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Modelling the distribution of waders in the Westerschelde

What is the predictive power of abiotic variables?

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Modelling the distribution of waders in the Westerschelde

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Summary	A variety of land and water development projects have been and are being executed in the Westerschelde. This report recounts the attempts to develop statistical models capable of describing and, more importantly, forecasting the effect of these projects on waders. Such models will prove useful when answering questions posed in the context of the Birds Directive and for MER. Studies show that the selected statistical method does not result in models suitable for effect forecasting. Recommendation for the near term is to develop, in addition to the current generation of statistical models, other (process oriented) models. Developmental costs for these models tend to run high but can produce, possibly in combination with the statistical models, enhanced effect forecasting
Samenvatting	In de Westerschelde zijn en worden diverse ingrepen gedaan. Dit rapport geeft een verslag van een poging statistische modellen te ontwikkelen waarmee het effect van deze ingrepen op steltlopers beschreven, en vooral, voorspeld kan worden. Dergelijke modellen kunnen een belangrijke rol gaan spelen bij het beantwoorden van vragen die bijvoorbeeld gesteld worden in het kader van de Vogelrichtlijn en bij de MER. Uit het onderzoek bleek dat de gekozen statistische techniek niet tot modellen leidt die zonder meer voor effectvoorspelling toegepast kunnen worden. Voor de toekomst wordt aanbevolen om naast de huidige generatie statistische modellen ook andere type modellen (procesgeoriënteerde modellen) te ontwikkelen. De ontwikkelkosten voor dit type modellen zijn vaak hoog, maar zij kunnen, eventueel in combinatie met de statistische modellen, de basis vormen voor een verbeterde effectvoorspelling.

Ver.	Originator		Date	REMARKS	REVIEW		APPROVED BY	
1	F. Twisk		6-6-2005	Final	B.J. Kater		J.A. van Pagee	

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ABSTRACT

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This report describes various models that predict the distribution of birds, mainly waders, feeding on the intertidal flats of the Westerschelde, SW Netherlands, during low tide. Abiotic predictor variables used in the models are e.g. emersion time, current velocity, silt content and salinity. Feeding densities of birds were determined from seven counts covering an entire low water period in 71 study plots at four locations in 2003 and 2004. Abiotic predictor variables were either measured in the study plots or derived from GIS-maps. Generalized linear modeling (GLM) was employed to fit models with total number of foraging hours of a particular bird species as the dependent variable. The predictive power, as judged from the explained deviance, was high for many of the models, but they performed poorly when the predictions were validated with low tide counts in other areas and high tide counts covering the entire Westerschelde. This mismatch was partly due to the fact that the models often predicted very high bird densities for abiotic conditions that were relatively rare in the Westerschelde and did not occur in the study plots. It was also investigated whether adding information on actual macrozoobenthos densities could improve the predictive power of the models. Generally, this was not the case, but the distribution of Oystercatchers showed a good correlation with the Cockle stocks.

Keywords: Westerschelde, habitat correlations, abiotic predictor variables, distribution model, generalized linear model (GLM), Shelduck, Oystercatcher, Avocet, Ringed Plover, Grey Plover, Curlew, Bar-tailed Godwit, Redshank, Dunlin, Sanderling, Knot

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Preface

This report describes the results of a project initiated by the Rijkswaterstaat National Institute for Coastal and Marine Management / RWS RIKZ under contract RKZ-1267 dealing with the development of models that predict the distribution of several bird species over the tidal flats of the Westerschelde during low tide. Alterra BV was the chief contractor and Bureau Altenburg & Wymenga and the Netherlands Institute of Fisheries Research (RIVO) were subcontractors.

RWS RIKZ supplied GIS-maps on abiotic predictor variables and took charge of analyzing the sediment samples. In the course of the project there were also regular meetings with employees of the RWS RIKZ (Jaap Graveland, Belinda Kater, Peter Meininger and Fred Twisk) to discuss the progress of the project. Throughout the project, Fred Twisk invested much effort. He also wrote the sections on the benthic sampling and the validation.

Alterra was in charge of the project as a whole, and the subtasks of handling the data, modelling and reporting. Elze Dijkman and Jenny Cremer were in charge of the database and making GIS-maps. Bert Brinkman and Erik Meesters performed the statistical modelling. Bruno Ens was the project leader.

Allix Brenninkmeijer, Marcel Kersten and other employees of Bureau Altenburg & Wymenga staked out the plots, performed the bird counts and took sediment samples. To reach study sites completely surrounded by water, they employed AquaTerra, who had a boat (the "Snoek") with an erectable hide, which was especially constructed for the project.

Josien Steenbergen from the Netherlands Institute of Fisheries (RIVO) developed a Cockle habitat model on the basis of their regular survey data and abiotic information provided by RWS RIKZ.

