher significantly increased with an increasing intertidal mussel stock (Figure 37; linear regression: $p < 0.05$, $R^2 = 0.92$, $F = 151.78$) (after elimination of mussel biomass estimates from the INTERECOS campaign and cockle survey). The relationship between mussel biomass and winter numbers of Oystercatchers was also significant, but gave a worse fit (linear regression: $p < 0.05$, $R^2 = 0.87$, $F = 80.90$). Caution should be taken in interpreting the relationship, however, since the relationship was largely determined by the seasons 1994/1995 and 1995/1996. Numbers of Oystercatchers were exceptionally high in the season 1995/1996 because of influx in the severe winter. After removal of this season, the relationship was still significant ($p < 0.07$, $R^2 = 0.50$, $F = 11.03$).

Because numbers of Oystercatcher showed a sudden decrease in numbers in the Central and Eastern compartments, we did not expect this drop to be related to the steady changes in the morphology of the intertidal foraging grounds. In the Western compartment, the decrease in Oystercatcher numbers was more gradual. This coincided with a decrease in relative area of tidal flats with exposure times higher than 40%. A causal relationship is impossible to conclude, nor does it seem likely.

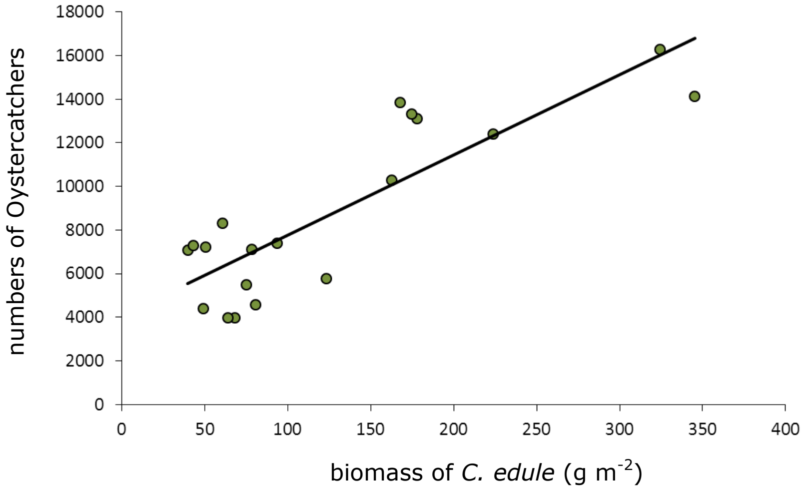

Figure 35. The number of Oystercatchers (average of November – February) related to the biomass of cockles in the preceding spring (all age classes; biomass in grams total wet weight per m^2) for the Eastern compartment (linear regression: $p < 0.05$, $R^2 = 0.73$).

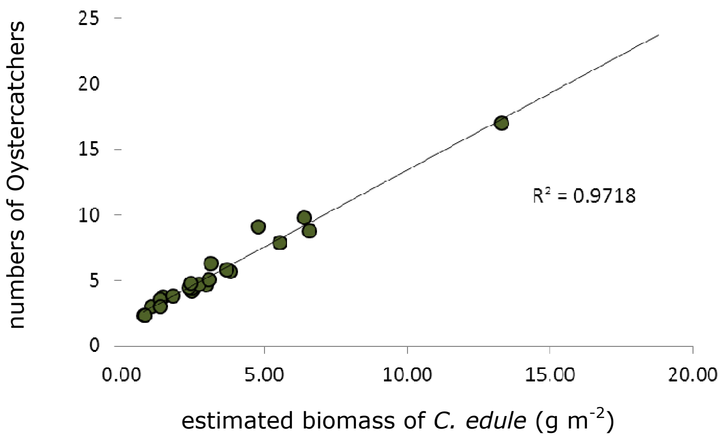

Figure 36. The number of Oystercatchers (average of November – February) related to the estimated biomass of cockles at densities higher than 50 m^{-2} in the preceding autumn (all age classes; biomass in grams total wet weight per m^2) for the Oosterschelde estuary (linear regression: $p < 0.05$, $F = 723.2$, $R^2 = 0.97$).

No relationships were found with other benthic species, such as *Arenicola marina* that was found to be preyed upon by Oystercatchers in the Oosterschelde during late summer (Zwarts 2009).

The strong decline in the Eastern and Central compartments coincides with the severe winter of 1996/1997. During the first severe winter, of 1995/1996, numbers of Oystercatchers were relatively high in all compartments. This is likely due to influx from birds which normally winter in wintering areas further north. Furthermore, the cockle stock did not yet show a decrease over this winter. By spring 1997 however, cockle stocks had decreased significantly. This may have been a combination of direct winter mortality in the winter of 1996/1997 and mortality during the summer of 1996 as a consequence of frost damage during the previous severe winter (Strasser et al. 2001). The significantly lower Oystercatcher numbers in the season 1996/1997 in the Central compartment is likely due to a combination of cold temperatures and low food availability, urging the birds to migrate further south and causing mortality among birds in times of ice cover. A part of the Oystercatchers may have switched to the Northern compartment where numbers were relatively high during the period 1995/1996 –

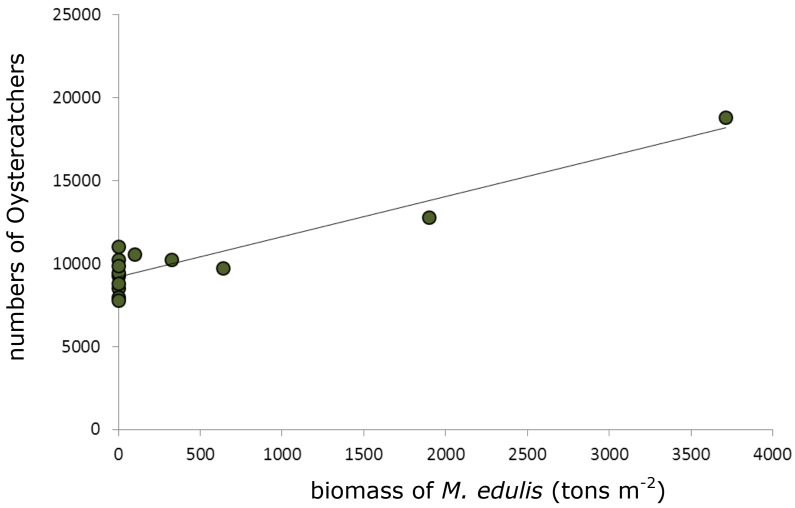

Figure 37. Relationship between mussel biomass (in tons fresh weight) in the intertidal (autumn), and numbers of Oystercatchers in the following winter (November – February; monthly average) in the Central compartment. The relationship is significant (linear regression: $p < 0.05$, $R^2 = 0.92$, $F = 151.78$). Data from the INTERECOS campaign and estimates from the cockle survey were not included.

1997/1998. The Northern compartment, together with the Western compartment, harbours the highest densities of cockles. In spring 1997, cockle densities in the Northern compartment were higher than in the other compartments, which may explain why Oystercatcher numbers did not decline here. After the severe winters of the mid-90s the cockle stock has not recovered in the Eastern compartment. This is likely due to a decreased carrying capacity for bivalve filter-feeders (Geurts van Kessel et al. 2003), but may also be related to the erosion of tidal flats. Simultaneously, 1995 was the last year in which substantial amounts of mussels were still present on intertidal culture plots. After 1995 practically all culture mussels are located on subtidal plots where they are unavailable for waders. Especially in the Central compartment, which harboured the most intertidal mussels, this resulted in a sudden decrease in the availability of mussels to waders.

In conclusion, the severe winters of the mid-90s seem responsible for the sharp decline in Oystercatcher numbers in the Central and Eastern compartments, but due the persisting absence of mussels in the Central compartment and cockles in the Eastern compartment numbers of Oystercatchers have not recovered since.

Numbers of Oystercatchers are expected to decline further in the near future. Due to the combined effects of erosion of tidal flats and sea level rise, cockles and other food sources will become less available. Simulations with the WEBTICS model demonstrated that cockle beds located at exposure times of at least 60% are of particular importance to Oystercatchers. At shorter exposure times, the birds simply have too little time to forage (Rappoldt et al. 2006).

Ringed Plover

In Europe there are three subspecies of Ringed Plover: the West European *Charadrius hiaticula hiaticula* breeds in the Netherlands, Germany, France and England, Scandinavia and the Baltic countries, and winters mainly along the shores of England, France and Northern Spain. *C. h. tundrae* breeds on the Arctic tundra's of Northern Europe and Russia and winters in tropical Africa. *C. h. psammodroma* breeds in Canada, Greenland and Iceland, and winters in Western and Southern Africa (Wetlands International 2002). Within the Oosterschelde estuary the Ringed Plover is observed year round (Figure 38). Maximum numbers are reached in the period August – October. In spring, migrants of the subspecies *C. h. hiaticula* pass in March and some remain in the area to breed. These are followed in May – June by migrants of *C. h. tundrae* and possibly also *C. h. psammodroma* (Meininger & Van Swelm 1989). A part of the population that breeds in the Oosterschelde estuary (70 pairs in 2009) also stays during winter (Strucker et al. 2010).

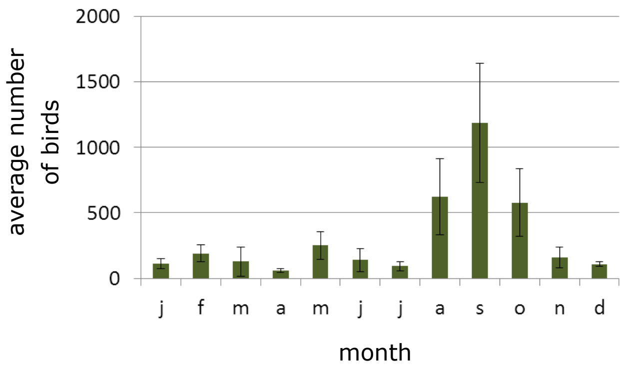

Figure 38. Seasonal occurrence of Ringed Plovers in the Oosterschelde estuary. Per month the average number of the seasons 2005/2006 – 2008/2009 is given.

The Ringed Plover showed no significant trend in the Oosterschelde estuary and the four compartments, which differs from the positive trend in the Wadden Sea and negative trend in the Westerschelde estuary (www.sovon.nl). Within the Oosterschelde estuary, numbers show large fluctuations from year to year without a significant trend in all four compartments (Appendix A). The Ringed Plover has been described to mainly feed on *Nereis* sp., crabs, insects, small worms such as *Scoloplos armiger* and *Heteromastus filiformis*, and mud snails (Leopold et al. 2004).

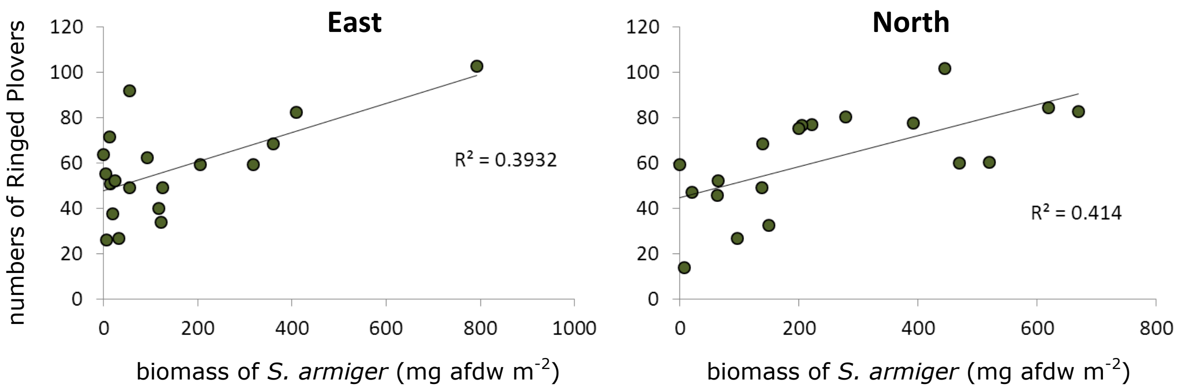

Figure 39. Relationship between biomass of Scoloplos armiger in the intertidal (MWTL, autumn), and seasonal average numbers of Ringed Plovers for the Eastern and Northern compartments. The relationships are significant (linear regression: East $p < 0.05$, $R2 = 0.39$, $F = 11.01$; North $p < 0.05$, $R2 = 0.41$, $F = 12.01$).

Within the Oosterschelde estuary we found a significant relationship with biomass (or density) of *Scoloplos armiger* in the Eastern compartment (linear regression: $p < 0.05$, $R^2 = 0.39$, $F = 11.01$) and Northern compartment (linear regression: $p < 0.05$, $R^2 = 0.41$, $F = 12.01$)(Figure 39). In the Northern compartment we furthermore found a significant relationship with the total density of all common polychaete species (*Aphelochaeta marioni*, *Arenicola marina*, *Capitella capitata*, *Heteromastus filiformis*, *Lanice conchilega*, *Nephtys* sp., *Nereis* sp., *Pygospio elegans*, *Scoloplos armiger*, *Spiophanes bombyx*, and *Urothoe poseidonis*) (Figure 40; linear regression: $p < 0.05$, $R^2 = 0.30$, $F = 7.10$). In the Western compartment we found a significant relationship with density (or biomass) of *Aphelochaeta marioni* (Figure 41; linear regression: $p < 0.05$, $R^2 = 0.24$, $F = 5.38$).

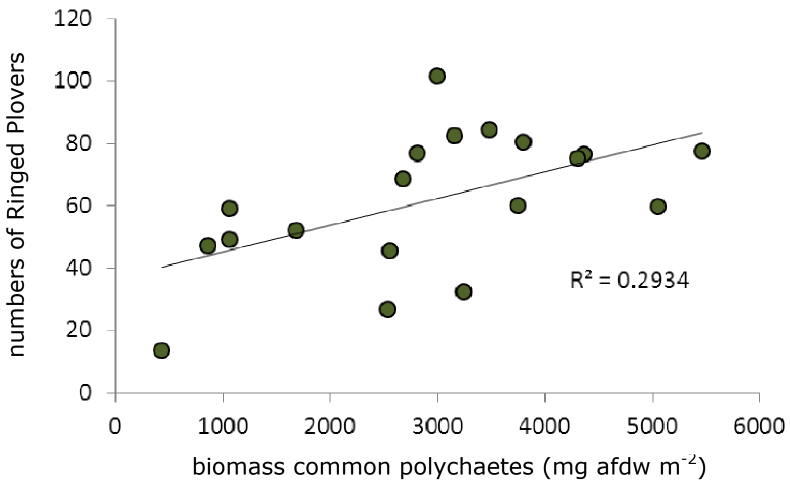

Figure 40. Relationship between the total biomass of common polychaetes in the intertidal (MWTL, autumn), and seasonal average numbers of Ringed Plovers for the Northern compartment. The relationship is significant (linear regression: $p < 0.05$, $R^2 = 0.30$, $F = 7.10$).

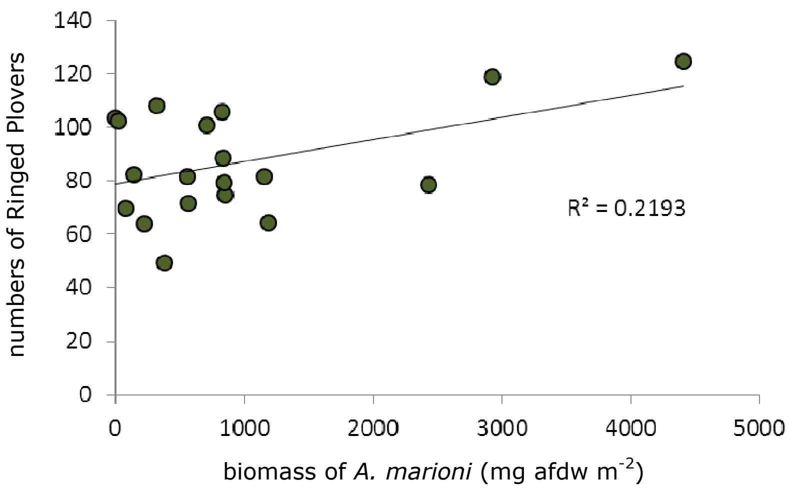

Figure 41. Relationship between the biomass of *Aphelochaeta marioni* in the intertidal (MWTL, autumn), and seasonal average numbers of Ringed Plovers for the Western compartment. The relationship is significant (linear regression: $p < 0.05$, $R^2 = 0.24$, $F = 5.38$).

Grey Plover

After the breeding season, Grey Plovers that breed in the Siberian arctic tundra's migrate to wintering areas in Northwest Europe and West Africa. The Wadden Sea and British estuaries are the most northerly wintering areas on the East-Atlantic flyway (Van Roomen et al. 2007). In the Oosterschelde estuary, the seasonal pattern does not differ between the different compartments and has been stable since 1987/1988 (Strucker et al. 2009).

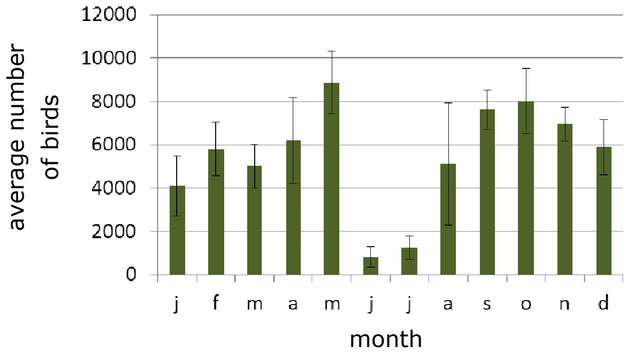

Figure 42. Seasonal occurrence of Grey Plovers in the Oosterschelde estuary. Per month the average number of the seasons 2005/2006 – 2008/2009 is given.

Two peaks in numbers can be discerned: one in spring and another in autumn (Figure 42). In June and July numbers are the lowest. Only birds remain that do not migrate to the arctic breeding grounds. In August the adult birds arrive from the breeding grounds and numbers increase. In September and October, when the juveniles also arrive, maximum numbers are reached. Most birds stay until November to complete their moult. After moulting about one third of the birds migrates further south, resulting in decreasing numbers. These birds, wintering in West Africa, return in May, again resulting in an increase in numbers in the Oosterschelde estuary. May is also the period in which almost all Grey Plovers leave the estuary for their breeding grounds up north. Within the Dutch south-western Delta area, the Oosterschelde estuary is the most important area for Grey Plovers. The Grey Plover showed large fluctuations in numbers in the Westerschelde estuary, and an increase in the Dutch Wadden Sea.

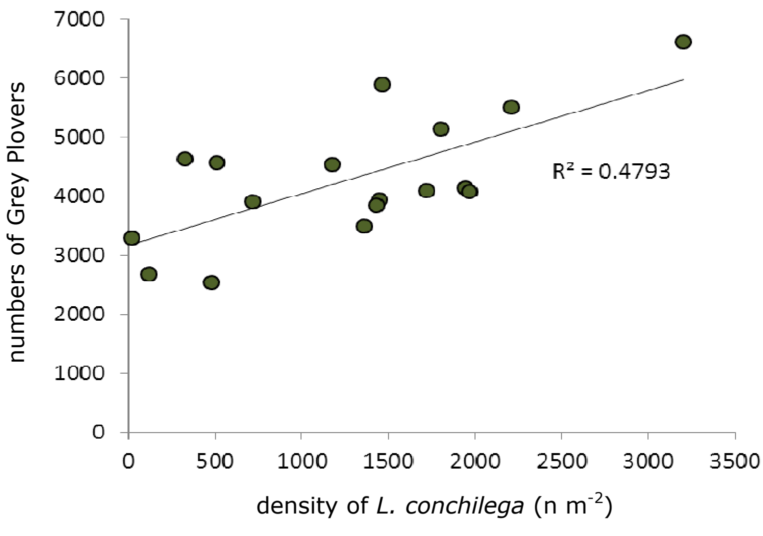

Figure 43. Relationship between the density of the Sand Mason *Lanice conchilega* and average numbers of Grey Plover in the winter months (January – February) in the Oosterschelde estuary as a whole. The relationship is significant (linear regression: $p < 0.05$, $R^2 = 0.48$, $F = 13.89$).

Within the Oosterschelde estuary, numbers have been increasing slightly in the last couple of years, following a decline during the severe winters of the mid-1990s. No clear differences between the compartments were observed (Appendix A). Highest numbers occurred in the Central and Western compartments.

Grey Plovers are very sensitive to cold winter temperatures that usually result in decreasing numbers. This resulted in a similarity with the trends observed for the Dunlin: in the season 1995/1996 of which the winter was severely cold, average numbers of Grey Plover were still relatively high. In the following year, during which the winter again was severely cold, numbers had dropped in all compartments, followed by a slow recovery in the following years. The winter effect was the strongest in the Central compartment and hardly detectable in the Northern compartment.