Summary

To help find the optimal balance between nature conservation, economic development and human safety in the Westerschelde, the Rijkswaterstaat National Institute for Coastal and Marine Management / RWS RIKZ has initiated a major project entitled ZEEKENNIS. This project seeks to increase the understanding of the physical and ecological processes that operate in the Westerschelde to improve predictions of the consequences of various human activities. The ZEEKENNIS project is divided into several themes, one of which deals with the birds that feed on the intertidal flats during low tide. Present predictions of human impact on birds depending on the flats of the Westerschelde, do not include emersion time as an important variable. Yet, emersion time is almost certainly a very important variable for the birds, as it determines how long they can feed on the flats. Other habitat variables may determine prey availability. This report describes the progress made in developing a tool to predict changes in the distribution and the numbers of birds as a result of man-induced changes in the morphology of the estuary.

The primary aim of the study was to use a correlation approach to develop models that directly link the feeding densities of the birds to abiotic features of the estuary that are potentially changed by human activities under study (mainly dredging and dumping of sediment).

A total of 63 study plots (later increased to 71) measuring approximately 50 by 50 m were staked out on the flats, spread over four different locations in the Westerschelde: Hooge Platen, Paulinaschor, Plaat van Baarland and Rug van Baarland. On seven dates between autumn 2003 and autumn 2004, the birds were counted during an entire low water period. The summed number of foraging hours of a particular bird species in a plot during one count was the dependent variable in our models.

Most abiotic variables (current velocity, emersion time, height and salinity) were derived from GIS maps provided by RWS RIKZ. Sediment composition (silt content and median grain size) was measured in the plots, as well as derived from GIS maps.

The original contract did not include taking samples of the benthic fauna in the plots. This additional information was collected by an institute outside the consortium and this information became available near the end of the project. During the project, prey choice of the birds was sometimes noted and financial resources were reallocated to allow a proper analysis of these observations.

It was hoped to obtain sufficient data to construct models for the following bird species: Shelduck *Tadorna tadorna*, Oystercatcher *Haematopus ostralegus*, Avocet *Recurvirostra avosetta*, Ringed Plover *Charadrius hiaticula*, Grey Plover *Pluvialis squatarola*, Knot *Calidris canutus*, Sanderling *Calidris alba*, Dunlin *Calidris alpina*, Bar-tailed Godwit *Limosa lapponica*, Curlew *Numenius arquata* and Redshank *Tringa totanus*. Too few

Avocets fed in the plots to build meaningful models. Sanderlings were sufficiently abundant during only one counting period.

We used Generalized Linear Modelling (GLM) to obtain models relating bird usage to abiotic variables. The deviance that was explained by these regression models for individual counting dates was generally higher than the deviance that was explained by models where all the data were lumped and where it was assumed that birds only changed their number in the course of the season, but not their distribution. However, in a way, the results of the monthly models were "too good to be true". The high explained deviances found when calculating these models, could be due to overparameterization. Perhaps, we had too many parameters and too few plots to produce meaningful models for a single count. We therefore assumed that the densities of the birds varied in the course of the season, but that this did not affect the basic relationship between bird usage and the abiotic predictor variables. For the majority of species, these models still explained more than 50% of the deviance.

Many of the abiotic variables were highly correlated, so we could use only a subset. In making this selection, we also took account of the fact that variables that are measured on a regular basis in the Westerschelde are more useful in predictive models, than variables that require a special effort to obtain measurements. For this reason, when deciding which of the two correlated variables current velocity or silt content should be incorporated in the models, we preferred current velocity. Depth and emersion time are also highly correlated, and in this case we preferred emersion time, as it is the more meaningful variable from the point of view of the birds.

Thus, we ended up with a model with the code name **Y3VM** that was based on three abiotic predictor variables (emersion time, current velocity and salinity) and monthly variation in the abundance of the birds, but not in their distribution. When this model was validated with counts in other low tide feeding areas and with counts made during high tide, the results were rather poor for the majority of bird species. In many cases, many more birds were predicted to occur than actually did. Close examination revealed a major problem with this model. For some abiotic predictor variables, the predicted bird hours steeply increased for either very low or very high values of the predictor variable. Thus, very high bird usage was predicted for relatively rare habitats where we did not have measurements. Since it was not possible to collect additional data in these rare habitats, this situation could not be remedied in a fundamental way. All we could do was to investigate if slightly different modelling approaches might alleviate the problem. Inspection of the data and the model suggested that in several cases a few data points with high bird usage were responsible for both the high explained deviance and the undesirable shape of the model. To minimize the effect of such outliers, we grouped the data by summing foraging hours of the birds for classes of emersion time and current velocity. This led to a model with the code name **GSY2VM** that was based on two abiotic predictor variables (emersion time and current velocity) and monthly variation in the abundance of the birds, but not in their distribution. The validation results were better for some species, but still rather poor for the majority of species.

As explained, the poor results of the validation were not due to the fact that the models had a poor fit to the data. In fact, for some species the model fit was spectacularly good. However, critics might argue that a very good correlation can still be a spurious correlation, and that what matters to the birds are not abiotic variables, but the stocks of the benthic food supplies. We therefore compared the performance of abiotic predictor variables with the performance of biotic (i.e. benthic) predictor variables. In most species, models with only abiotic variables explained more variation in bird usage than models with only biotic variables. When it was investigated whether adding biotic variables to a model with abiotic variables significantly improved the model fit, the answer was negative for most species, except for Redshank, Bar-tailed Godwit and Oystercatcher. In the case of Redshank and Bar-tailed Godwit the explained variance increased only by a few percent, but in the case of Oystercatcher, the explained variance increased by more than 10%.

Observations on Oystercatchers indicated that Cockles were the main prey for this species in the Westerschelde and the distribution of this species over the study plots was clearly determined by the density of Cockles, especially the larger size classes.

Summarizing, we succeeded in deriving models that can "explain" quite well the data that we collected to construct these models, i.e. explained deviances often exceeded 50%. However, the validation indicated that for many species, the predictive power of these models was rather poor. Reasonably reliable predictions can only be obtained for Dunlin and Grey Plover. These two species are both common and do not suffer from the problem that high bird usage is predicted for relatively rare habitats that we did not encounter in our study locations. Since we think that the partial failure of our study can be remedied, we see no need to abandon the idea that bird usage can be predicted directly from abiotic variables to a considerable degree.

The obvious solution to remedy the poor performance of models that predict high bird usage in habitats that are relatively uncommon is to selectively study bird usage in these rare habitats. The plots used for validation with low tide counts might be useful in this respect, as it turned out that they had combinations of emersion time and current velocity that we did not encounter in the plots used to construct the models. Additional counts are also needed to test if the birds systematically change their distribution pattern in the course of the season.

The above recommendations amount to a counting programme encompassing 15 study locations and at least 12 counts per year. The financial resources and the extra time needed to conduct this programme may be a problem. Some quick and cheap improvement of the models might be possible by including the low tide counts used for validation. To estimate the extent of the improvement the high tide counts can be used for validation, but for validation with low tide counts it will be necessary to collect new data.

An alternative option is available for the Oystercatcher. For this species, a model exists that can calculate how the birds will distribute their foraging effort with respect to a particular food supply. With some additional assumptions, the model can calculate the carrying capacity of a particular estuary. This model, called WEBTICS, is not built on correlations, but on knowledge of the processes known to govern the distribution of the birds (Rappoldt *et al.* 2004).

1 Introduction

The Westerschelde is an estuary with high natural values, including large numbers of birds feeding on the intertidal flats at low tide (Berrevoets *et al.* 2003). For this reason the area receives special protection from the EU Birds Directive and the EU Habitat Directive. At the same time the Westerschelde links the economically important port of Antwerpen to the open sea whereas high dikes protect polders, consisting of reclaimed land bordering the Westerschelde, against flooding. Thus, the natural values of the Westerschelde have been and still are under pressure from economic developments and the need to provide sufficient protection to the people living behind the dikes.

To help find the optimal balance between nature conservation, economic development and human safety, the Rijkswaterstaat Institute for Coastal and Marine Management / *RWS RIKZ* has initiated a major project entitled ZEEKENNIS. This project, which was commissioned by RWS Zeeland, seeks to increase the understanding of the interdependent physical and ecological processes that operate in the Westerschelde so that it may be possible to predict the consequences of various human activities. An obvious activity is dredging the Westerschelde to a greater depth, but ZEEKENNIS is not restricted to this activity. In fact, the aim is to predict the impact of any human activity that potentially influences the physical and/or ecological processes operating in the Westerschelde, including management and restoration projects. Scenario studies can be envisaged where it is investigated which locations are most suitable for restoration. Such scenario calculations are not part of ZEEKENNIS but could be part of the coming MER (environmental impact study) on the plans to substantially increase the depth of the Westerschelde.

The ZEEKENNIS project is organised around the themes depicted in Figure 1-1. At the knowledge and instruments level morphological and hydrological aspects are studied and morphological and hydrodynamical models built. The output of the models are maps, for instance of bottom level and current velocities, which are used as input for the ecological GIS-modules. Habitat maps for species of macrozoobenthos, fish, birds and marine mammals are produced by combining those maps with definitions of their habitat requirements. The instruments are used to simulate and predict effects of natural developments and human activities on the aspects 'safety against flooding, accessibility and natural qualities', which are the main management goals for the estuary. After integration the results can be used at the assessment and advisory levels, to support estuarine management decisions.

This project contributes to the knowledge and instruments level and deals with the birds that feed on the tidal flats during low tide. These tidal flats, and therefore the birds, are influenced by changes in the morphology of the estuary as a result of embankments in the past, widening of the shipping channel (dredging and dumping) and sea level rise. A tool is needed to predict changes in the distribution and the numbers of birds as a result of man-induced changes in morphology of the estuary.