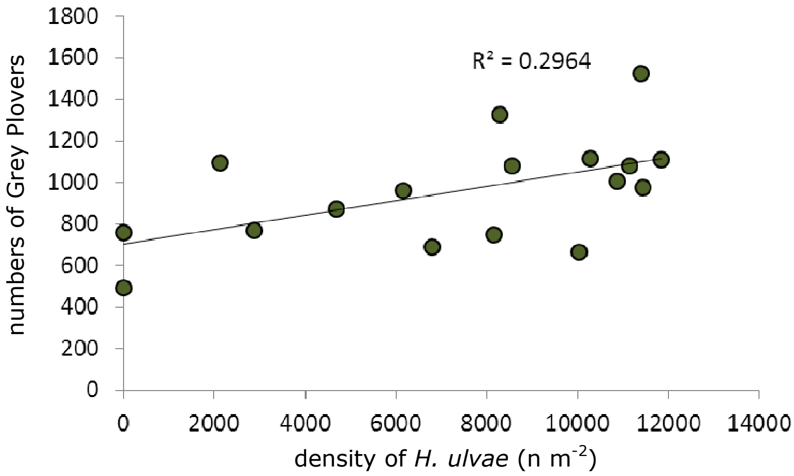

Figure 44. Relationship between the density of mud snails and seasonal average numbers of Grey Plover in the Northern compartment of the Oosterschelde estuary. The relationship is significant (linear regression: $p < 0.05$, $R^2 = 0.30$, $F = 6.31$).

For the Oosterschelde estuary as a whole, we found a significant relationship between the density (or biomass) of *Lanice conchilega* in autumn and numbers of Grey Plover (seasonal average,July-June) (linear regression: $p < 0.05$, $R^2 = 0.27$, $F = 5.47$). The severe winters of 1995/1996 and 1996/1997 were removed from the dataset. The relationship was stronger when only plovers that remained in the estuary during the winter months (January – February) were included (Figure 43; linear regression: $p < 0.05$, $R^2 = 0.48$, $F = 13.89$). The relationship with *L. conchilega* was only significant on the scale of the entire estuary but not for the separate compartments (North, West and East).

For the separate compartments (excluding the Central compartment due to a lack of data) we found a significant relationship between the density of the ragworm *Nereis diversicolor* and average numbers of Grey Plover during winter (January-February) in the Eastern compartment (linear regression: $p < 0.05$, $R^2 = 0.42$, $F = 10.69$), and a significant relationship between the density of the mud snail and seasonal average numbers of Grey Plover in the Northern compartment (Figure 44; linear regression: $p < 0.05$, $R^2 = 0.30$, $F = 6.31$). Again, the seasons with severe winters (1995/1996 and 1996/1997) were removed from the analysis. Both *Nereis diversicolor* and the mud snail are known prey species of the Grey Plover (Leopold et al. 2004). The significant relationship with *N. diversicolor* was, however, entirely determined by only one year with a relatively high abundance of ragworms: 1992. For the Western compartment, where *N. diversicolor* is more abundant, we found no relationships between ragworms and Grey Plovers at all.

Knot

Two subspecies of Knot visit the Oosterschelde estuary. These are *Calidris canutus canutus* and *Calidris canutus islandica*. *C. c. canutus* breeds on the tundra's of Siberia and winters mainly along the coasts of western Africa. It visits some Western European estuaries for resting and feeding during its southward migration. They also pass the Netherlands in spring when they migrate back north, but then they stay shorter and in lower numbers. *C. c. islandica* breeds on the tundra's of Greenland and Canada. Its main wintering areas are located along the coasts of North-western Europe (Germany to NW France and the UK) including the Oosterschelde estuary (Strucker et al. 2009). The largest numbers of Knot in the Oosterschelde estuary are found in November – February (Figure 45). There are some conspicuous differences between the four compartments. In the Western compartment the highest numbers are found in late summer and autumn. The numbers present in this area consist of Knot migrating further south, as well as moulting adults (pers. comm. P.L. Meininger). Compared to the other compartments, the Western compartment is not important for wintering Knot. Most Knots foraging in the Northern compartment spend the high tide period on roosts in Lake Grevelingen (at Slikken van Flakkee near Herkingen) and also on the flats of Dwars in de Weg in the Krabbenkreek area in the Northern compartment if the tides are not too high (pers. comm. R. Strucker).

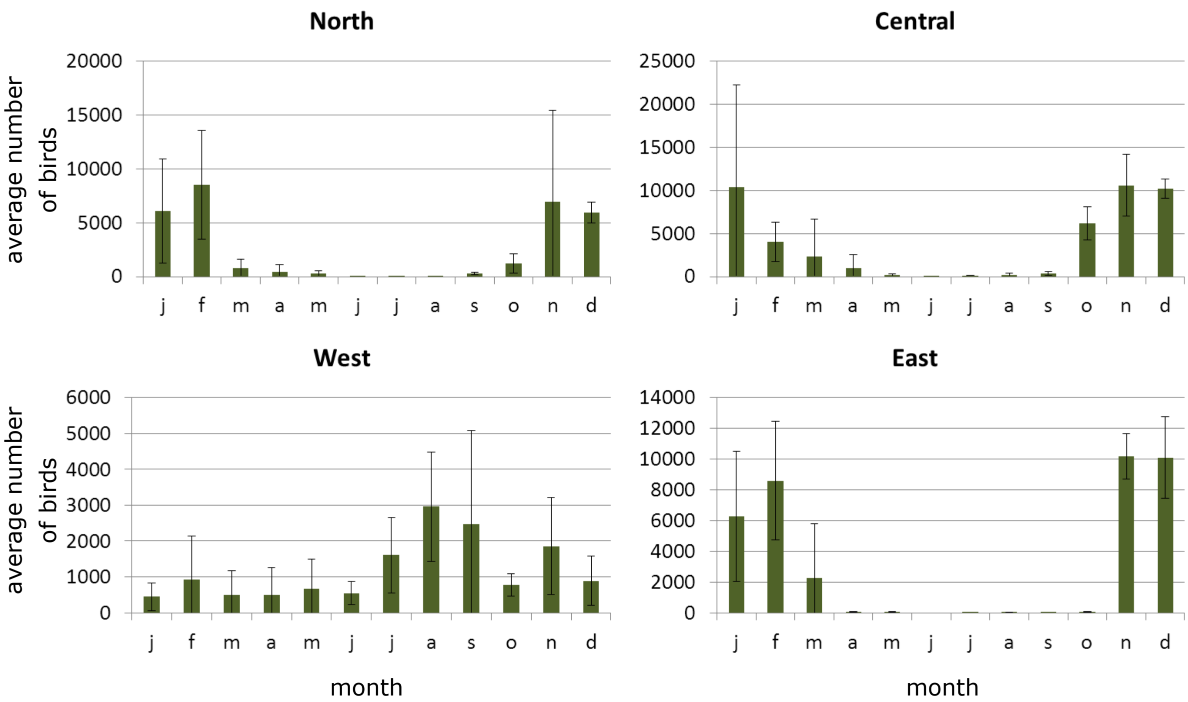

Figure 45. Seasonal occurrence of Knots in the different compartments of the Oosterschelde estuary. Per month the average number of the seasons 2005/2006 – 2008/2009 is given.

Trends in numbers of Knot showed large differences between the different water bodies and between the different compartments. Numbers increased in the Oosterschelde estuary and in the Eastern part of the Dutch Wadden Sea, but remained stable in the Western Dutch Wadden Sea and Westerschelde estuary. Within the Oosterschelde estuary numbers appear to decline again after 2006, the most pronounced in the Western and Central compartments (Figure 46). In the Westerschelde estuary, numbers show an increase over the past six years (www.sovon.nl).

Although Knots are known to be highly dependent on the availability of Baltic tellins and cockles in the Dutch Wadden Sea (Zwarts and Wanink 1993; Seys et al. 1994), we found almost no relationships between biomass and abundance of Baltic tellins and numbers of Knots in the Oosterschelde estuary. Only in the Eastern compartment, numbers of Knots increased significantly with the density of Baltic tellins, but this relationship was weak (linear regression: $p = 0.049$, $R^2 = 0.24$, $F = 4.60$). The years with severely cold winters (1995/1996 and 1996/1997) were removed from the analysis since severe winters are known to affect numbers of Knots (Strucker et al. 2009).

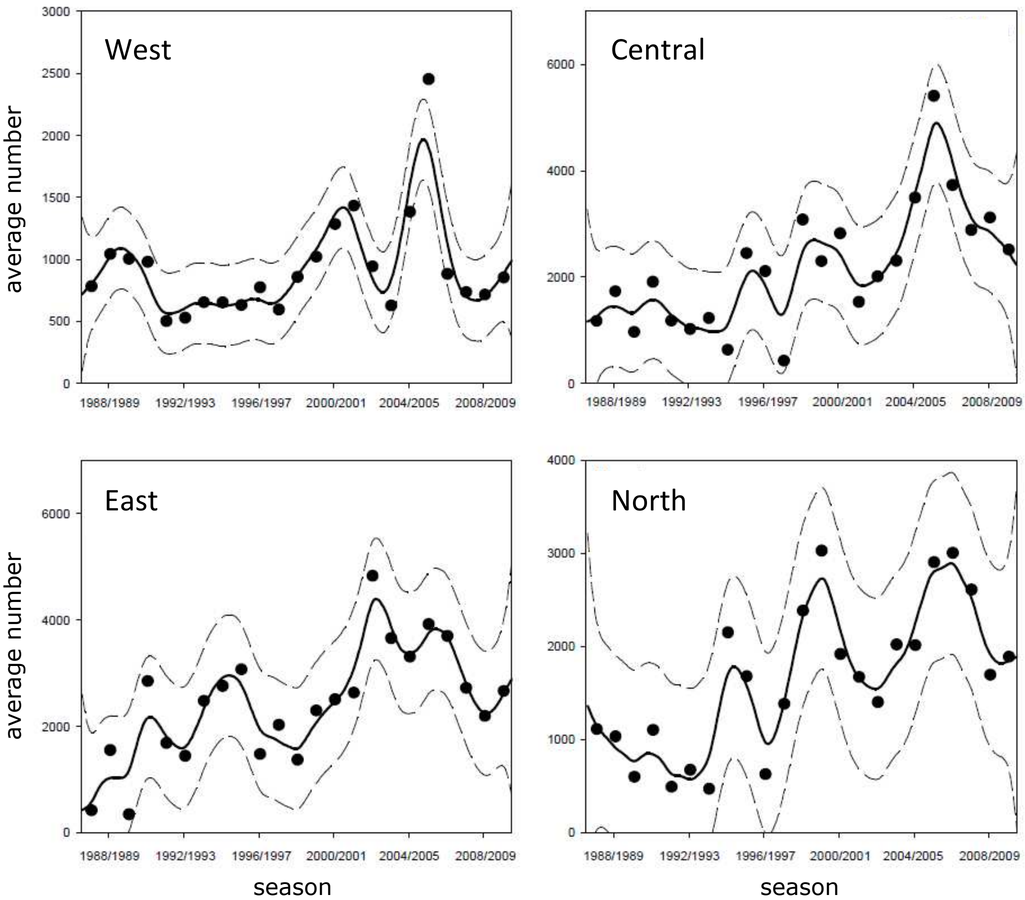

Figure 46. Trends in numbers of Knot in the four compartments of the Oosterschelde estuary (Trendspotter, with 95% confidence intervals).

On the other hand we did find a relationship between the density of mud snails in autumn and average numbers of Knot per counting season (linear regression: $p < 0.05$, $R^2=0.57$, $F=19.94$), but only for the Northern compartment (Figure 47). Densities of mud snails follow largely the same pattern in the Eastern compartment as in the Northern compartment, with the distinction that densities were much higher in the period 2000 – 2003 (Figure 18). This peak in density is not reflected in numbers of Knot and no relationship between the two was found for the Eastern compartment. In the Eastern compartment, numbers of Knot are expected to be determined by the availability of Baltic tellins, even though the relationship was weak, rather than by mud snails. It is not clear why Knot numbers appear to be determined by mud snail densities in the Northern compartment, but not in the Eastern compartment. Densities of both mud snail and the Baltic tellin are comparable between the two compartments. The Eastern compartment differs in the peak in mud snail densities in 2000 – 2003, and in harbouring higher densities of juvenile Baltic tellins (animals with a shell length < 5 mm) (Figure 16).

In the Western compartment, where only very low numbers of Knot winter, no relationships with benthic prey species were found. In the Central compartment, where only dominant bivalves are monitored, we also found no relationships.

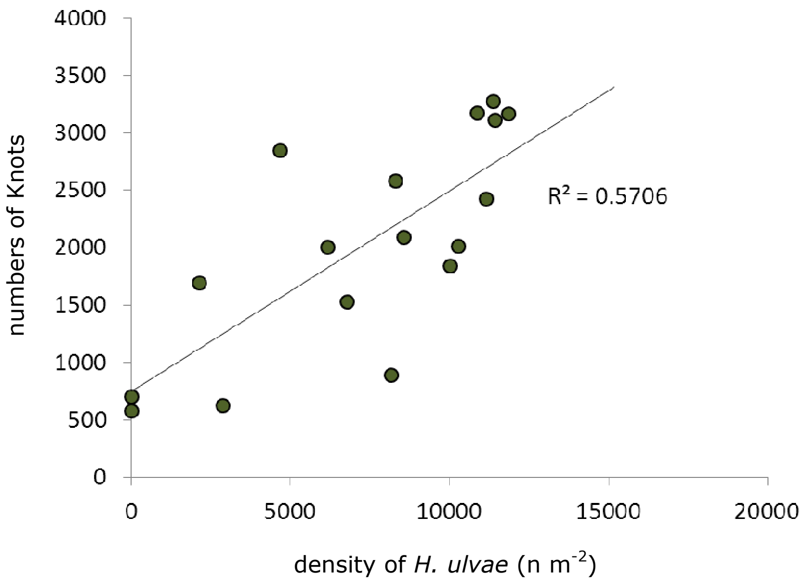

Figure 47. Relationship between density of mud snails (*Hydrobia ulvae*) in autumn in the Northern compartment (n m^{-1}) and season average numbers of Knot (n). The relationship is significant (linear regression: $p < 0.05$, R^2=0.57, F=19.94).

The fact that no relationships were found between Knot numbers and Baltic tellins and cockles may be due to a large variation in determining parameters from year to year. For instance, in the winters of 1995 and 1996, numbers of Knot were exceptionally low in the Oosterschelde estuary because the animals migrated further south. These two winters were therefore excluded from the analysis. In the remaining years, however, apart from the availability of mollusc prey other parameters may be determining in different years. Parameters inside the estuary, but also parameters that influence the population size on a larger scale. For example, in the 2005/2006 season exceptionally high numbers of Knot were counted in the Oosterschelde estuary. During that season, all months showed an increase, and all compartments except for the Eastern compartment. This peak was also observed in the Westerschelde estuary and Western Wadden Sea, which renders a relationship with food availability in the Oosterschelde estuary unlikely. Furthermore, Knots are very mobile. Within the same winter season they may change their preferred high tide roost location frequently (pers. comm. R. Strucker). Shifts between compartments will therefore also occur frequently, which makes it difficult to detect relationships with food availability within compartments. This is in accordance with observations from the Wadden Sea (Piersma et al. 1993).

Dunlin

For Dunlin, the most important wintering areas are the estuaries of the UK, the French Atlantic coast, the Wadden Sea area, the coasts of Ireland and Portugal, and the Dutch “Delta” area, among which the Oosterschelde estuary (Meire et al. 1994b). In the Oosterschelde estuary, Dunlins start to arrive in significant numbers in October, and maximum numbers are reached in November – January (Meire et al. 1994b)(Figure 48). During severe winters and following years, winter numbers are significantly lower because high numbers of Dunlin leave the Oosterschelde estuary in November to migrate further south, possibly due to food shortage (Meire et al. 1994b).

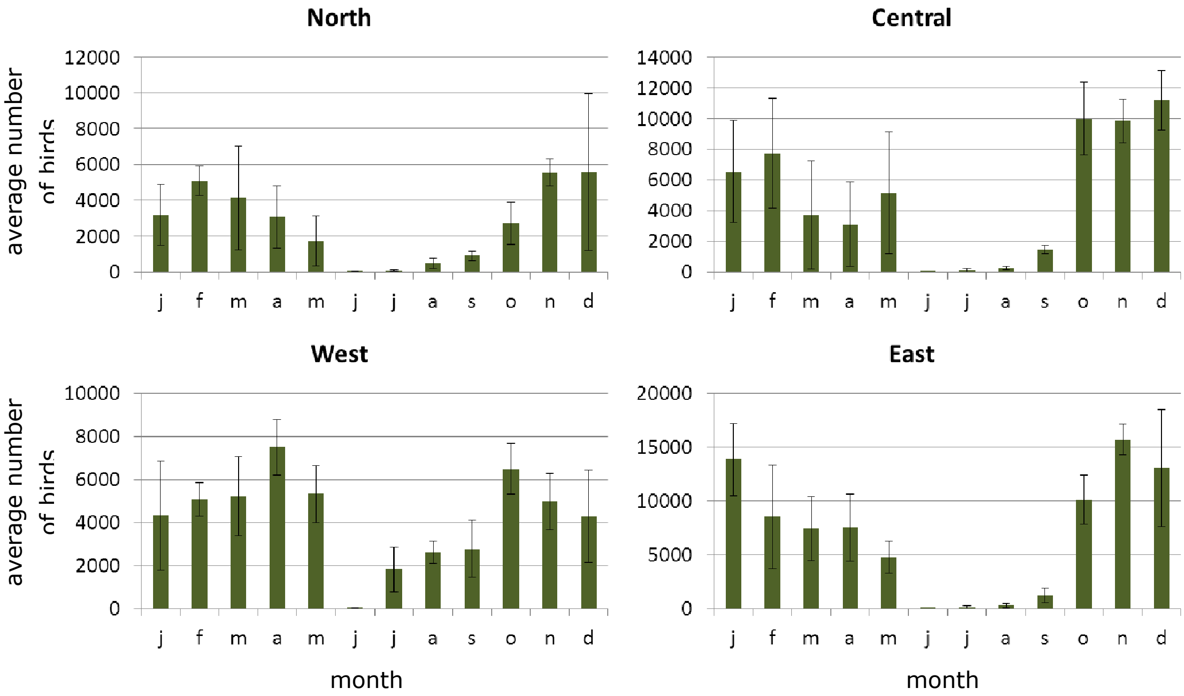

Figure 48. Seasonal occurrence of Dunlins in the Oosterschelde estuary. Per month the average number of the seasons 2005/2006 – 2008/2009 is given.

Three subspecies of Dunlin visit Dutch coastal waters: *Calidris alpina alpina*, *C. a. schinzii* and *C. a. arctica*. Of these, *C. a. alpina* is the most frequently encountered migrant, and the only subspecies that winters along Dutch waters (Meire et al. 1994b). In the Dutch Delta area, numbers increase in October and maximum numbers are reached in November – January. In the Western compartment, numbers are relatively high in late summer (July – September). This is due to the passage of migrating birds that do not stay during winter.

The Dunlin shows a significant increase in numbers in all marine water bodies within the Netherlands (Western Wadden Sea, Westerschelde and Oosterschelde estuaries). Trends in the Oosterschelde and Westerschelde estuaries are comparable, but these differ from the Western Wadden Sea. Between the different compartments of the Oosterschelde estuary no clear differences were found, except for a conspicuous sudden increase in the Eastern compartment starting in 1999/2000 (Figure 49). This raises the question what changed in the Eastern compartment to make it more interesting for Dunlins? The sudden increase follows a few years after the severe winters of 1995/1996 and 1996/1997. For the Dunlin the phenomenon is described that numbers drop in the years after severe winters, and take a few years to recover (Meire et al. 1994b). Indeed, while numbers in all compartments were still relatively high in the season 1995/1996, numbers dropped in the following years. This was less pronounced in the Eastern compartment. The most conspicuous difference with the Northern and Western compartment in terms of densities of benthic prey species seems to be the high numbers of the mud snail in 2000 – 2003. A significant although weak relationship was found between density or biomass of mud snails and numbers of Dunlin in the Eastern compartment (Figure 50) linear regression: $p < 0.05$, $R^2 = 0.26 / 0.25$, $F = 5.96 / 5.65$). The high numbers of mud snails may explain why recovery after the severe winters of the mid-1990s appears to have been more successful in the Eastern compartment than in the other compartments.

Mud snails were described by Goss-Custard et al. (1977) and later by Santos et al. (2010) to be an important prey species of the Dunlin. Santos et al. (2010) observed that Dunlin in the Tagus estuary, Portugal, mainly fed on mud snails in dry patches and that they mainly cropped siphons of *Scrobicularia plana* in wet patches. Animals that were not skilled enough in siphon cropping resorted to mainly feeding on mud snails.