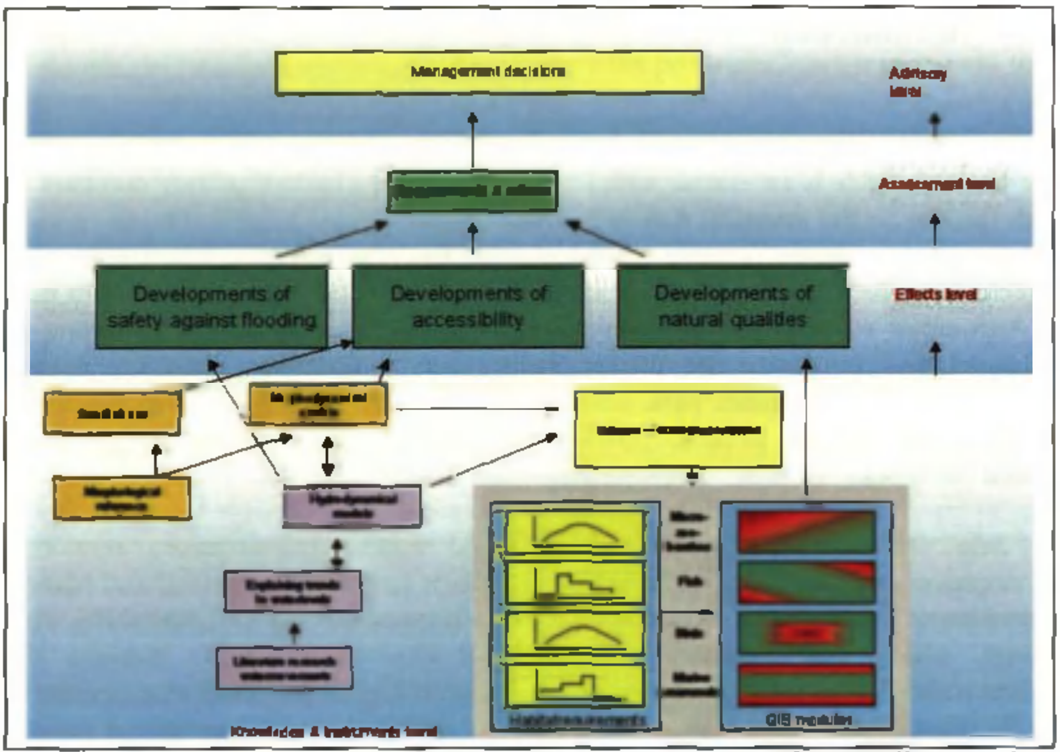

Figure 1-1. Depiction of the interrelationships between the various themes in the ZEEKENNIS *project. Source: RWS RIKZ.*

1.1 Making predictions: process-based versus correlation models

There are many ways to try to predict the impact of human activities on the birds that feed on the tidal flats during low tide. Ideally, we would have knowledge on how the human activities not only affect the morphology, but also on how this change in morphology impacts the distribution and population dynamics of each of the benthic animal species living at the surface of the flats. Finally, we should know how this change in benthic food stocks affects the foraging distribution and population dynamics of the various bird species. This is the approach advocated by Goss-Custard (1985), Meire (1993), Ens *et al.* (1994), Goss-Custard *et al.* (1995) and Sutherland (1996). Considerable progress with this approach has been made for two species of shellfish-eating shorebird: the Oystercatcher (Stillman *et al.* 2000; Stillman *et al.* 2001; Rappoldt *et al.* 2003a; Rappoldt *et al.* 2003b; Rappoldt *et al.* 2004) and the Knot (Zwarts & Blomert 1992; van Gils *et al.* 2003; van Gils & Piersma 2004). While such an approach based on a fundamental understanding of the various interlocking underlying ecological processes is the best guarantee for reliable predictions, the resources needed to build and parameterize a model for each of the wader species feeding on the tidal flats of the Westerschelde, would be immense. *Thus, the process-based approach is not suitable if resources are limited and a quick answer is needed.*

An alternative approach, requiring fewer resources, is to rely on correlation methods that directly link the feeding densities of the waders to abiotic features of the estuary that are potentially changed by the human activity under study. Clearly, shorebirds eat prey items, not abiotic variables. However, the density and the availability of the prey items are likely to be linked to abiotic variables like sediment composition and emersion time. We may expect birds to become adapted to the habitat where they most commonly feed and this will reinforce their preference for that habitat. There is variation in the foot pressure between different bird species for instance, and the birds with the lowest foot pressure tend to feed on the softest substrates (Figure 1-2). Blomert (2002) reviewed the correlation approach and the available evidence, and concluded that there were good reasons to believe the approach to work, but that so far there were only three empirical studies conducted along these lines.

One of these studies was by Brinkman & Ens (1998), who successfully predicted the effects of soil subsidence and sea level rise on the waders feeding on the intertidal flats of the Dutch Wadden Sea; see Ens & Brinkman in Oost *et al.* (1998). The approach did not work for all species, but for a majority of species feeding densities in late summer showed clear, often bell-shaped, relationships with the abiotic variables silt content and emersion time. These relationships were obtained from data collected by Zwarts and co-workers at low tide in a small study area along the Frisian coast (Zwarts 1988; Blomert 2002). Given the restrictions with regard to size and geography of that study area, it was all the more surprising that when the models were used to predict the number of birds in the Dutch Wadden Sea as a whole, these numbers were in many cases in the same order of magnitude as the numbers counted during high tide (Meltofte *et al.* 1994). *Thus, the correlation approach may be a feasible approach to apply to the Westerschelde.*

If the relationship between habitat characteristics and bird densities did not depend on the geographical area, the Wadden Sea model might simply be used to predict densities in the Westerschelde. However, a first trial with the distribution models based on data from the Wadden Sea Brinkman & Ens (1998) showed that the resulting distribution maps did not resemble the patterns observed by Van Kleunen (1999) in the Westerschelde (RWS RIKZ, unpublished). Both the models and observations regarded bird densities at low tide. However, the models where mainly based on late summer observations, whereas the data reported by Van Kleunen were for the mid-winter situation. One example is shown in Figure 1-3: the relative distribution of Grey Plover in the model shows densities in the mid and eastern area that are much higher than observed. This mismatch between predictions and observations provided further support to follow the advice of Blomert (2002) to initiate empirical investigations in the Westerschelde itself on the relationship between the feeding densities of birds and abiotic variables characterizing the tidal flats. *Thus, models specific to the case of the Westerschelde need to be built.*

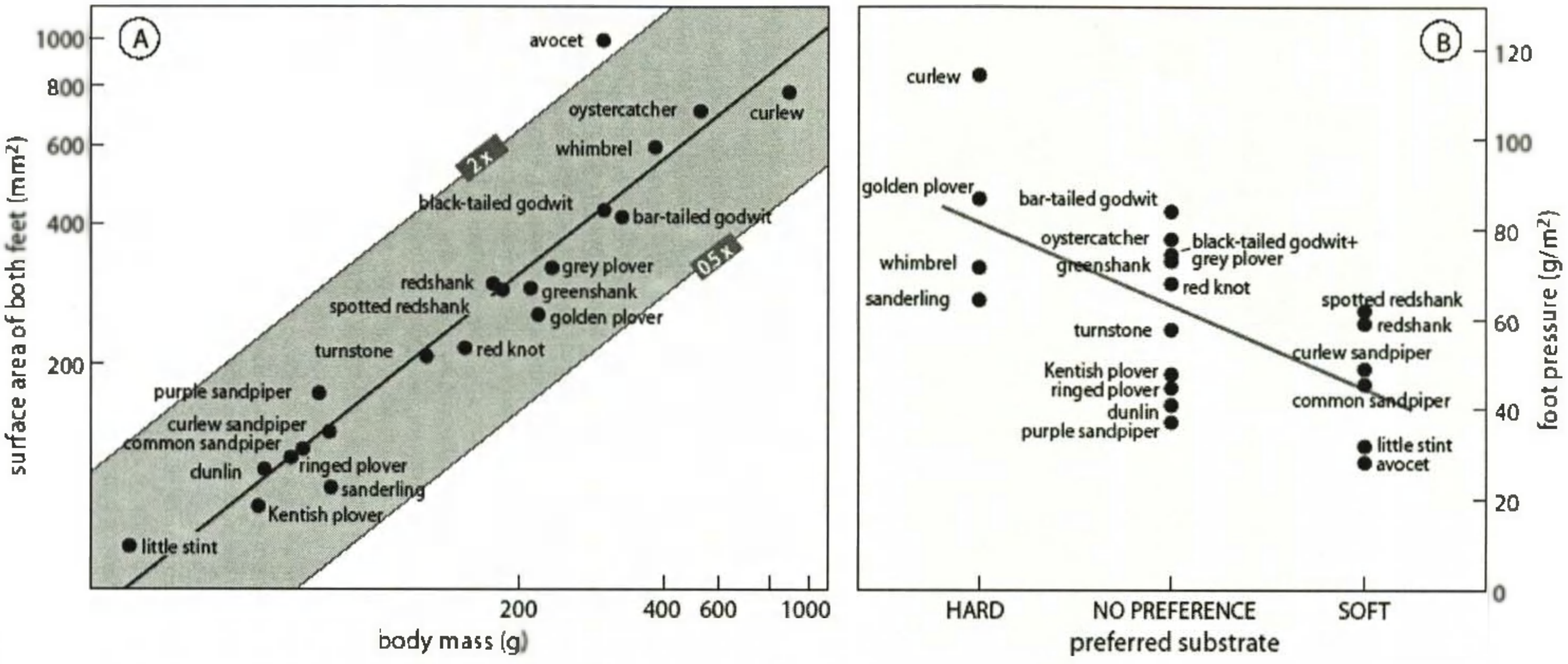

Figure 1-2. (a) Relationship between surface area of both feet (mm²) and body mass for selected wader species. (b) Foot pressure (g/m²) in relation to the softness of the preferred feeding substrate. From: Van de Kam et al. (2004).