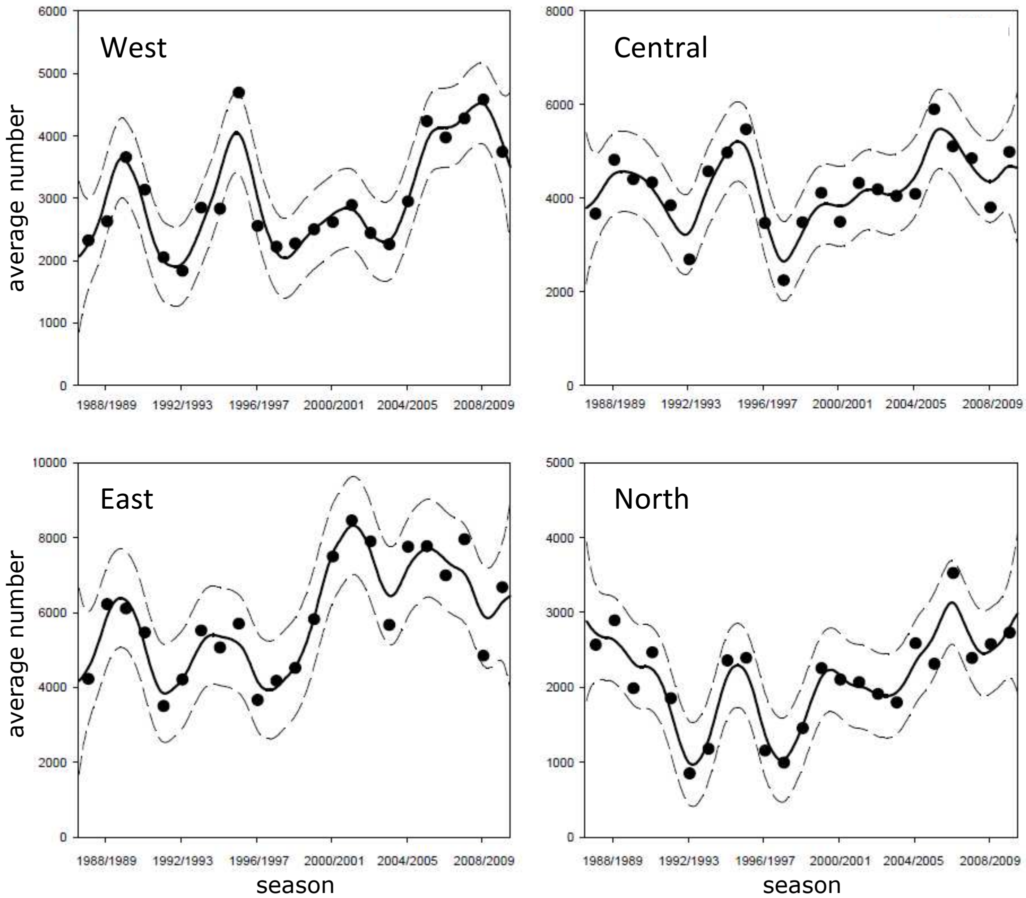

Figure 49. Trends in numbers of Dunlin in the four compartments of the Oosterschelde estuary (Trendspotter, with 95% confidence intervals).

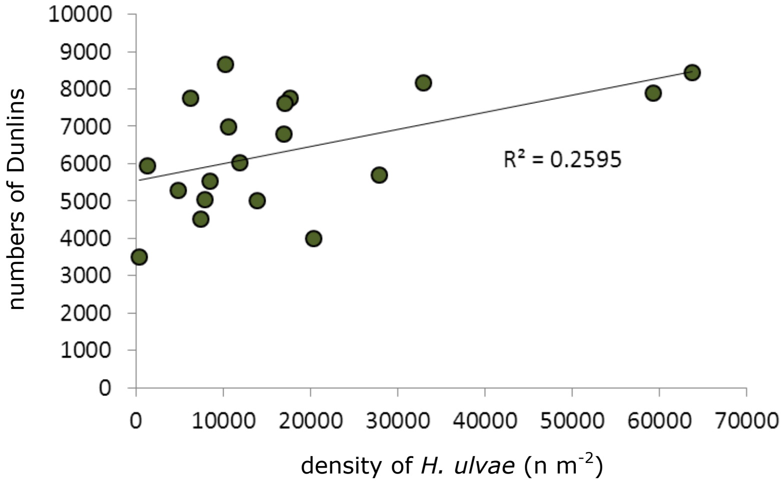

Figure 50. Relationship between density of mud snails (*Hydrobia ulvae*) in autumn in the Eastern compartment (n m^{-1}) and season average numbers of Dunlin (n). The relationship is significant (linear regression: $p < 0.05$, $R^2 = 0.26$, $F = 5.96$).

In the Northern compartment, recovery after the severe winters of the mid-1990s was quick. Here, we found a significant relationship between numbers of Dunlin and density or biomass of the polychaete *Lanice conchilega* (Figure 51; linear regression: $p < 0.05$, $R^2 = 0.44 / 0.40$, $F = 13.53 / 11.24$). However, this relationship more likely represents a relationship with *Lanice* beds and their accompanying fauna, than a direct predator-prey relationship (Goss-Custard et al. 1977; Petersen and Exo 1999). Zwarts (2009) also found that *L. conchilega* itself was hardly eaten by waders. *Lanice* beds may also be preferred as foraging grounds because *L. conchilega* is an ecosystem engineer that creates spatially heterogeneous soft-bottom areas that are easier to probe in search of prey species preferred by Dunlin. A similar effect may be expected for other ecosystem engineers such as the mussel *Mytilus edulis* and the Pacific oyster *Crassostrea gigas.*

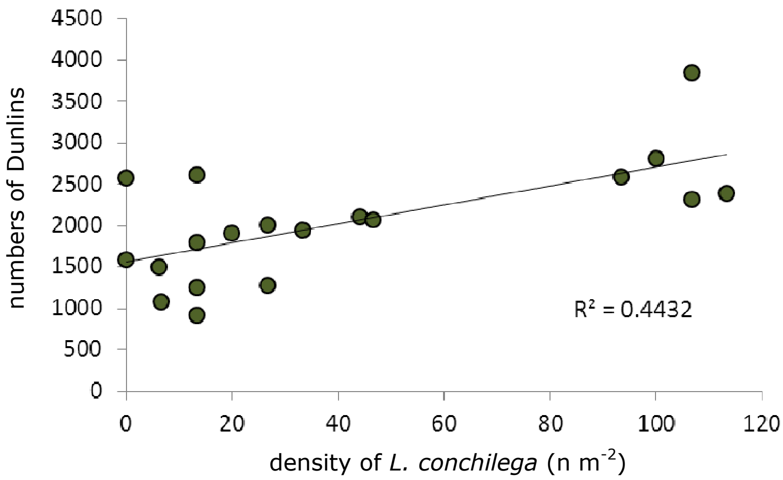

Figure 51. Relationship between density of the polychaete tube worm *Lanice conchilega* (Sand Mason) in autumn in the Northern compartment (n m^{-1}) and season average numbers of Dunlin (n). The relationship is significant (linear regression: $p < 0.05$, $R^2 = 0.44$, $F = 13.53$).

No relationship with benthic prey species was found in the Western compartment. Here, polychaete worms occur in higher densities and biomass than in the Northern and Eastern compartments. The Dunlin is known to feed on polychaetes such as *Nereis diversicolor* and *Nephtys* sp.. However, no relationships with these species, nor with *L. conchilega* or with the total of all common polychaetes were found. For the Central compartment, data on benthic prey species other than the common bivalves (IMARES survey) were not available.

Bar-tailed Godwit

Two subspecies of the Bar-tailed Godwit, visit Dutch estuaries: *Limosa lapponica lapponica* breeds in Northern Fennoscandinavia, the Northern part of the White Sea and the Kanin peninsula, and winters in the Wadden Sea and Delta area; *L. l. taymyrensis* breeds more easterly from the Yamal peninsula to the delta of the Anaber river, and only passes through the Netherlands on its way to wintering areas in Western Africa and on its way back to the breeding quarters (Rappoldt et al. 2004). Within the Oosterschelde estuary, two peaks in numbers are discerned: in spring and autumn (Figure 52). In June, numbers are lowest. Rather few birds remain in the Delta wintering area. In July, the first birds arrive from the breeding grounds in the North. In August, migrating birds cause an increase in numbers. In September, numbers have decreased again since most of the migrants from the *taymyrensis* subspecies have passed to Western Africa. In the months following , numbers gradually decrease. From the end of April onwards numbers suddenly increase again due to birds passing from their wintering areas in Africa to their breeding grounds up North.

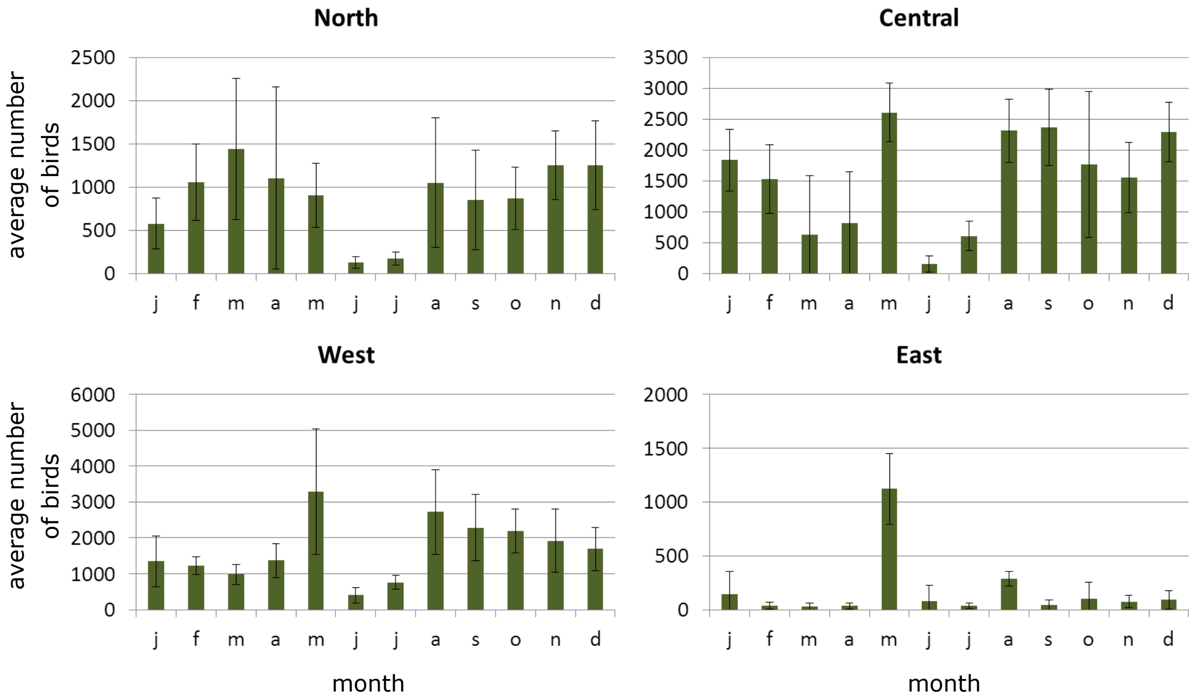

Figure 52. Seasonal occurrence of Bar-tailed Godwits in the Oosterschelde estuary. Per month the average number of the seasons 2005/2006 – 2008/2009 is given.

Between the different compartments of the Oosterschelde estuary some differences can be observed. The Eastern compartment is not of high importance to Bar-tailed Godwits, especially *L. l. lapponica*. The whole year through numbers are very low. Only in May, when the maximum is reached due to large numbers of migrating birds, numbers are comparable with the Northern compartment. In the Western and Central compartments the maximum number is reached in May as well, but in the Northern compartment where lower numbers of Bar-tailed Godwits are present the maximum number is reached in March. From January until March numbers increase in this compartment whereas they decrease in the other compartments during this period.

Over the period 1990/1991 – 2009/2010, numbers of Bar-tailed Godwits remained stable in the Oosterschelde estuary and its Northern, Western and Central Compartments. In the Eastern compartment, however, that harbours the lowest numbers, numbers dropped sharply around 1988/1989

(Figure 53). In the period 1988/1989 – 1992/1993 a (non-significant) decrease was observed in all but the Central compartment. Trends were somewhat different in the Dutch Wadden Sea and Westerschelde estuary. In the Wadden Sea, numbers of Bar-tailed Godwits increased over the entire period of 1987/1988 – 2009/2010 whereas numbers showed a steady decrease in the Westerschelde estuary.

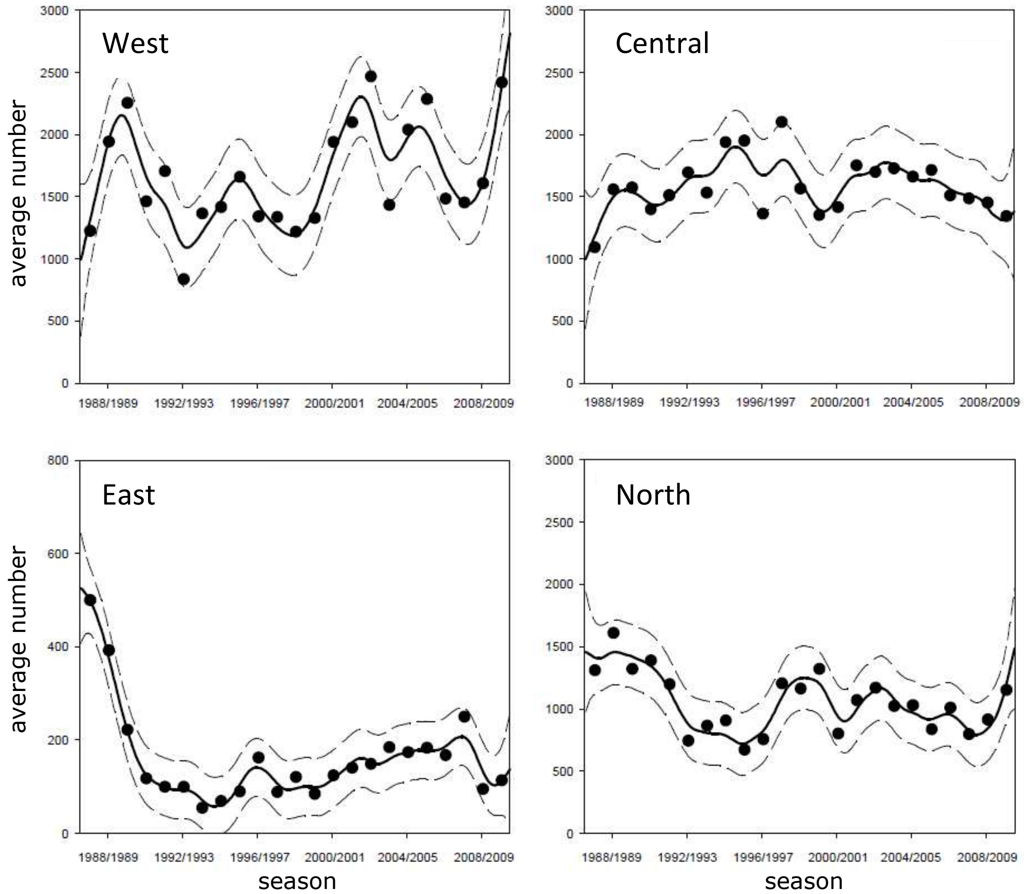

Figure 53. Trends in numbers of Bar-tailed Godwit in the four compartments of the Oosterschelde estuary (Trendspotter, with 95% confidence intervals).

The Bar-tailed Godwit is mainly considered a worm eater, but is observed to utilise many different prey species such as shrimps, crabs, and lugworms *Arenicola marina* (Zwarts 2009), Baltic tellins *Macoma balthica*, mud snails, polychaete worms *Heteromastus filiformis*, *Nereis* sp., *Nephtys* sp., and many other species (Meire et al. 1994a; Leopold et al. 2004). In some areas they are seen to specifically feed on one prey species, but in another area they may have a preference for other prey species (references in Leopold et al. 2004).

We only found a significant relationship between numbers of Bar-tailed Godwits and the density (or biomass) of the polychaete worm *Capitella capitata* in the Western compartment (linear regression: $p < 0.05$, $R^2 = 0.33$, $F = 8.31$). The significance of this relationship was, however, dependent on one year: 2005. Removal of this year from the analysis resulted in a significance of $p = 0.067$ ($R^2 = 0.20$, $F = 3.88$).

Bar-tailed Godwits appear to be opportunistic feeders, which makes it difficult to find causal relationships with prey species abundance. Furthermore, males and females have differently shaped bills and therefore have different preferences for certain prey items (references in Leopold et al. 2004).

Curlew

The Curlew breeds in the Netherlands, but mainly in the Eastern part of the Netherlands and hardly in the South-western Delta area. Of the population that breeds in the Netherlands, a large proportion migrates to Southern England and the Atlantic coasts of France, Spain, Portugal and Morocco. The South-western Delta area, and specifically the Oosterschelde estuary, is mainly visited by Curlews that breed in Finland and North-western Russia. They appear in the area as migrant and winter guest (Strucker et al. 2010). The seasonal pattern is very similar for the different compartments although the Northern compartment harbours lower numbers. Lowest numbers are present in May and June (Figure 54). In the period July – October maximum numbers are reached. In this period, the South-western Delta area is important for moulting Curlews. After October, numbers decrease until January when numbers start to increase again. In the period February – March maximum spring numbers are reached.

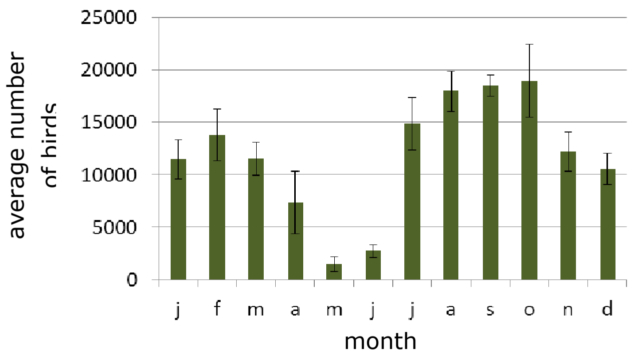

Figure 54. Seasonal occurrence of Curlews in the Oosterschelde estuary. Per month the average number of the seasons 2005/2006 – 2008/2009 is given.

The Curlew showed a strong increase in winter in all Dutch coastal water bodies (except for the Ems-Dollard estuary) and all compartments of the Oosterschelde estuary (Appendix A). The increase was steady in the Wadden Sea since the mid-1970s and more abrupt in the Oosterschelde and Westerschelde estuaries since around 2000/2001. While numbers in the Netherlands showed an increase, internationally numbers are decreasing, as is also the case in the Schleswig-Holstein German part of the Wadden Sea. The Netherlands harbours almost half of the international flyway population (Aarts et al. 2008).

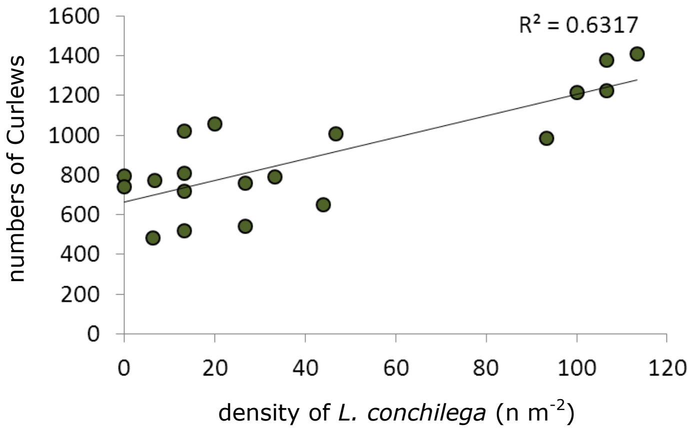

Figure 55. Relationship between density of the polychaete tube worm *Lanice conchilega* (Sand Mason) in autumn in the Northern compartment (n m^{-1}) and season average numbers of Curlew (n). The relationship is significant (linear regression: $p < 0.05$, $R^2 = 0.63$, $F = 29.15$).

The Curlew has a varied diet, which mainly contains larger prey species. In the Wadden Sea they were observed to feed on larger polychaetes such as *Lanice conchilega*, *Nereis* sp., and *Arenicola marina*, and also bivalve shellfish, crabs and shrimps (Leopold et al. 2004; Zwarts 2009). Within the Oosterschelde estuary we found a significant relationship between Curlew numbers and the density (or biomass) of the sand mason *Lanice conchilega* in the Northern compartment (Figure 55; linear regression: $p < 0.05$, $R^2 = 0.63$, $F = 29.15$) and the density (or biomass) of *Capitella capitata* in the Eastern compartment (linear regression: $p < 0.05$, $R^2 = 0.46$, $F = 14.6$). The relationship with *Lanice conchilega* may well be a causal relationship since Curlew have been observed to feed in *Lanice* fields and on large numbers of *Lanice conchilega* itself (references in Leopold et al. 2004). However, whether the increase in numbers of Curlew can be explained by an increase in abundance of *L. conchilega* and *C. capitata* cannot be concluded yet. Curlew and the both potential prey species may have shown an increase due to (an)other factor(s). The significant relationships are almost entirely dependent on the last four years of the time series. In these last four years numbers of Curlew were stable while *C. capitata* showed a strong increase in the Eastern compartment. Furthermore, there are no indications from literature that Curlew feed on *C. capitata*. *Lanice conchilega* did show an increase over the entire period, and more stable densities on a higher level in the last five years. This species is commonly known to be eaten by Curlew, and Curlew are described to feed in *Lanice* fields. On the scale of the Northern compartment numbers of Curlew may be determined by the availability of *Lanice conchilega* or the area of *Lanice* fields. The cause for increasing Curlew numbers may, however, rather be found on the larger scale of the Netherlands regarding the increasing numbers in the Wadden Sea. In the Central and Eastern compartments the Curlew appears to have reached its maximum already, which should be determined by the local carrying capacity for this species in terms of available foraging area and prey availability.

For the Central compartment there are no data available on trends in time of potential prey species. For the Western compartment we found no relationships with potential prey species.

Spotted Redshank

Spotted Redshanks that breed in the open wooded tundra's of Northern Scandinavia and Russia migrate broadly scattered over Europe to the wintering areas in Africa. Relatively low numbers winter in Europe.

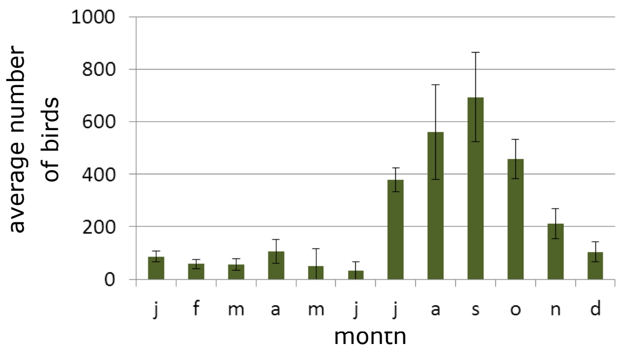

Figure 56. Seasonal occurrence of Spotted Redshanks in the Oosterschelde estuary. Per month the average number of the seasons 2005/2006 – 2008/2009 is given.

In the Netherlands, largest numbers are counted in the migration periods July-September and April-May (Figure 56). In the Oosterschelde estuary maximum numbers are counted during the autumn migration, in August – September. Only few birds stay during winter. Numbers passing through in April-May are much lower. Already in June the females start to arrive from the breeding grounds after having spent only 4-5 weeks there, and in July the males and juveniles follow (references in Meire et al. 1994b).

During the last decade numbers of Spotted Redshank have decreased in the Wadden Sea, Westerschelde and Oosterschelde estuaries. In the Oosterschelde estuary numbers show larger fluctuations from year to year than the Wadden Sea. Changes from year to year are quite similar between the Westerschelde and Oosterschelde estuaries, which suggests that changes are mainly caused by population fluctuations. Within the Oosterschelde estuary, the decline was primarily caused by a decline in the Central compartment. Numbers in the Western compartment remained stable. In the period of the strongest decline in the Central compartment, around 2002, numbers suddenly increased in the Eastern compartment (Figure 57). This is largely due to the construction of the nature reserve Scherpenissepolder which offers good foraging opportunities for Spotted Redshanks (pers. comm. R. Strucker). In the Northern compartment a sudden increase was observed around 1993-1994. This increase was concentrated in the Rammegors nature reserve in the Krabbenkreek area. After the increases in the Northern and Eastern compartment, numbers appeared to gradually decrease again.

The diet of the Spotted Redshank contains *Nereis* sp., *Corophium* sp., crabs, shrimps, small fish, and bivalve shellfish (*Macoma* and *Mya*) (Leopold et al. 2004). Of these, the sampling methods of the MWTL programme (BIOMON) are not well suited to larger vagile epifauna such as crabs, shrimps and small fish, and larger infauna that occurs in low densities such as *Mya*. We found a significant but weak relationship in the Northern compartment between numbers of Spotted Redshank and density (or biomass) of the shrimp *Crangon crangon* (linear regression: $p < 0.05$, $R^2 = 0.22$, $F = 4.81$) and density of the polychaete *Nephtys hombergii* (Figure 58; linear regression: $p < 0.05$, $R^2 = 0.34$, $F = 8.91$). The weak relationship with *C. crangon* was almost entirely determined by one season (1999/2000).

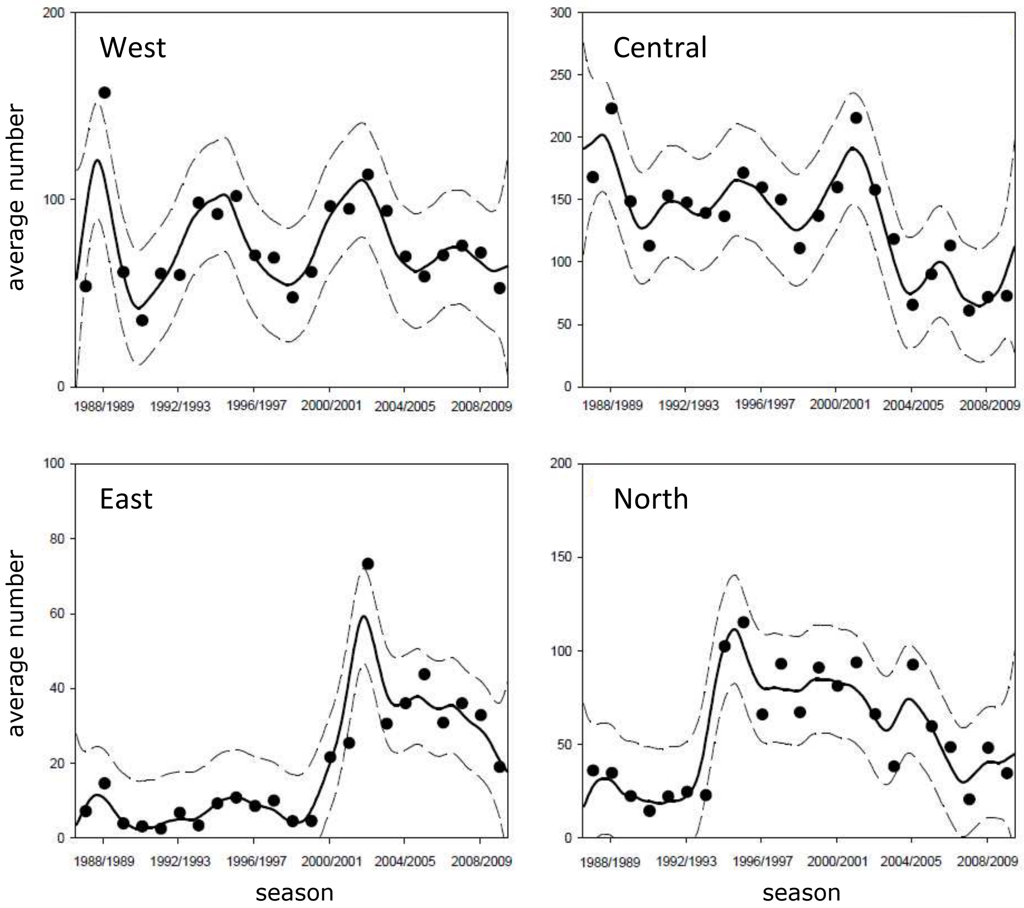

Figure 57. Trends in numbers of Spotted Redshank in the four compartments of the Oosterschelde estuary (Trendspotter, with 95% confidence intervals).

We also tested the relationship with the mud snail, which is described as an exceptional prey item (references in Strucker et al. 2010). The relationship with mud snail density was significant for the Northern compartment (linear regression: $p < 0.05$, $R^2 = 0.42$, $F = 12.08$) and the Eastern compartment (linear regression: $p < 0.05$, $R^2 = 0.34$, $F = 8.89$) (Figure 59). If this indeed means that mud snail is an important prey item for the Spotted Redshank, an increase in the abundance of mud snails in these two compartments may explain why numbers of Spotted Redshank increased here, whereas they showed a decline in the Central compartment. Whether the abundance of mud snails showed a decline in the Central compartment is not known, since benthic fauna is not sampled annually here.

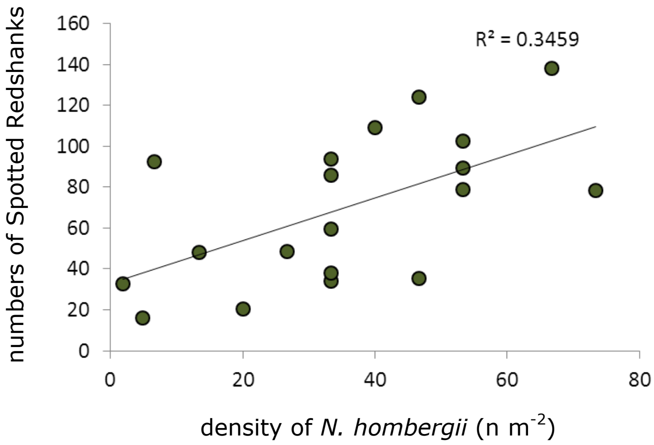

Figure 58. Relationship between density of the polychaete *Nephtys hombergii* in autumn in the Northern compartment (n m^{-1}) and season average numbers of Spotted Redshank (n). The relationship is significant (linear regression: $p < 0.05$, $R^2 = 0.34$, $F = 8.91$).

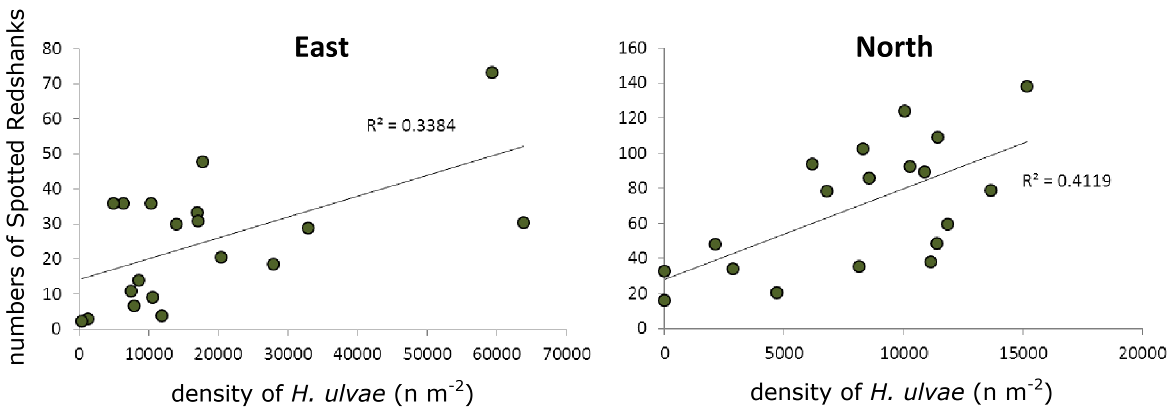

Figure 59. Relationship between density of the mud snail *H. ulvae* in autumn and season average numbers of Curlew (n) in the Eastern and Northern compartments. The relationships are significant (linear regression: East: $p < 0.05$, $R^2 = 0.34$, $F = 8.89$; North: $p < 0.05$, $R^2 = 0.42$, $F = 12.08$).

4. Discussion and conclusions

Numbers of waders could not be related to direct effects of erosion of tidal flats (decrease in foraging area and foraging time), yet. Also indirect effects of erosion of tidal flats, through effects on food composition and availability, could not be demonstrated yet. We therefore conclude that wader numbers in general did not decrease because they still have enough foraging are left. Foraging area and foraging time are expected not to be limiting still, but this may change rapidly in the future. Up until present eroded sediments from the higher intertidal have replenished the lower tidal flats with the result that the area of lower intertidal flats has not decreased yet. As soon as the upper intertidal has eroded completely, the mid and lower intertidal area will start to erode as well. Since the mid and lower intertidal harbour a higher biomass of prey species in general, erosion of this part of the tidal zone is expected to lead immediately to decreasing bird numbers. As a result of erosion of tidal flats the tidal flats have become flatter. Therefore the expected future decrease in area of relatively profitable tidal flats may occur at a faster rate than observed until present, and will be augmented by any rise in level. There is, therefore, a realistic chance that we may see a relatively sudden change in the carrying capacity of the Oosterschelde estuary for waders. A change that may be very difficult, or even impossible, to turn around. Oystercatchers do show a decline already, and numbers are expected to decrease further in the near future.

Changes in morphology of intertidal flats

Erosion of the intertidal area of the Oosterschelde estuary, with a subsequent decrease in average exposure time (≈ foraging time for birds) and total intertidal area (≈ foraging area for birds) was already described by Van Zanten and Adriaanse (2008) and Jacobse et al. (2008). Geurts van Kessel et al. (2004) analysed changes in exposure time as a consequence of erosion of tidal flats in the Oosterschelde estuary, and found that the average emerge time has decreased until 2001. They also found that areas with exposure times longer than 60% (of the time) had disappeared, compared to areas with shorter exposure times (<40%). In other words, the tidal flats are topped off; they are becoming flatter. Based on the available elevation maps (1990, 2001 and 2007) Jacobse et al. (2008) already concluded that the area of the higher intertidal decreased faster than the area of lower intertidal because net erosion rates in the lower intertidal were limited by sediment transport from higher areas. They showed higher erosion rates in the lower intertidal at locations where no sediment transport from higher locations took place anymore and predicted that in the future, as soon as the higher areas are completely eroded, erosion of the lower intertidal will occur much more rapidly than is the case at present. This supports our hypothesis that erosion of tidal flats has not yet led to decreasing bird numbers because the relatively more important lower intertidal has as yet not decreased substantially. Jacobse et al. (2008) do, however, question the reliability of the elevation maps, especially the map of 1990. Elevations in 1990 seem to be overestimated, whereas elevations in the lower intertidal in 2001 and 2007 may be underestimated. We mainly focussed our analyses on the RTK transect measurements of Rijkswaterstaat to refine the analysis in time and space. Advantages of using these measurements are a higher reliability (pers. comm. Ir. J.G. de Ronde, Deltares) and a higher frequency (up to 2 times per year since 1987). However, results cannot be translated to the entire intertidal area of the Oosterschelde estuary and some areas are covered in larger detail than others. For example, the transects in the Eastern compartment were designed to monitor mainly erosion of the salt marshes and are therefore located in the higher intertidal whereas the majority of the Eastern compartment is situated below NAP. Our results confirm the results by Jacobse et al. (2008) in the sense that we see a relative decrease in areas with exposure times longer than 40% and a relative increase in areas with exposure times shorter than 40%. Because our results cannot be fully translated to the entire intertidal, we cannot conclude whether the increase in lower intertidal area was absolute. Since the study by Jacobse et al. (2008) shows that all intertidal flats showed net decreases in total area rather than increases, we can conclude that there was an absolute decrease in intertidal area with exposure times > 40%, but no decrease in areas with exposure times < 40%. Locally there may have even been a net increase of the area with < 40% exposure time, but this cannot be proven with our results.

Jacobse et al. (2008) concluded, based on the elevation maps of 1990, 2001 and 2007, that erosion rates are the fastest for the larger tidal flats in the Eastern compartment. This is contra-intuitive since the Eastern compartment is more sheltered than the Western and Central compartments, and erosion rates are therefore expected to be slower. Our study of the RTK profiles shows that out of all compartments, observed changes were the least in the Eastern compartment. There are, however, problems with both methods. Jacobse et al. (2008) show that the sediment balance is far from closed in the Eastern compartment. Sediment is in fact disappearing from the entire system and nobody knows where it disappears to. This may be an artefact due to errors in the elevation maps. The RTK profiles are located in the higher intertidal whereas the majority of the Eastern compartment consists of lower intertidal. The RTK profiles are therefore not representative for the entire compartment.

We found the largest changes in (relative) intertidal area within different classes of exposure time in the Western compartment at Roggenplaat, in the Central compartment at Slikken van de Dortsman and in the Northern compartment at Slikken van Viane South. Especially increases within the lower exposure time classes were visible (in the isohypses of Figure 13).

What may furthermore be highly relevant for the suitability of the different compartments as foraging areas for waders and the Shelduck, is the distribution of elevations (and exposure times). The different compartments show large differences. Whereas the Eastern compartment is situated below NAP for 94% (in 2007), the Northern and Western compartments shows a more equal distribution with respectively 54% to 65% of the area below NAP. The Central compartment is intermediate, with 80% of the intertidal area below NAP. The optimum combination of foraging time (exposure time) and foraging area (intertidal) area is found below NAP in the Eastern and Central compartments, and above NAP in the Northern and Western compartments. Because food availability for waders is a product of prey abundance, foraging time and foraging area, a more balanced distribution of the different tidal zones is believed to offer better foraging opportunities than areas where either the higher or lower intertidal dominates.

Since 94% of the the Eastern compartment already now is situated below NAP and Jacobse et al. (2008) show that the erosion rates of the tidal flats in this compartment are higher than elsewhere , this compartment is expected to be the first to lose its suitability for foraging waders . However, this conclusion cannot be drawn before it becomes clear why the sediment balance is not closed for this compartment. Furthermore Jacobse et al. (2008) predict that an equilibrium may soon be reached in the upper reaches of the Northern compartment: in Slaak and Krabbenkreek. Suitability for foraging by birds in these areas is therefore expected to be maintained. Slikken van Viane in the lower reaches of the Northern compartment, an important tidal flats for foraging birds, is a dynamic location that still shows high erosion and sedimentation rates. Based on current knowledge the future of this area is more uncertain.

Changes in prey abundance

Only few long-term trends were observed in terms of benthic invertebrate abundance in the different compartments (North, West and East; Central not sampled). Cockles *C. edule* suddenly declined in the Eastern compartment and the stock was never restored. Mussels *M. edulis* on intertidal culture plots were all relocated to subtidal culture plots in the mid-1990s. This mainly had an effect in the Central compartment where most intertidal mussel culture took place before 1995. In the entire study period there were almost no natural mussel beds in the intertidal. Polychaetes suddenly became very abundant in the Western compartment in the mid-1990s, and showed a slow decrease in the following years. Differences in abundance between compartments are more conspicuous. *Lanice conchilega* is completely absent in samples from the Eastern compartment. It is relatively abundant in the Northern compartment at Slikken van Viane, but was completely absent at Krabbenkreek in 1989. This illustrates large differences on relatively small spatial scales, although of course an absence in samples taken in 1989 does not mean the species was absent in the entire study period. In general, densities are dominated by polychaetes in the Western compartment and by molluscs in the Northern and Eastern compartments (mainly mud snails). Biomass is dominated by molluscs in all compartments (mainly larger bivalves such as *C. edule*).

Corresponding with our observations, Escaravage et al. (2003) found no conspicuous long-term trends in the occurrence of benthic invertebrates as well. They concluded that erosion of tidal flats will most likely affect the distribution and abundance of benthic invertebrates to a large extent, but that effects of erosion of tidal flats on benthic biomass and distribution could not (yet) be demonstrated because the total loss in area of tidal flats up until 2002 was still small.

Benthic biomass in the intertidal is concentrated at exposure times lower than 60%. Therefore, based on total abundance of benthic prey species alone, the middle and lower intertidal would be expected to be more important for waders than the higher intertidal (> 60% exposure time). However, the different species of waders have different diets, ranging from opportunistic generalist feeders to specialists on certain prey species. Based on the distribution of benthic species in 1989 in the different compartments of the Oosterschelde estuary (except the Eastern compartments), birds that are dependent on The mud snail, *Corophium* sp., *Bathyporeia* sp., *Scoloplos armiger*, or *Nereis* sp. are expected to be dependent on foraging opportunities in the higher intertidal (> 40% exposure). This is also expected for birds dependent on smaller *Macoma balthica* (Hiddink 2002; Escaravage et al. 2003). Birds that are dependent on *Crangon crangon*, *Nephtys* sp. or *Mytilus edulis* are expected to be dependent on foraging opportunities in the lower intertidal (< 40%). This is also expected for birds dependent on *Aphelochaeta marioni*, *Lanice conchilega*, or *Mya arenaria* (Escaravage et al. 2003). Specialists on other benthic invertebrate species studied here, as well as generalist and opportunistic feeders, are expected to utilise the entire intertidal range with more flexibility. But also for these species generally more food is to be found at exposure times shorter than 60%. Our study only shows the occurrence of prey species, but we cannot conclude anything about actual food availability for birds since we did not take into account profitable densities, size classes and burying depth.

Finally, analyses of changes in abundance of benthic fauna in the Eastern compartment may not be representative for the entire compartment. The majority of the 10 fixed intertidal sampling stations in the MWTL programme are situated at levels above NAP while 94% of the compartment is situated below NAP. Relationships found between wader numbers and abundance of benthic fauna, and between abundance of benthic fauna and tidal elevation, should be interpreted with caution. Also data on larger, less abundant and vagile epifauna should be interpreted with caution since the sampling technique is not optimized for such species. For example, the lugworm *A. marina* is an important prey species in late summer, but because the sampling technique is not suited to this species it is very difficult to find causal relationships with wader numbers. These data do not really allow for statistical analyses of trends and relationships with elevation and predator numbers.

Changes in other factors

Apart from changes in the morphology of tidal flats and benthic biomass, primary production and corresponding carrying capacity for filter feeders are also important factors that changed over time. Carrying capacity already appears to have been reached which may explain the reduced cockle biomass observed in the Eastern compartment (Geurts van Kessel et al. 2003). Within the framework of a transition in mussel culture from bottom seed fisheries to mussel seed collection on suspended ropes and nets (SMC's: seed mussel collectors) the carrying capacity of the Oosterschelde is currently under study (IMARES, commissioned by the ministry of EL&I). In our dataset, effects of a reduced carrying capacity appear visible for cockles but not (yet) for other benthic invertebrates.

We did not use data on the expansion of the Pacific oyster *C. gigas* in the Oosterschelde estuary since the role of Pacific oyster beds for foraging waders is yet unknown and causal relationships will be impossible to find. Besides, the oyster showed an ongoing increase and potential effects will be very difficult to isolate from ongoing effects of erosion of tidal flats. The Pacific oyster mainly occurs in the lower intertidal where the reef structures cause sedimentation resulting in an accumulation of fine sediments. The Pacific oyster itself is not used as an important food source by waders, but has a profound effect on habitat structure. This may stimulate the occurrence of species such as the mud snail and *Corophium* sp. (Troost 2010 and references therein). Furthermore, Pacific oyster beds increase habitat heterogeneity and biodiversity and may therefore enhance foraging opportunities for waders. This will, however, depend on the oyster density in a bed. In very dense oyster reefs only little bare sediment remains and prey items will be more difficult to reach between the sharp oyster shells. Pacific oyster reefs are also argued to restore natural mussel biomass in the intertidal by offering the mussels a settlement substrate and refuge. Because of an increase in the area covered by oyster beds, more mussels may again become available for foraging Oystercatchers (Troost 2010). Within the oyster reefs tidal pools may form attractive feeding areas for species feeding of small fish and shrimps, such as Greenshank and Spotted Redshank.