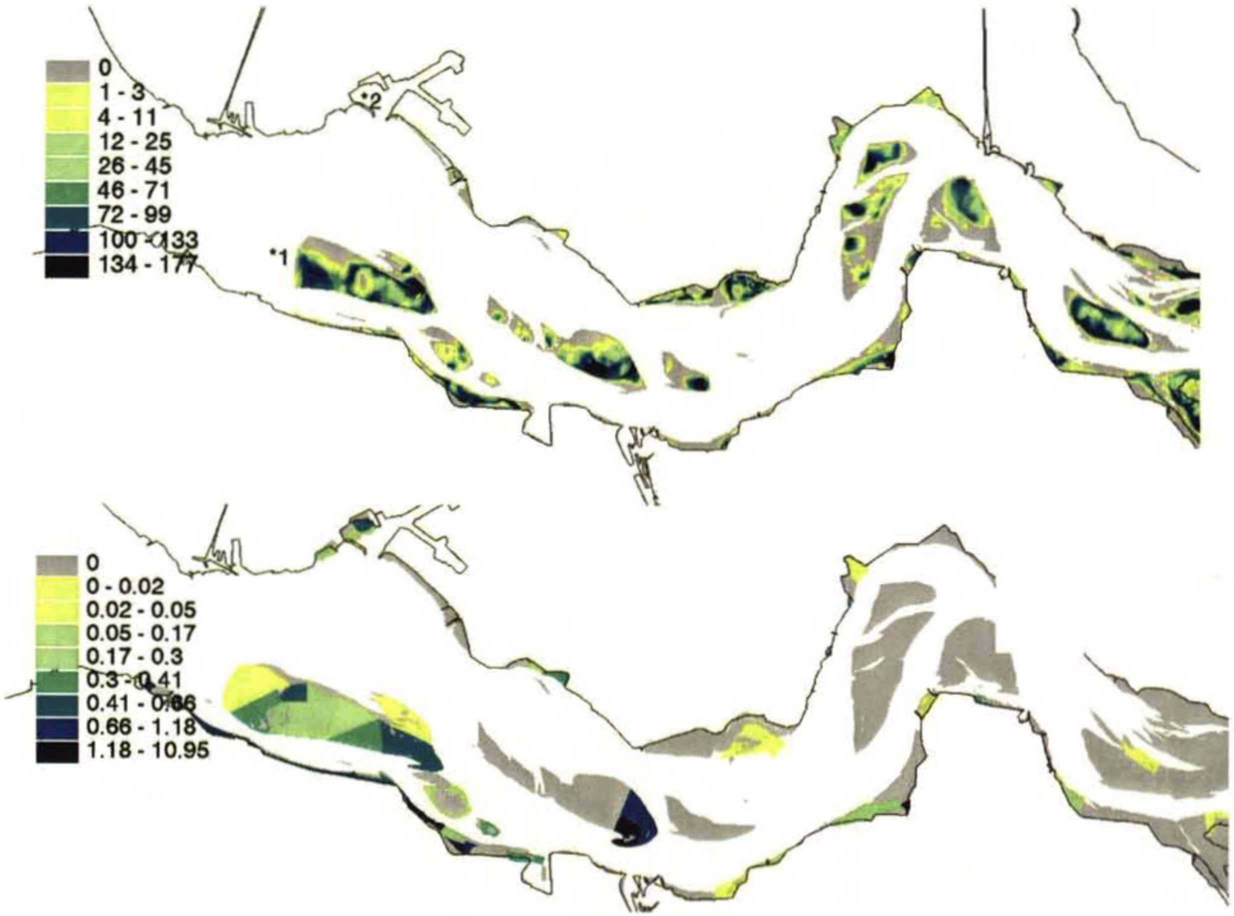

*Figure 1-3. Distribution of Grey Plover predicted by a distribution model derived for the Wadden Sea by Brinkman & Ens (1998) (top; number of birds per hectare * 1000) and as observed by Van Kleunen (1999)(bottom; number of birds per hectare). *1 and *2 in the top map are no-data areas. See text for further explanation. Source:* RWS RIKZ.