The intertidal area occupied by Pacific oyster beds differs between the compartments. Based on survey data up until 2005 (IMARES, unpublished), oyster beds covered from 115 hectares in the Western compartment to 365 ha in the Eastern compartment. In the Eastern compartment, roughly 15% of the intertidal is covered by oyster beds. In the other compartments oyster cover is around 7%. Pacific oyster beds mainly occur in the lower intertidal.

Changes in shorebird occurrence (and distribution) explained

The numbers of a migratory bird species in a certain area is determined by many factors, acting on different spatial and temporal scales. In this study we were interested in factors acting on a local scale: in the Oosterschelde estuary itself. We therefore mainly focussed on species that showed a different long-term trend in the Oosterschelde estuary compared to other Dutch estuaries. We hereby assumed that a different trend in the Oosterschelde estuary was caused by characteristics of the estuary itself that may have changed over time. As for species that showed a similar trend in the Oosterschelde estuary as on the Dutch Wadden Sea and/or Westerschelde estuary, factors acting in the Oosterschelde estuary may still explain bird numbers on compartment scale. Relative importance of the different compartments may have changed over time, even though the total number in the estuary was mainly determined by factors acting on a larger spatial scale.

Based on observed changes in relative wader abundance (expressed as estimated wader density) in the different compartments, more particularly the stable wader abundance in the Eastern compartment and strongly increasing abundance in the Northern compartment, two alternative and contradicting hypotheses are possible: either the Northern compartment is a more profitable area for waders than the Eastern compartment explaining the increase, or the carrying capacity of the Eastern compartment was already reached around 1990 forcing increasing wader numbers to other compartments. Especially according to the latter hypothesis, first effects of further erosion of tidal flats are likely to be observed in the Eastern compartment. This expectation also corresponds to the predicted near-equilibrium of intertidal area in the Northern compartment while the intertidal of the Eastern compartment is predicted to erode further (Jacobse et al. 2008).

Based on differences in temporal trends between the Oosterschelde estuary and Westerschelde estuary and/or Wadden Sea alone, numbers of the following bird species appear to be (partially) determined by factors acting in the Oosterschelde estuary: Oystercatcher, Avocet, Ringed Plover, Grey Plover, Knot, Bar-tailed Godwit, Spotted Redshank, Redshank, Greenshank and Turnstone. Of these, the Oystercatcher, Bar-tailed Godwit and Spotted Redshank showed clear differences between compartments within the Oosterschelde estuary. Also the Shelduck, that showed a similar trend in the Oosterschelde and Westerschelde estuaries and Dutch Wadden Sea, showed differences between compartments. Of the above mentioned species, the Shelduck, Oystercatcher, Ringed Plover, Grey Plover, Knot, Bar-tailed Godwit, and Spotted Redshank were studied in more detail, as well as the Dunlin and Curlew.

Numbers of the selected bird species could not be related to direct or indirect effects of erosion of tidal flats (decrease in foraging area and foraging time), yet. We did find relationships with the abundance of certain prey species. Especially the mud snail turned out to be of relatively high importance. The density of mud snails appears to be determining for several bird species in the Northern compartment (Knot, Grey Plover, and Spotted Redshank) and Eastern compartment (Shelduck, Dunlin, and Spotted Redshank). *Lanice conchilega* was the other prey species that appeared to be determining for more than one species of wader, in the Northern compartment (Dunlin and Curlew) and entire Oosterschelde estuary (Grey Plover). For the Curlew, this relationship may be direct since this species is known to feed on *L. conchilega* itself. For the Grey Plover and Dunlin the relationship more likely represents a relationship with *Lanice* beds and its accompanying fauna, than a direct predator-prey relationship (Goss-Custard et al. 1977; Petersen and Exo 1999). *Lanice* beds may especially be preferred as foraging grounds because *L. conchilega* is an ecosystem engineer that creates spatially heterogeneous soft-bottom areas that are easier to probe in search of prey and/or have a higher prey density. Furthermore, the Oystercatcher showed, as expected, relationships with mussels (Central compartment) and cockles (Eastern compartment). For the Ringed Plover, a known worm-eater, several polychaete species appeared important: *Scoloplos armiger* (Northern and Eastern compartments), *Aphelochaeta marioni* (Western compartment), and the total of eleven common polychaete species (Northern compartment).

Bird species that are dependent on prey species that mainly occur in the upper intertidal, such as the mud snail, *Corophium* sp. and *S. armiger*, are expected to be affected by the effects of erosion of tidal flats before species that are generalists or dependent on prey that is distributed homogeneously throughout the tidal zone or that mainly occurs in the lower intertidal. The mud snail occurs in the highest densities in the Eastern and Northern compartments, and is negligible in the Western compartment. The Eastern and Northern compartments greatly differ in the relative (and total) area of the higher intertidal zone, and also seem to differ greatly in the rate of erosion and expected end-scenario. Whereas the Northern compartment, that has a large area of higher intertidal, may almost reach an equilibrium state, erosion rates may be the highest in the Eastern compartment where higher intertidal zones are already scarce. Species depending on prey species living in the higher intertidal of the Eastern compartment may therefore be among the first to be affected by the effects of erosion of tidal flats. However, this will also be dependent on the ability of these bird species to switch to other prey that may not be restricted to the higher tidal zones. For the Oystercatcher, that is a specialist predator of cockles and mussels, modelling with WEBTICS showed a high dependence on the availability of cockle beds at higher tidal levels (exposure times at least 60%; Rappoldt et al. 2006). This species will not be able to switch to other prey species in winter and is therefore very vulnerable for further erosion of tidal flats.

Species that may be highly dependent on mud snails are the Shelduck and Knot. For the Shelduck a relationship with mud snails was found in the Eastern compartment. For the Knot, a relationship with mud snails was found in the Northern compartment, and with *M. balthica*, of which the smaller and younger individuals also show a preference for the higher intertidal (Hiddink 2002), in the Eastern compartment. Although a decrease in numbers of both species is not yet apparent in these compartments, the Shelduck and Knot foraging in the Eastern compartment may well be among the first waders to be affected by erosion of tidal flats. The Dunlin and Spotted Redshank also showed a relationship with mud snails in the Eastern compartment and may therefore be among the first to show a decrease in this compartment as a result of further erosion. Especially wintering birds are expected to be dependent on shellfish such as bivalves and mud snails, since many other prey species are more difficultly available in winter. Also based on this extra dependence in winter, the most vulnerable species in particularly the Eastern compartment are expected to be the Shelduck, Knot, Oystercatcher and Dunlin.

The Ringed Plover showed a relationship with *S. armiger* in the Eastern compartment but does not seem highly dependent on just this one polychaete species and may easily switch to polychaetes that are not dependent on the higher intertidal.

For birds that are dependent on prey species and communities occuring lower in the intertidal, such as *Lanice conchilega*, *Mytilus edulis*, *Crangon crangon* and *Aphelochaeta marioni*, the abundance of their main prey species is expected not to be affected until locally the higher intertidal areas are completely eroded. At that point, sedimentation from the higher intertidal will halt and the lower intertidal will also start to decrease in area. In the Eastern compartment, where only a small area of higher intertidal remains, and erosion rates may be the fastest (Jacobse et al. 2008), the lower intertidal may be first affected. Species belonging to this category are mainly the Grey Plover, Dunlin, and Curlew (all dependent on *Lanice conchilega* fields). However, even if the preferred prey species occur in the lower intertidal, availability of prey in higher intertidal areas may still be of key importance for survival of certain waders since foraging time in the lower intertidal may be too limited to gather enough food.

Some groups of prey species were not included in the analyses because the determined density and biomass were expected to have a large sampling error. These groups were: larger species that occur in relatively low densities and that are vagile epifauna, such as bivalves *Mya arenaria*, *Scrobicularia plana*, *Ensis directus*, and *Crassostrea gigas*, the polychaete *Arenicola marina*, and crustaceans *Crangon crangon*, *Carcinus maenas*, and *Hemigrapsus* sp. We found no relationships with the lugworm *A. marina*, although Zwarts (Zwarts 2009) showed that the lugworm is consumed in considerable amounts by the Grey Plover, Oystercatcher, Curlew, and Bar-tailed Godwit (especially females). Furthermore, Zwarts (2009) showed that also *Crangon crangon* and *Carcinus maenas* are preyed upon by many species. Zwarts made his observations in late summer / early autumn. Therefore, *A. marina*, *C. crangon* and *C. maenas* are expected to be at least of importance in summer and fall, and likely also in spring when they return to the tidal flats and reproduce. The crustacean prey species are largely unavailable in winter and therefore probably of no importance to wintering birds.

Acknowledgements

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Justification

Report C063/11
Project Number: 4303100401

The scientific quality of this report has been peer reviewed by the a colleague scientist and the head of the department of IMARES.

Approved: drs. C.J. Smit
researcher

Signature:

Date: May 26, 2011

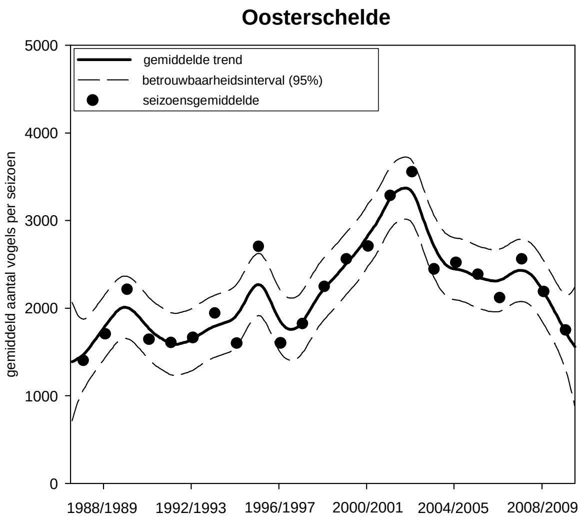
Approved: Dr. B. Dauwe
Head of Department Delta

Signature:

Date: May 26, 2011

Appendix A. Trends in bird numbers in the Oosterschelde estuary

Bergeend



Oosterschelde
gemiddelde trend
betrouwbaarheidsinterval (95%)
seizoensgemiddelde
gemiddeld aantal vogels per seizoen
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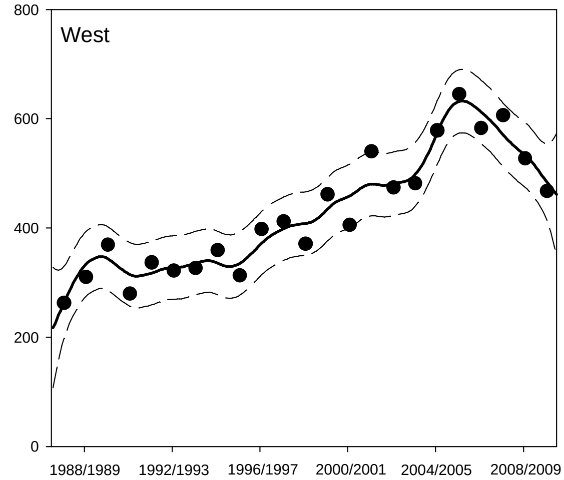
4000
5000
1988/1989
1992/1993
1996/1997
2000/2001
2004/2005
2008/2009



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1988/1989
1992/1993
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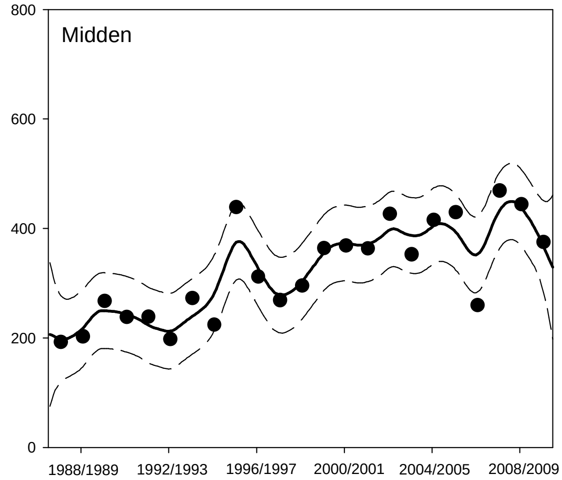
2000/2001
2004/2005
2008/2009



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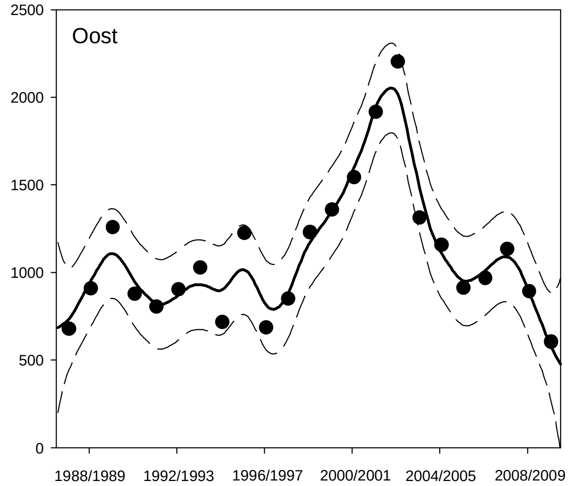

Oost
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500
1000
1500
2000
2500
1988/1989
1992/1993
1996/1997
2000/2001
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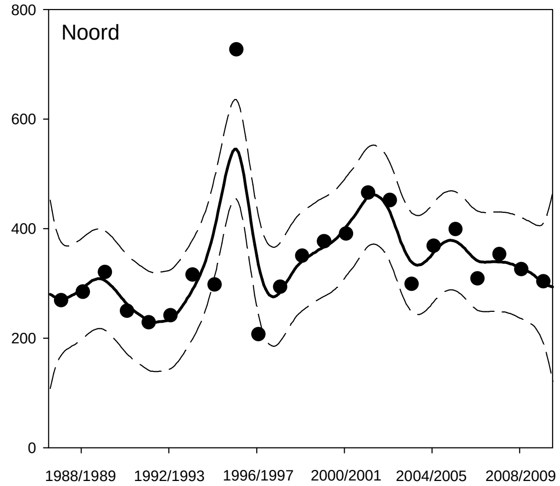
2008/2009



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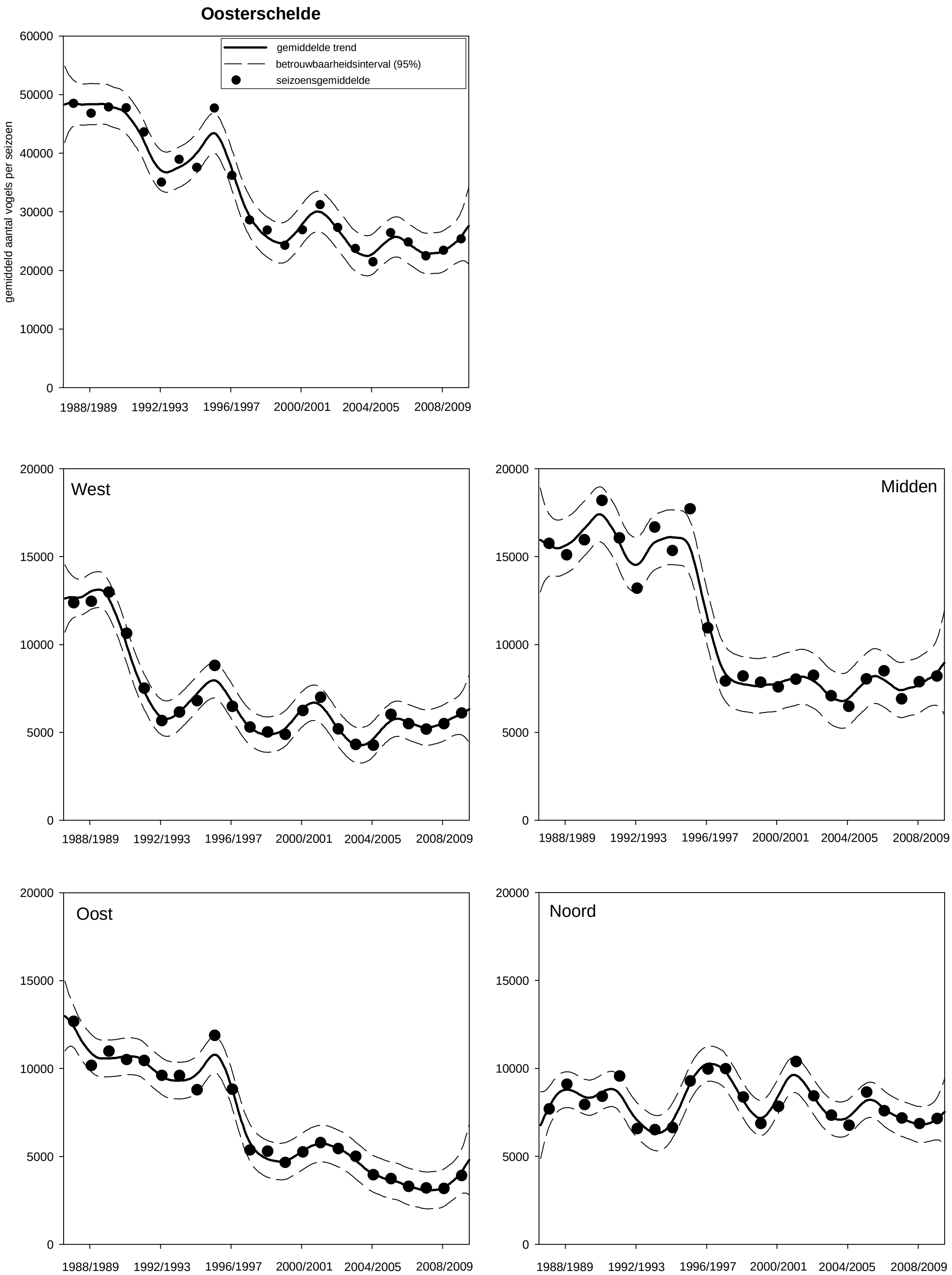
2008/2009

Scholekster



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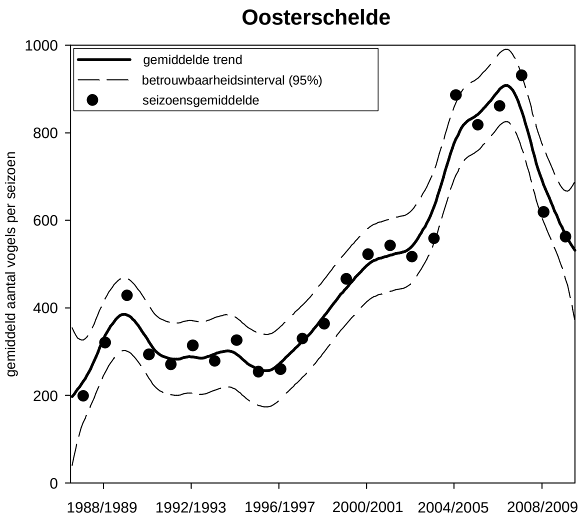
Oosterschelde
gemiddelde trend
betrouwbaarheidsinterval (95%)
seizoensgemiddelde
gemiddeld aantal vogels per seizoen
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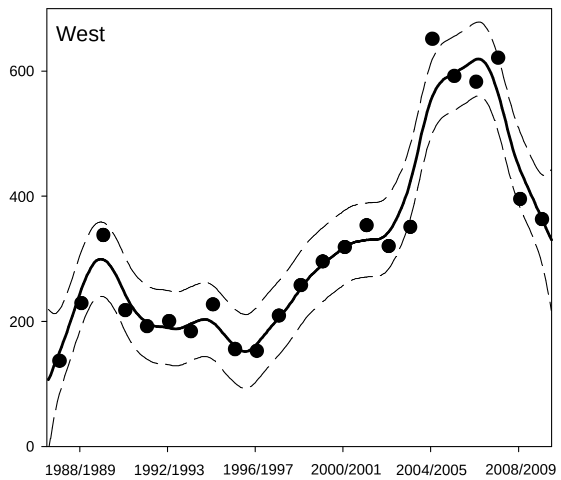
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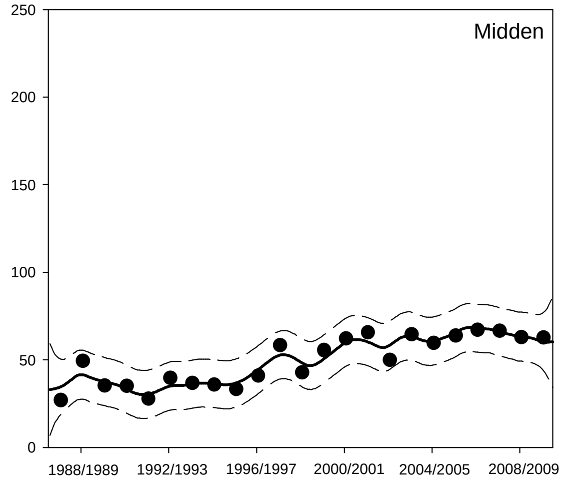
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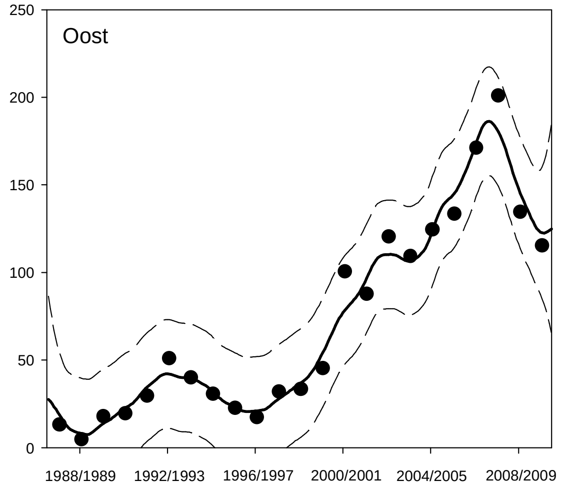
Oost
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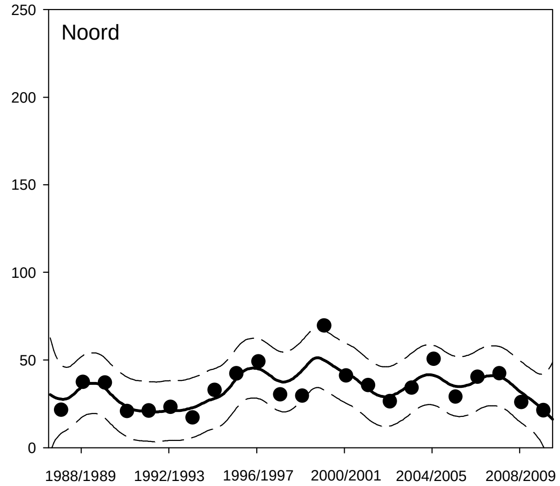
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1988/1989
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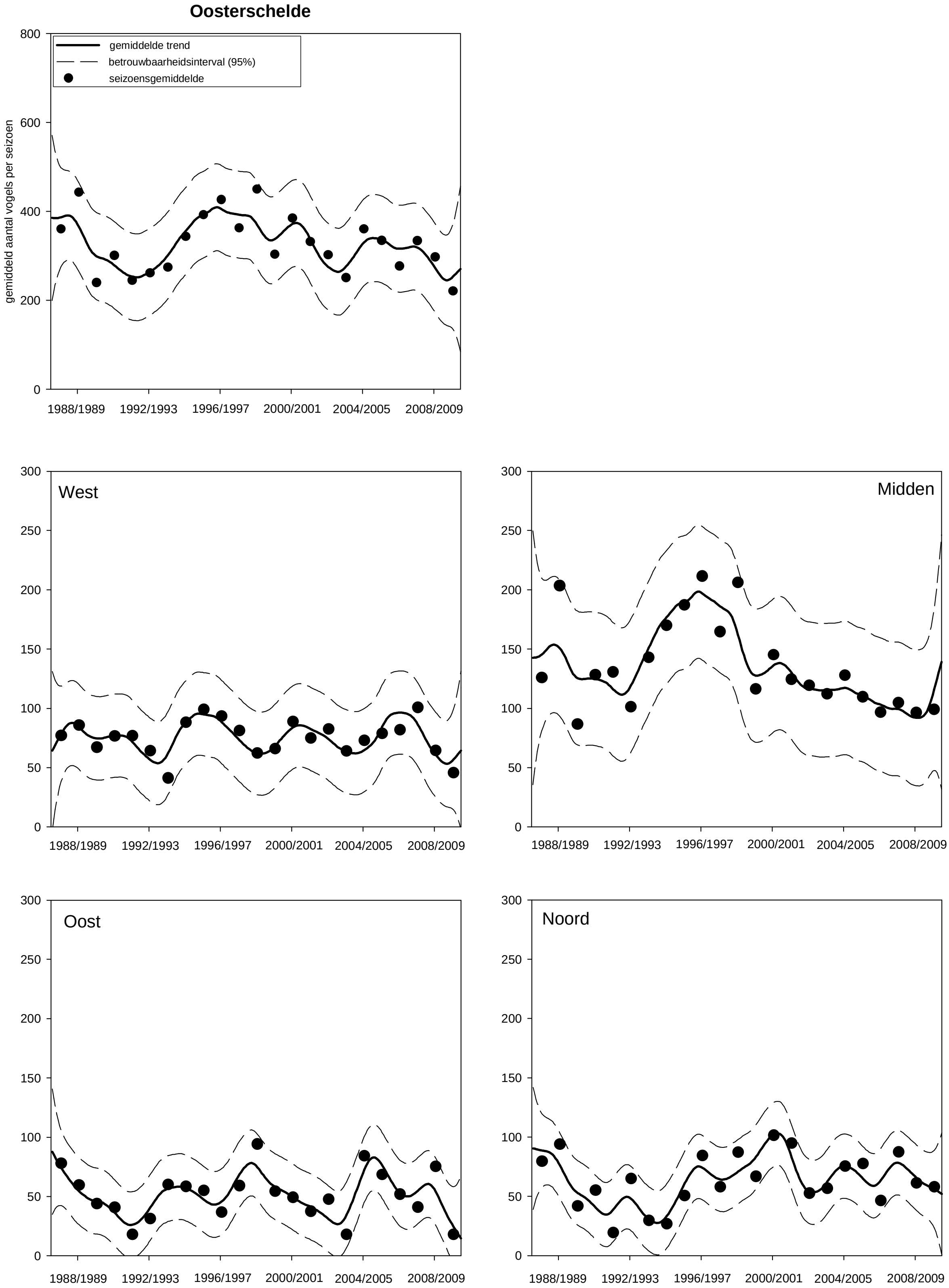
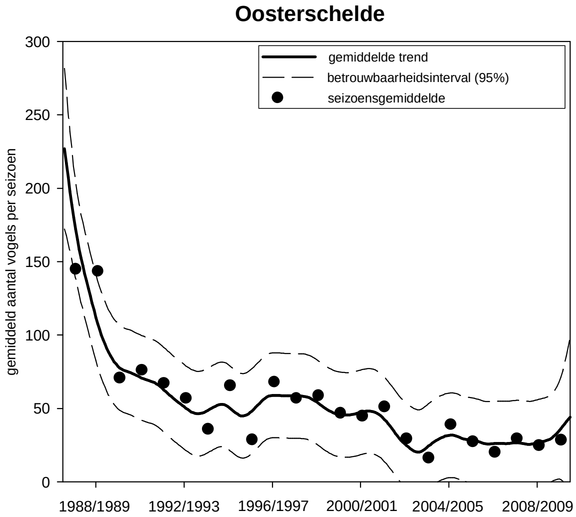
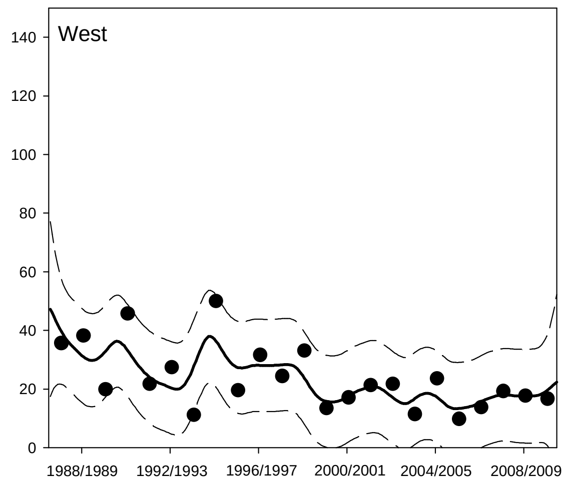
2008/2009

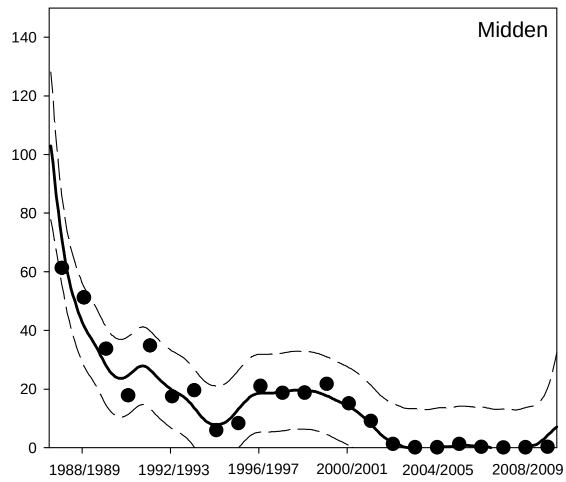
Bontbekplevier

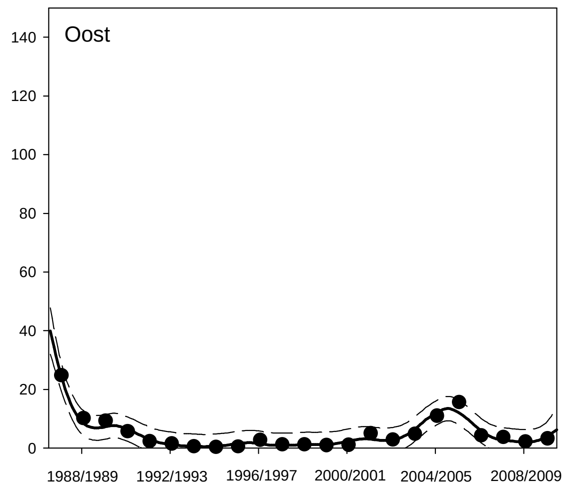


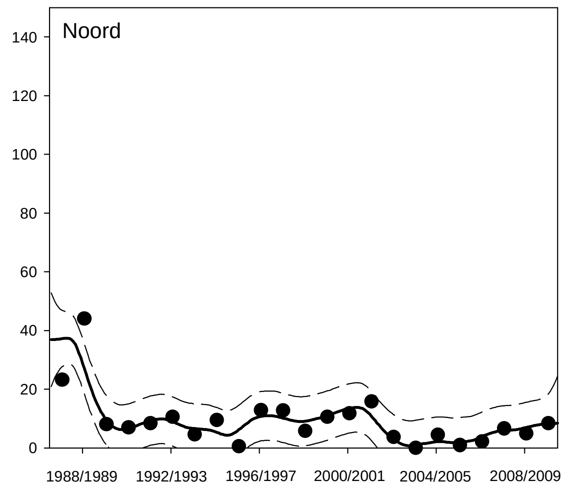
Strandplevier











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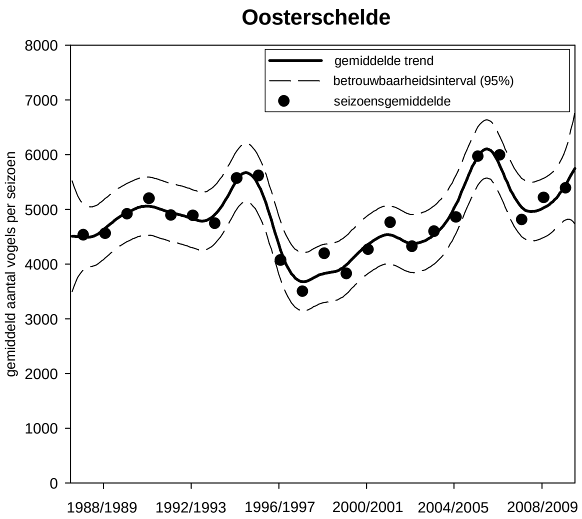
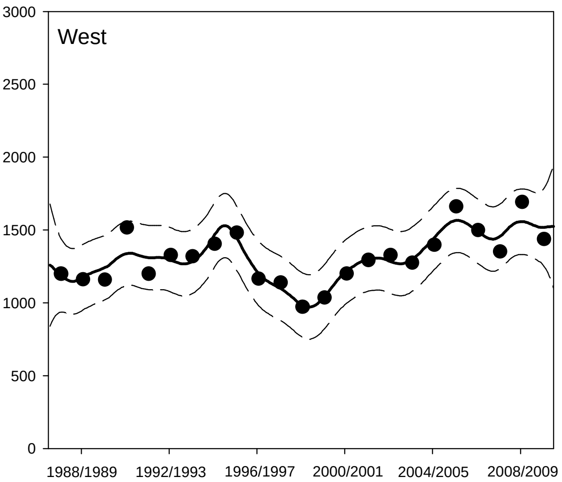
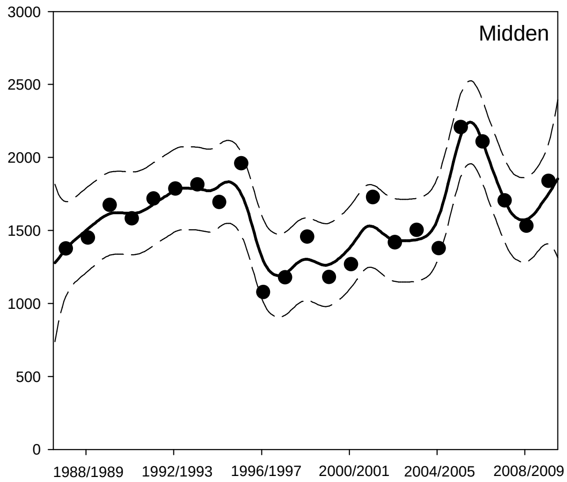
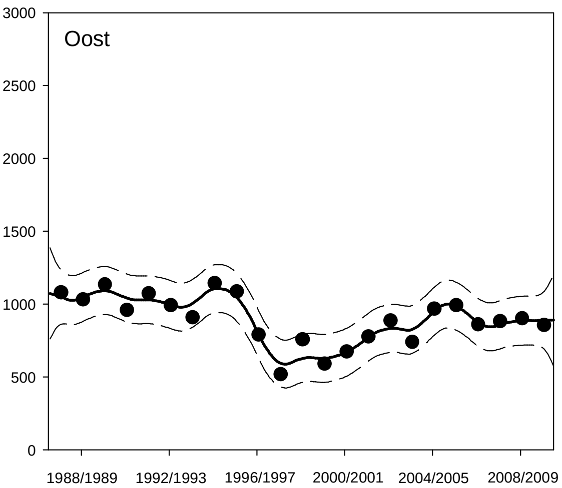
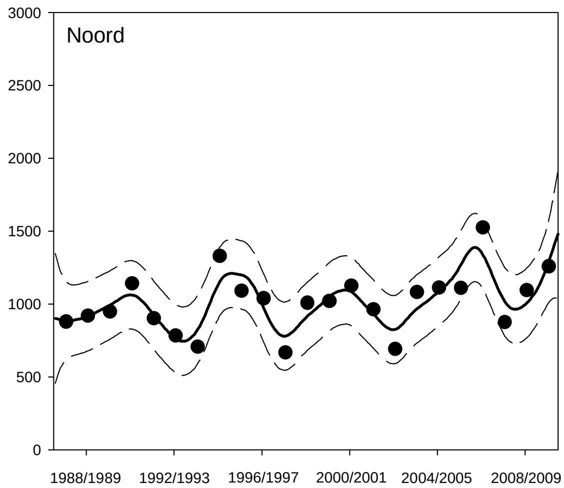