1.2 Modelling approach

1.2.1 Foraging hours as the dependent variable

The aim of the study was to relate the feeding densities of the birds to environmental variables like sediment type and emersion time as was done for instance by Scheiffarth *et al.* (1996), Yates *et al.* (1996), Brinkman & Ens (1998) and Granadeiro *et al.* (2004). This required the derivation of quantitative relationships between environmental variables (the predictor variables) and the usage of the study plots by the birds (the dependent variable), which we measured as the number of foraging hours summed over a tide. This variable does not distinguish between a small number of birds feeding a long time in an area and a large number of birds feeding a short time in an area. Our argument for this choice is that we take a population perspective. The average feeding time of the birds during a tide, multiplied by the number of birds, yields the total number of foraging hours that must be spent by the population to keep all individuals in the population healthy. The importance of a site to feed the population can therefore be gauged by the number of foraging hours spent in the site.

1.2.2 Statistical model

There are different ways to link bird usage to environmental variables via correlation. Yates *et al.* (1993), Yates *et al.* (1996) and Scheiffarth *et al.* (1996) all used standard multiple regression techniques. They performed logarithmic transformations of bird densities to satisfy the demand that the dependent variable has a normal distribution, and included quadratic terms of the predictor variables to allow for non-linear relationships. However, non-linear models can also be obtained using GLM (generalized linear modelling) and the advantage of this approach is that it is not necessary to assume that the dependent variable has a normal distribution (McCullagh & Nelder 1989). Many different distributions can be assumed for the dependent variable, including the Poisson distribution, which is the natural choice for bird counts. Therefore, Brinkman & Ens (1998) used GLM to relate bird densities to environmental variables.

A wide variety of relationships can be modelled via GLM, but any model must first be specified mathematically, before it is possible to test if it fits the data better than alternative models. According to Granadeiro *et al.* (2004) this is a major drawback and they advocate the use of Generalised Additive Modelling or GAM (Hastie & Tibshirani 1990). GAMs are data-driven regressions that yield smooth functions between the dependent variable and the predictor variable that can take on virtually any form. A demand on the models that we produced was that they could be employed in the program HABIMAP of the RWS RIKZ to draw the predicted distributions of birds under different scenarios. Since HABIMAP[1] requires explicit

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[1] A detailed description of HABIMAP can be found on the following internet site: http://gis.esri.com/library/userconf/proc98/PROCEED/TO850/PAP820/P820.HTM. A recent version of the software includes an option to use multiple regression models.

mathematical relationships between the dependent variable and the predictor variables, we could not employ GAM (Generalized Additive Modelling). Furthermore, as we will argue in the discussion, contrary to Granadeiro *et al.* we see no major advantages of GAM over GLM (Generalized Linear Modelling). Thus, we employed GLMs in this study to model the relationship between bird usage (measured as foraging hours) and habitat variables.

The variables that we included in the model were all local. That means that in principal all these variables can be measured in the site where the birds are feeding even though in practice most of the values were derived from GIS-based maps. Thus, we did not include distance to high tide roosting sites for instance, as this would involve an evaluation of roosting sites in the surrounding area. We did not differentiate between variables with regard to the time scale over which they may vary. Sediment composition for instance, may vary considerably on a short time scale. Current velocity will vary over even shorter time scales, i.e. within a tide. However, the current velocity that we used was the maximum for an average tide, derived from model calculations. A detailed description of the abiotic variables that were part of this study, including the reasons for inclusion or exclusion from the models, is provided in chapter 2.3.

1.3 Bird species studied

The designation of the Westerschelde as a Special Protection Area under the EU Birds Directive is primarily based on the large numbers of migratory waterbirds that depend on the area in winter and during migration in spring and autumn. The importance of the area for a particular species can be gauged from the percentage of the flyway population of that species that uses the area during its migrations. The usual criterion is 1% of the flyway population. Estimates of the flyway population of the various species of waterbirds are provided by Wetlands International (2002). According to Berrevoets *et al.* (2005) the norm is exceeded in the Westerschelde for 12 species of waterbirds. Some of the species, like Greylag Goose and Pintail, primarily occur in the eastern brackish part of the Westerschelde. This study deals with the species that depend on the intertidal flats of the polyhaline central and western part of the Westerschelde. These species are listed in Table 1-1.

Table 1-1. List of species studied. For those species that exceed the 1% level (i.e. the number of birds that comprises 1% of the flyway population) in the Westerschelde, it is indicated how many times and in which seasons this level was exceeded. From Berrevoets et al. (2005).