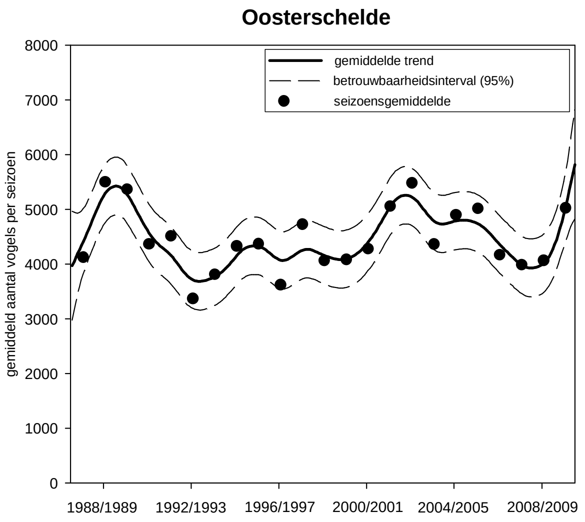


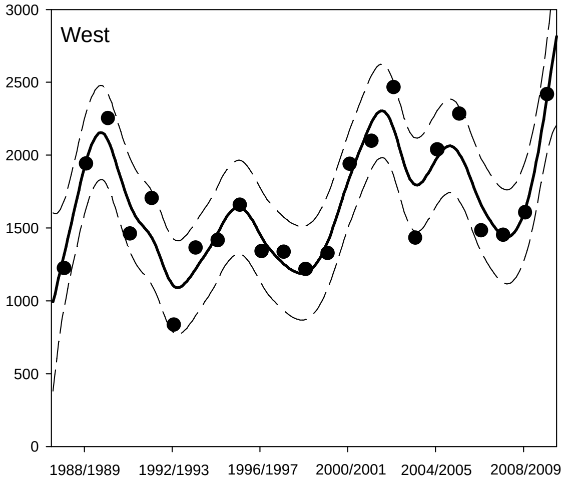


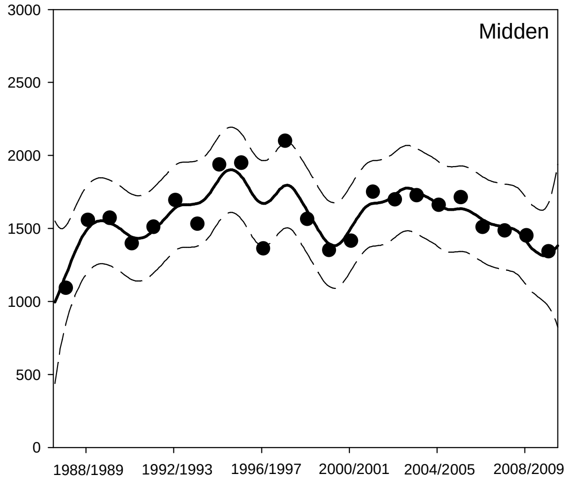


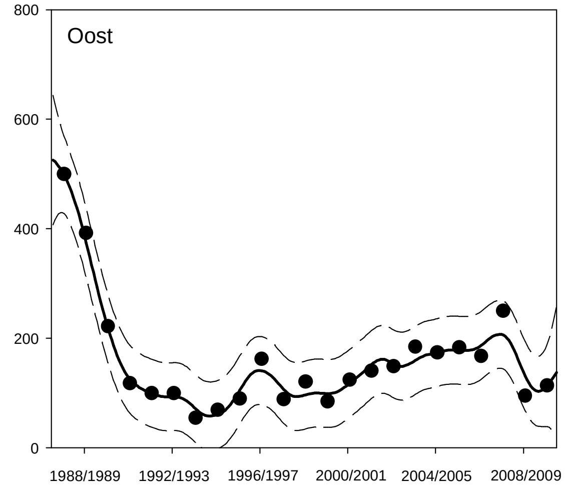


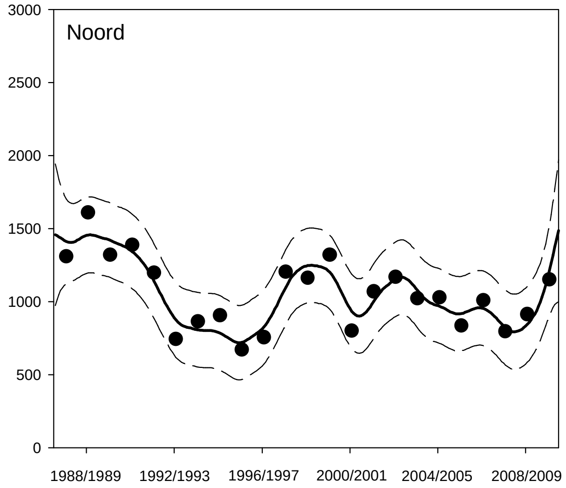
Rosse Grutto



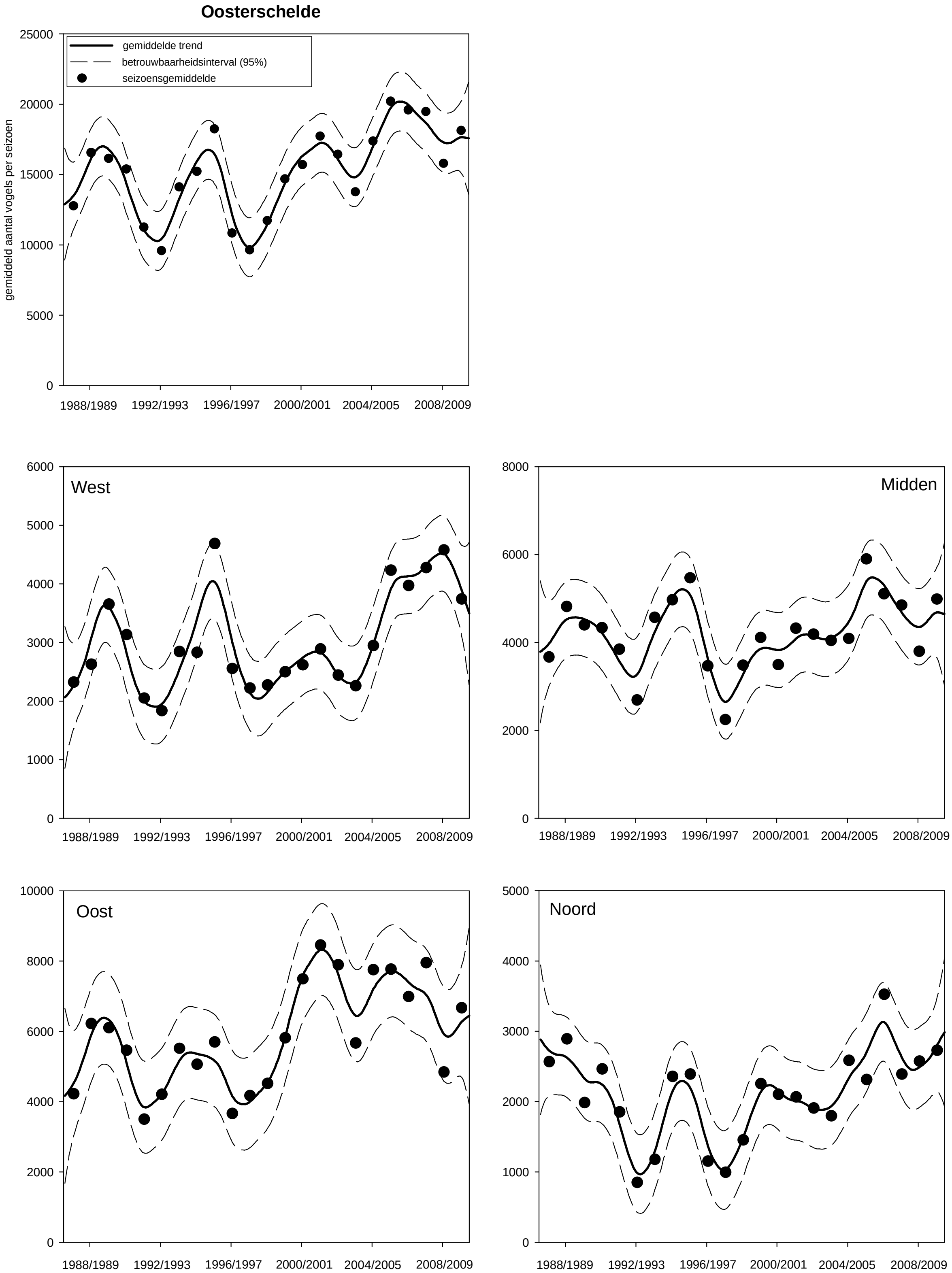








Bonte Strandloper



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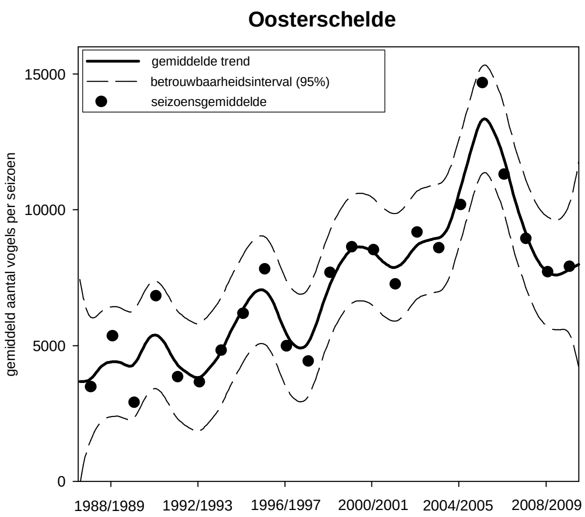
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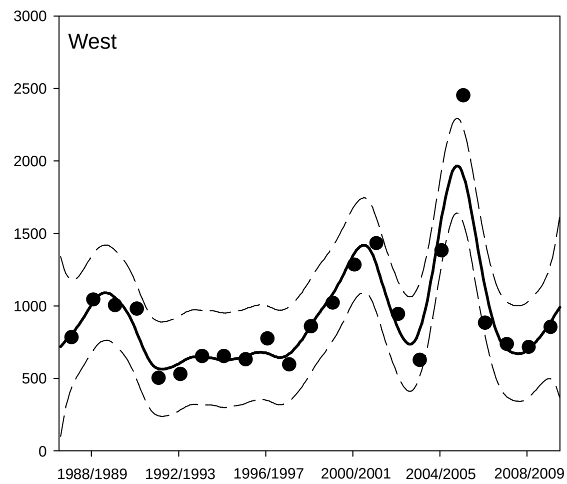
gemiddelde trend
betrouwbaarheidsinterval (95%)
seizoensgemiddelde
gemiddeld aantal vogels per seizoen
0
5000
10000
15000
1988/1989
1992/1993
1996/1997
2000/2001
2004/2005
2008/2009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1996/1997
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2004/2005
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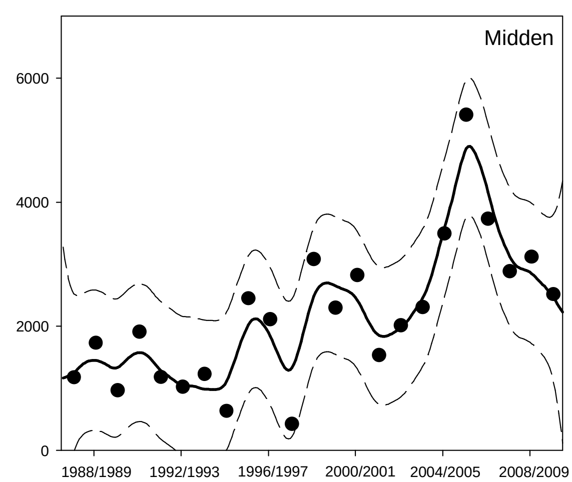
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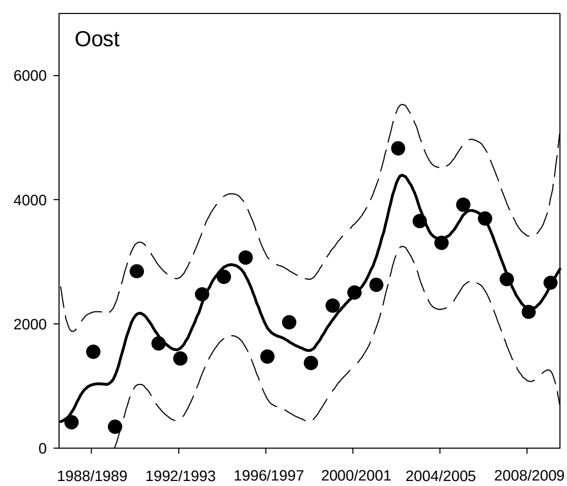
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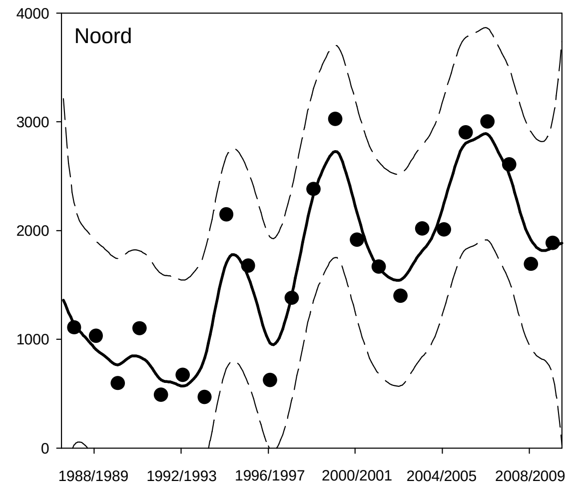
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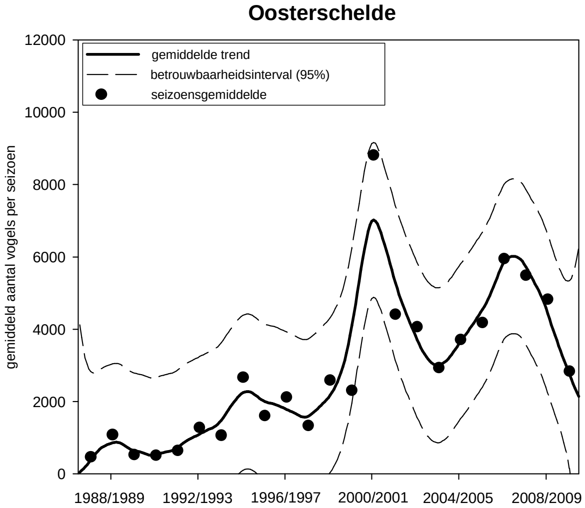
Kievit



Oosterschelde
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betrouwbaarheidsinterval (95%)
seizoensgemiddelde
gemiddeld aantal vogels per seizoen
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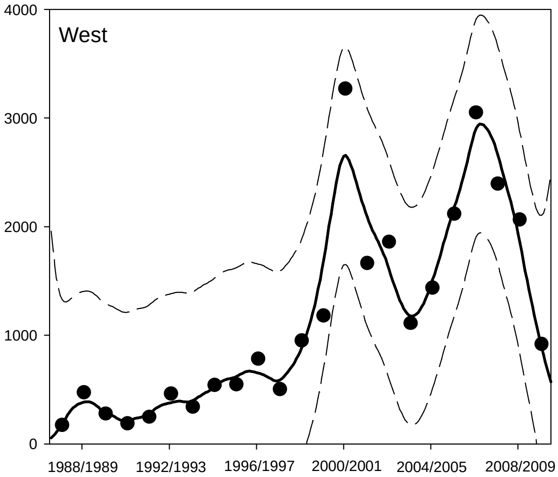

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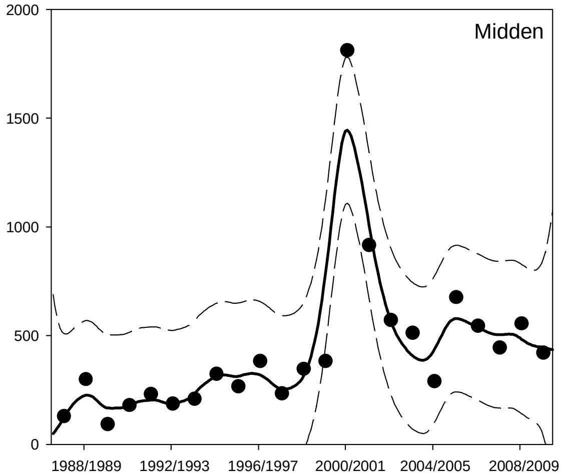

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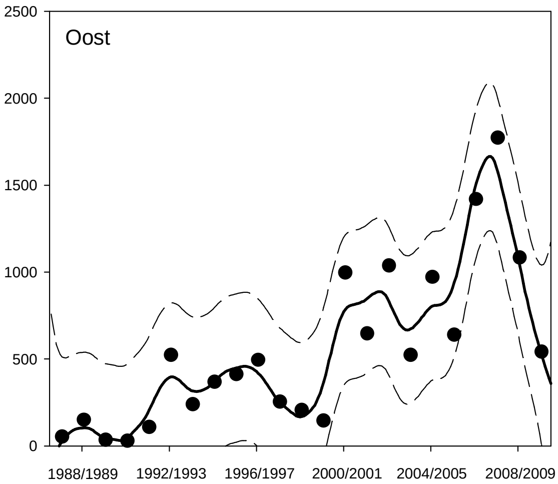

Oost
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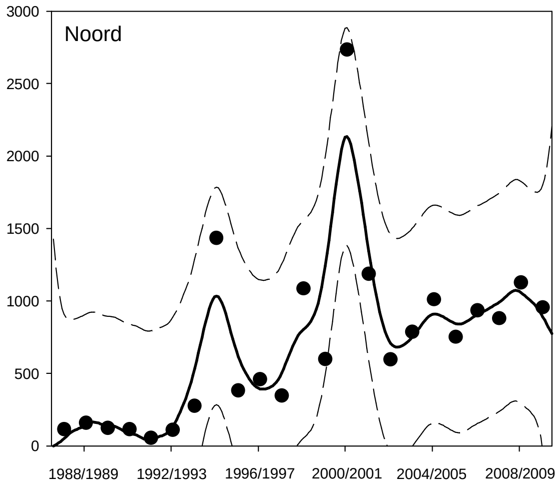

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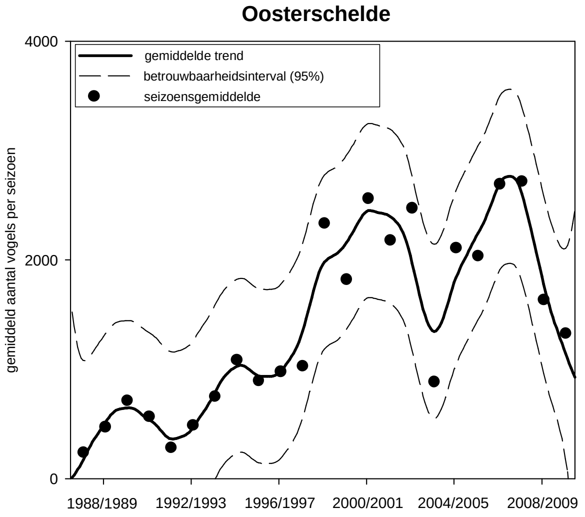
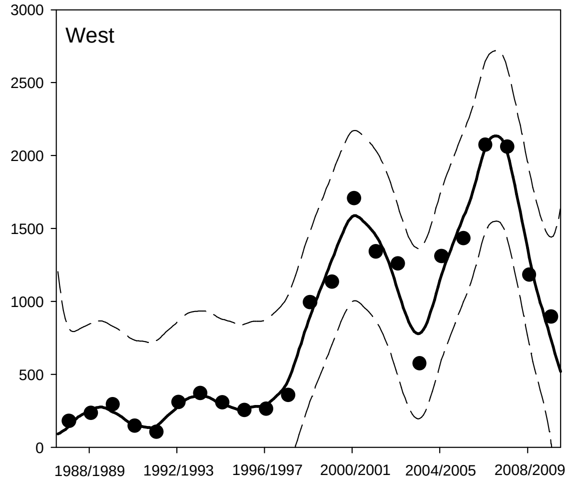
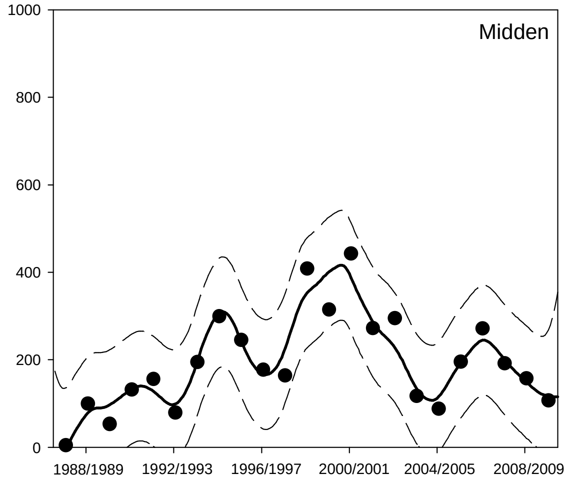
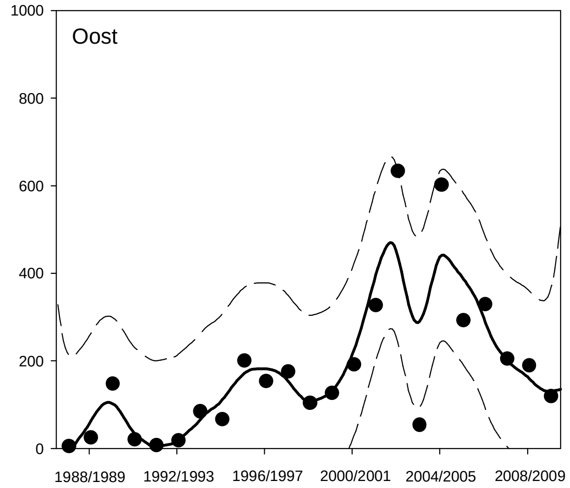
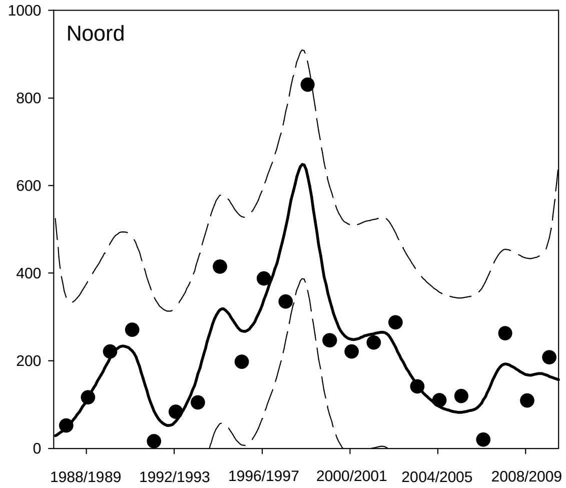
Goudplevier



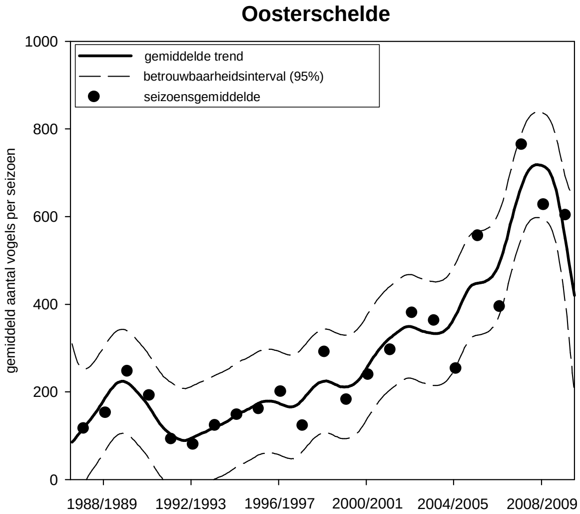


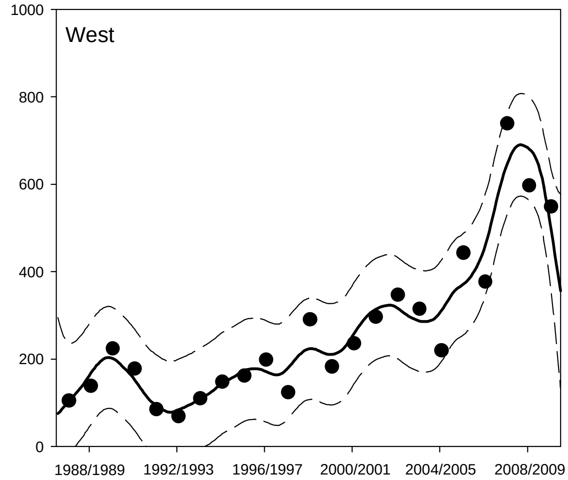


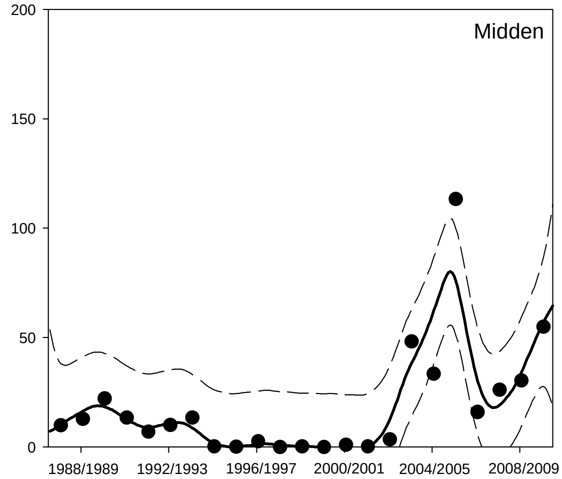


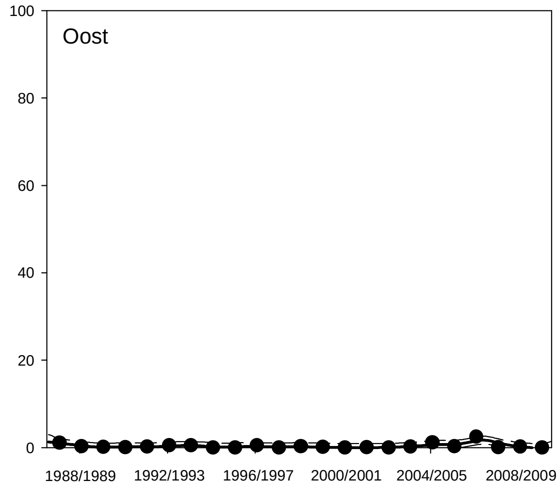


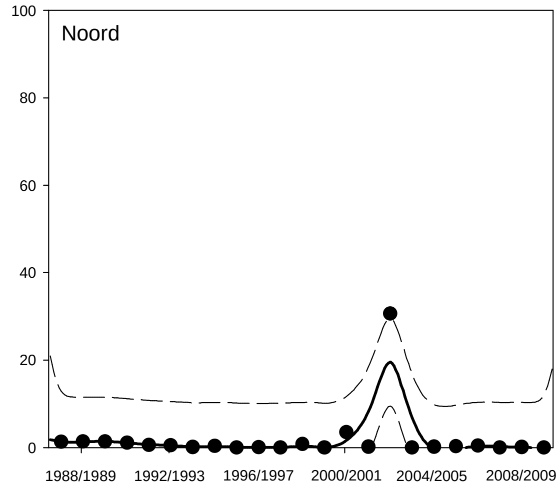
Drieteenstrandloper











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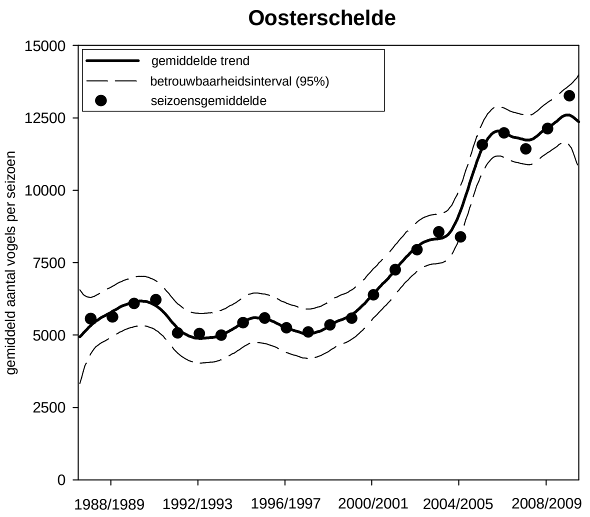

Oosterschelde
gemiddelde trend
betrouwbaarheidsinterval (95%)
seizoensgemiddelde
gemiddeld aantal vogels per seizoen
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1992/1993
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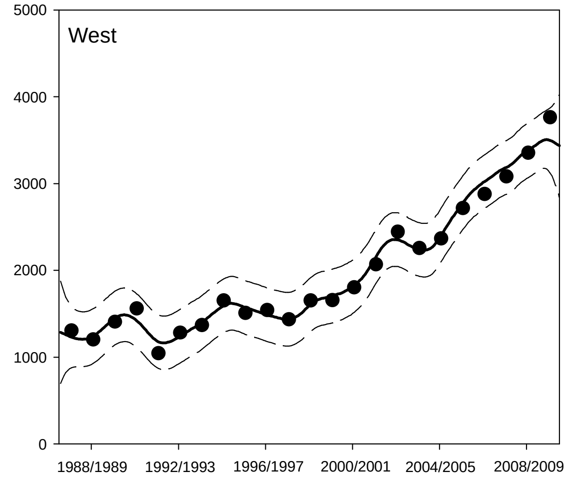
2000/2001
2004/2005
2008/2009



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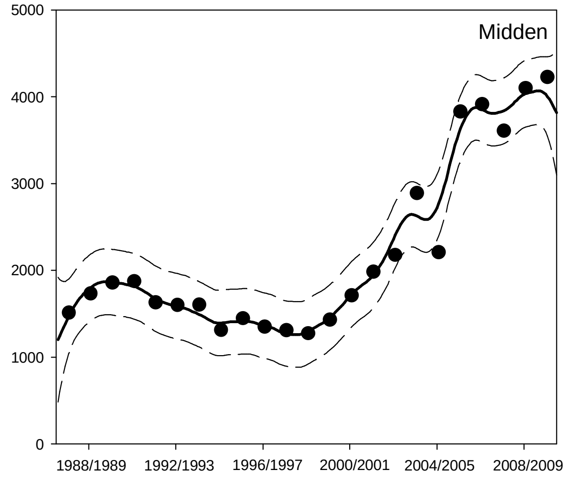

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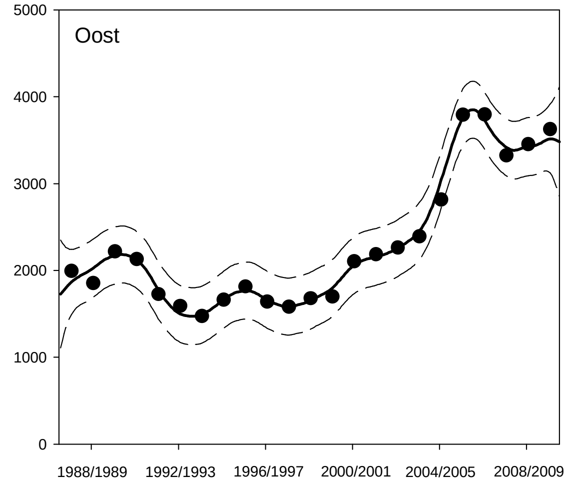

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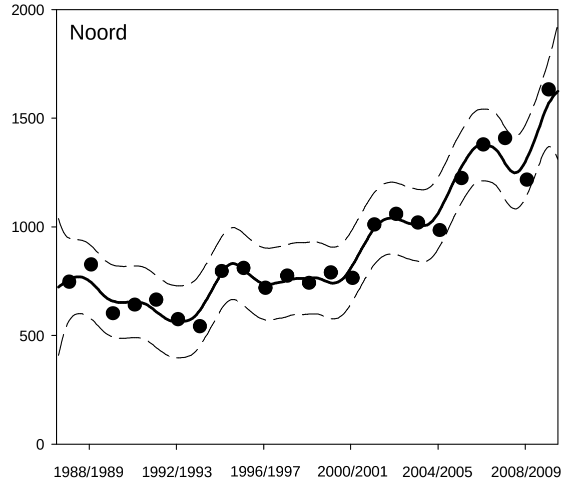

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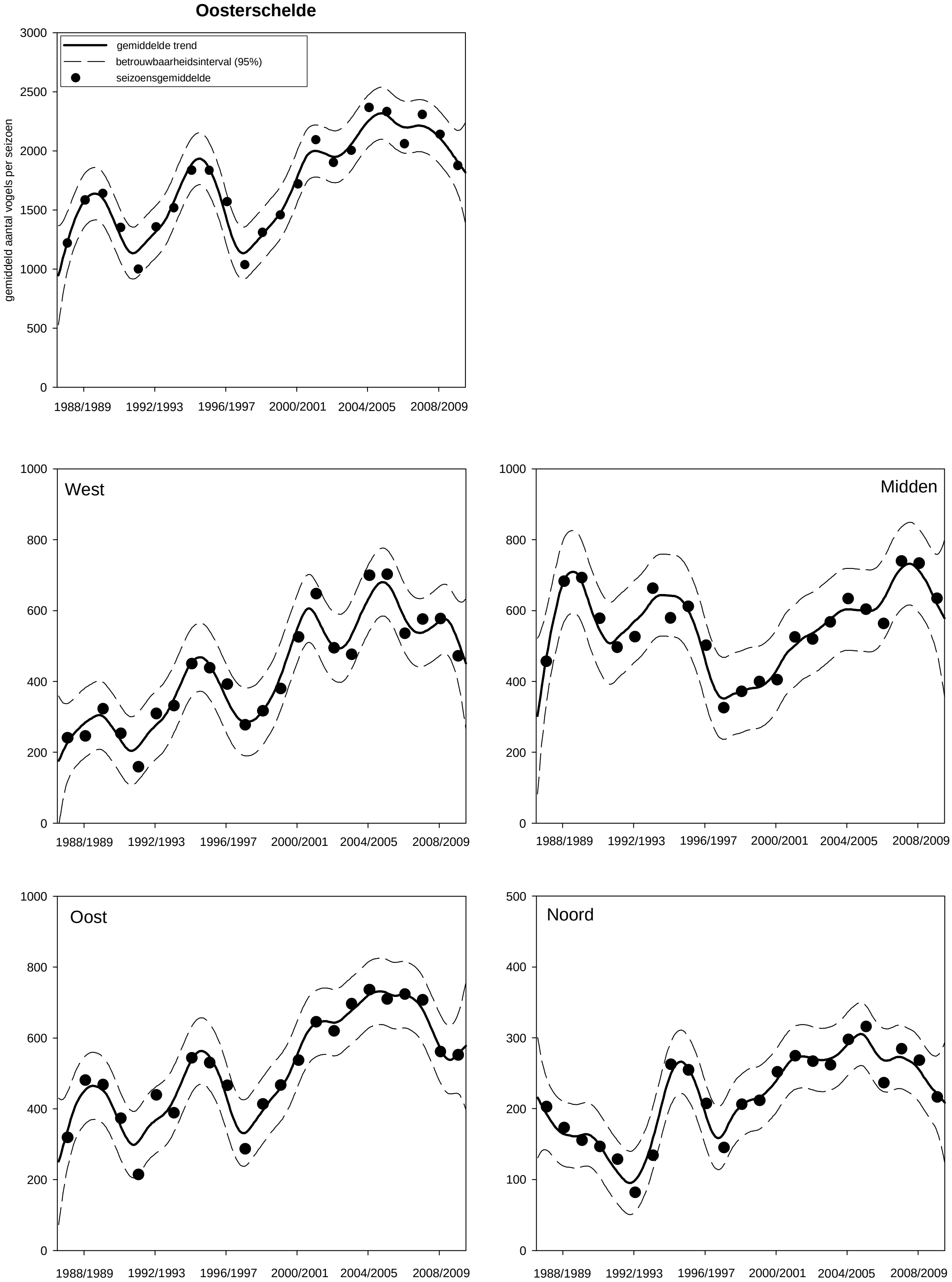
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betrouwbaarheidsinterval (95%)
seizoensgemiddelde
gemiddeld aantal vogels per seizoen
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2004/2005
2008/2009
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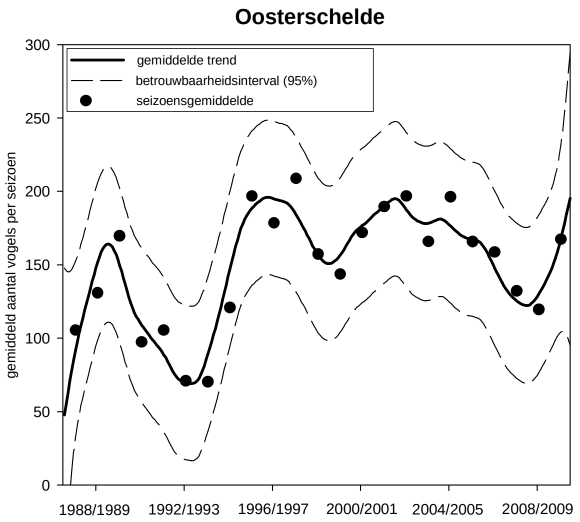
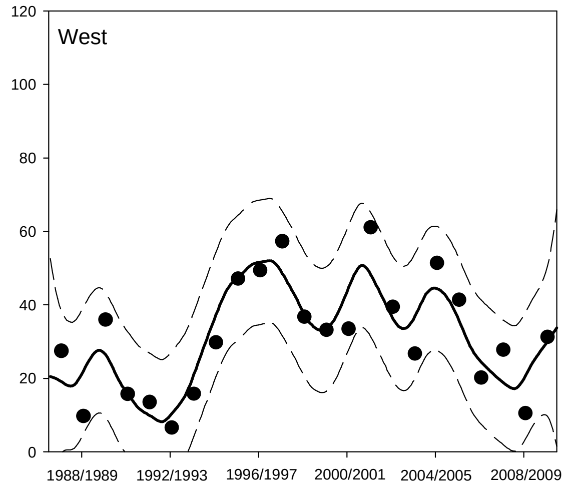
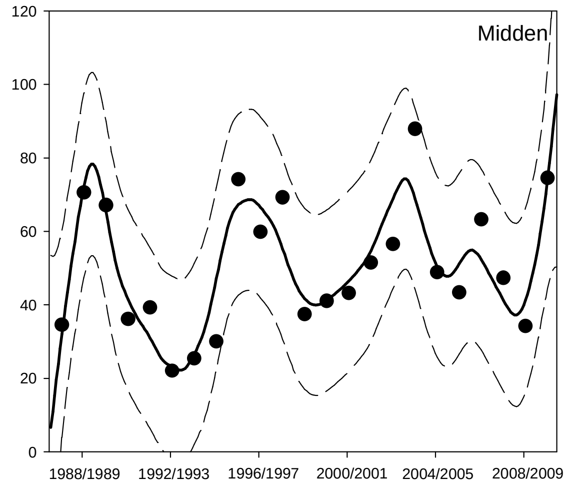
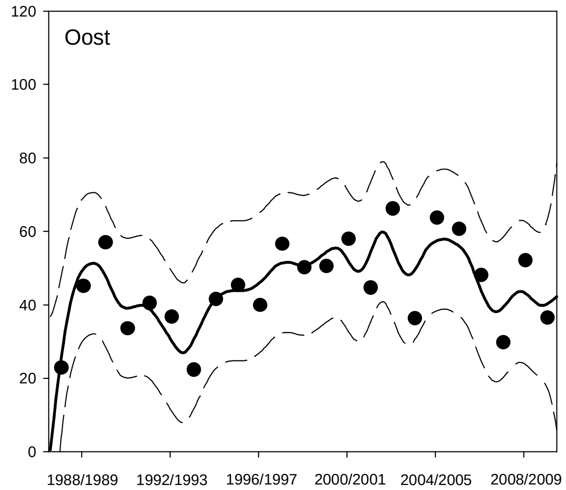
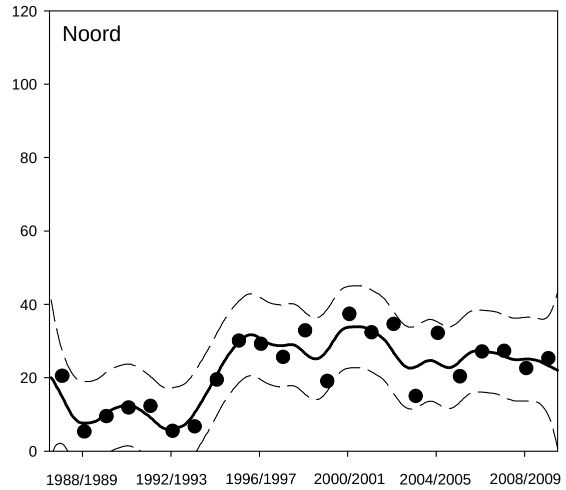


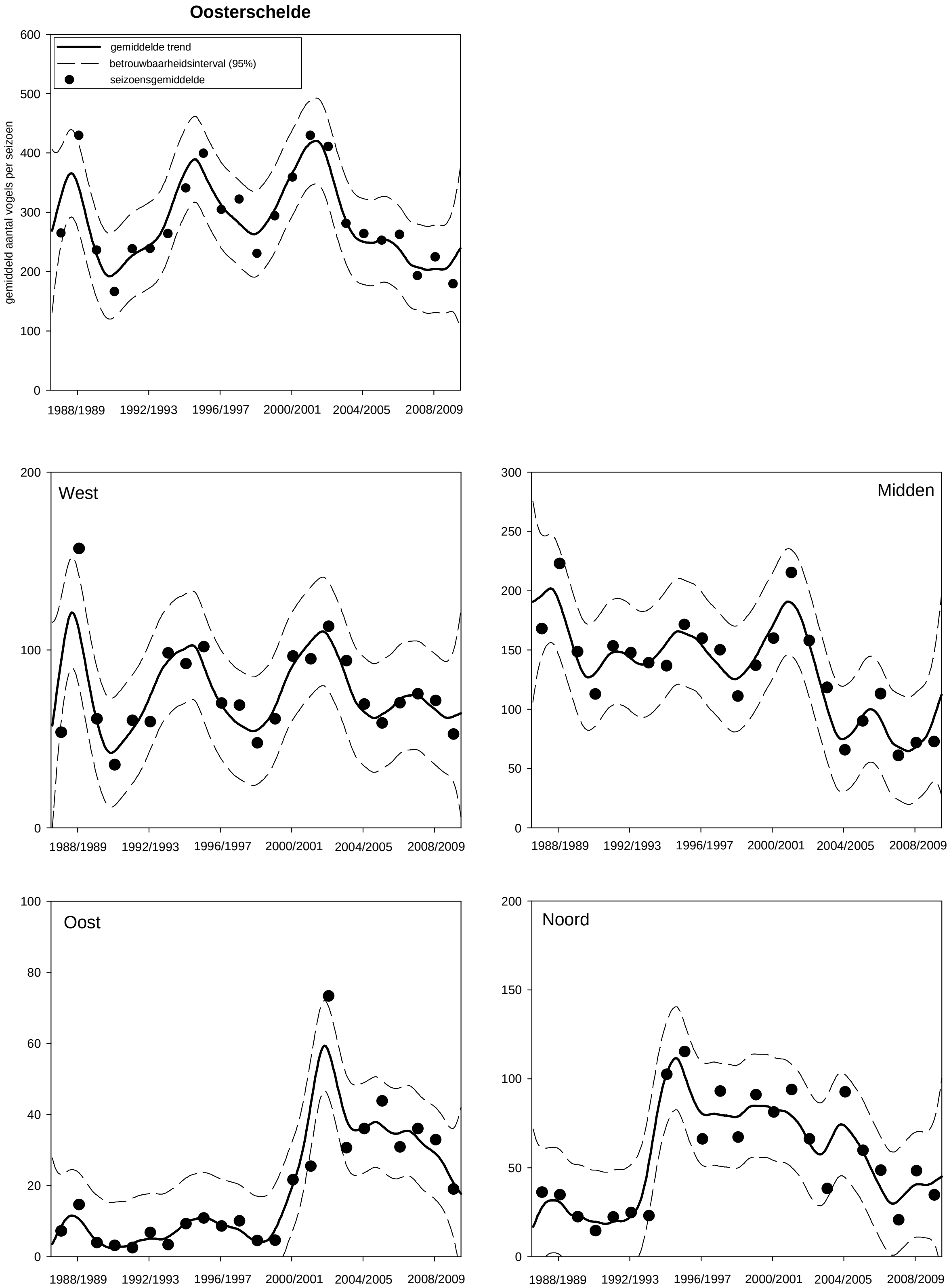




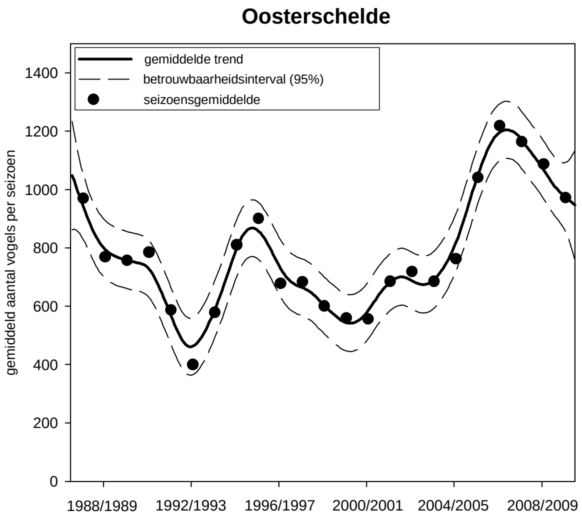




Zwarte Ruiter



Steenloper



Oosterschelde
gemiddelde trend
betrouwbaarheidsinterval (95%)
seizoensgemiddelde
gemiddeld aantal vogels per seizoen
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1988/1989
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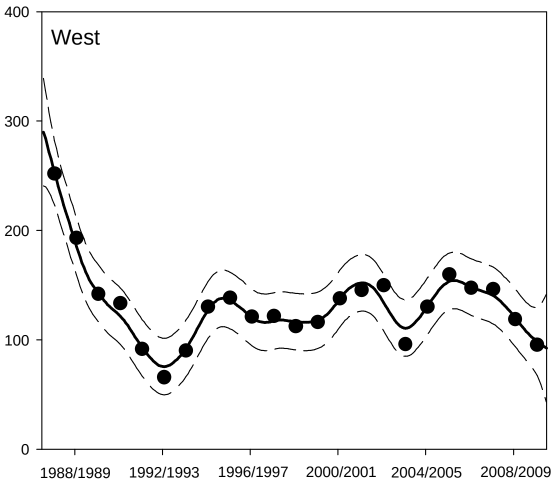
1996/1997
2000/2001
2004/2005
2008/2009



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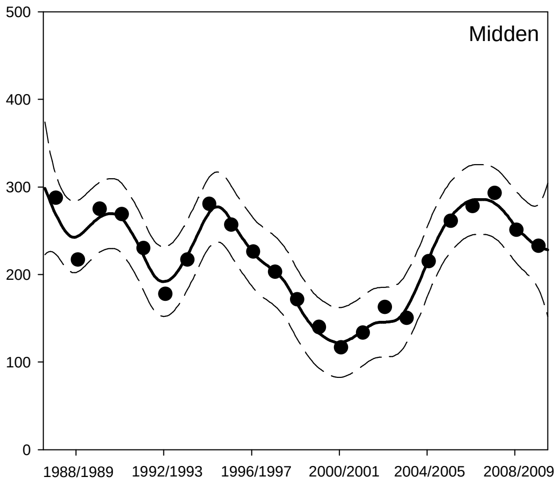

Midden
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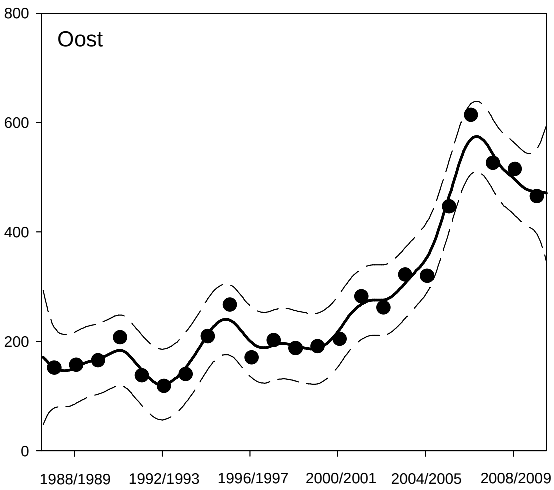

Oost
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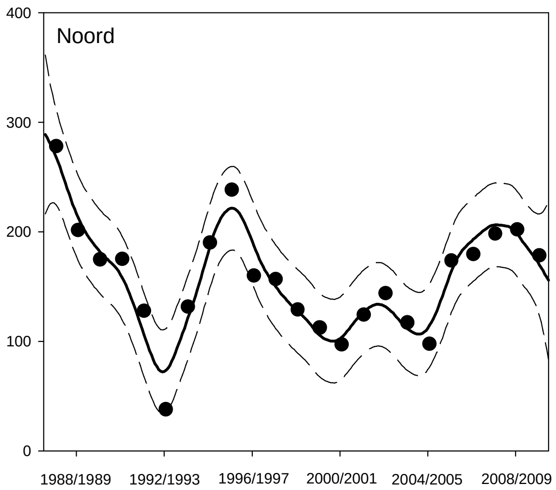

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