Species	season	Norm	autumn	winter	spring	summer	maximum
Shelduck		3000	4.0		1.3	4.5	4.5
Oystercatcher		10200	1.4				1.4
Avocet		730	1.1		1.0		1.1
Ringed Plover							
Grey Plover		2500			1.2		1.2
Knot							
Sanderling		1200	1.9		3.1		3.1
Dunlin	winter	13300	2.1	3.0			2.6
Bar-tailed Godwit							
Curlew		4200	1.4			1.0	1.4
Redshank							

1.4 Prey choice of the bird species studied

Even though the primary aim of the study was to link bird densities to abiotic habitat variables, it is useful to keep the prey choice of the birds in mind. Recently, Leopold *et al.* (2004) summarized the literature of the prey choice of the birds that feed on the tidal flats during low tide (Figure 1-4, Table 1-2). Most of the bird species feeding on the tidal flats of the Westerschelde depend mainly on worms. Only Oystercatcher and Knot depend mainly on bivalves and Curlew and Redshank have a mixed diet. More details on prey choice are given in the species accounts, including the prey observations conducted as part of this study. Compared to the other species, our accounts of prey choice are quite detailed for Oystercatcher and Curlew, as these are the two species on which we collected the largest number of prey observations in the Westerschelde.

It is clear that different bird species have different diets and since the various benthic animals differ in their distribution over the estuary (van Damme *et al.* 1999; Ysebaert 2000; Ysebaert & Herman 2002), it seems rather likely that the birds will also differ in their distribution over the estuary.

We made some observations on the type of prey that different bird species took, but we did not attempt to measure the intake rate of food and relate this intake rate to the density of prey and the density of competitors, i.e. we did not attempt to measure the generalized functional response as defined by Van der Meer & Ens (1997).

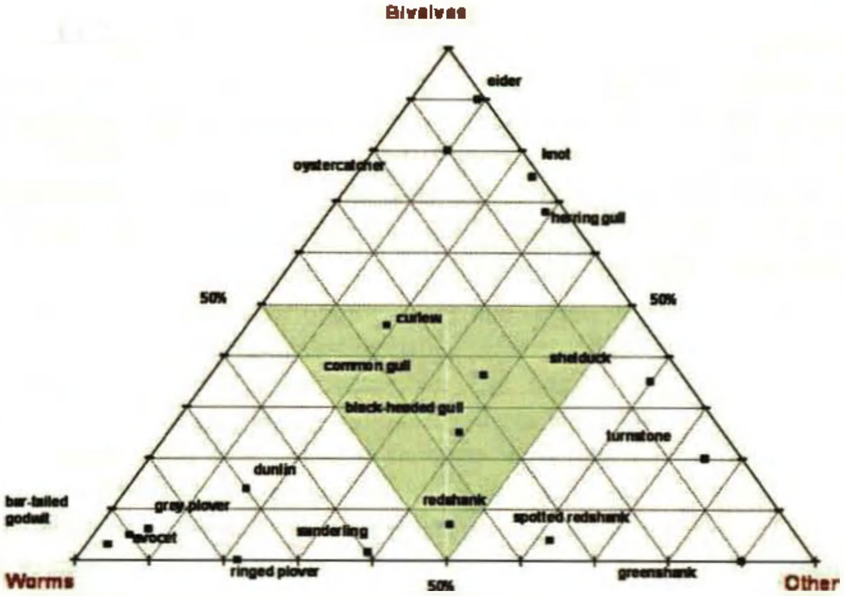

Figure 1-4. The diet of birds that feed on the intertidal flats during low tide. For each species the diet is represented by a dot in the triangle, where the distance to each of the corners represents the relative importance of bivalves (top), worms (lower left) and other prey (lower right) in the diet. The closer the data point is to the corner, the greater the relative importance of that type of prey in the diet. From Leopold et al. (2004)

Table 1-2. Summary of the prey choice in coastal areas of the bird species studied in this report as determined by Leopold et al. (2004) on the basis of a survey of the literature. The percentage values refer to an expert judgement, not a properly quantified biomass proportion.

Bird species	**Scientific name**	**Main prey**	**%-bivalves**	**%-Worms**	**%-other foods**
Oystercatcher	*Haematopus ostralegus*	Bivalves	80	10	10
Knot	*Calidris canutus*	Bivalves	75	1	24
Bar-tailed Godwit	*Limosa lapponica*	Worms	3	94	3
Avocet	*Recurvirostra avosetta*	Worms	5	90	5
Grey Plover	*Pluvialis squatarola*	Worms	6	87	7
Ringed Plover	*Charadrius hiaticula*	Worms	0	78	22
Dunlin	*Calidris alpina*	Worms	14	70	16
Sanderling	*Calidris alba*	Worms	1	60	39
Curlew	*Numenius arquata*	Mixed	46	35	19
Redshank	*Tringa totanus*	Mixed	7	46	47
Shelduck	*Tadorna tadorna*	Otherwise	35	5	60

1.5 Using a community approach

Instead of studying for each bird species how it distributes its foraging effort with respect to the different habitats, it is also possible to investigate how the community of birds differs in different habitats. We used Principal Component Analysis (PCA) and non-metric Multi-Dimensional Scaling to explore which combination of habitat variables yielded the best prediction. Because of the exploratory nature of this analysis we refer to Brinkman et al. (2005) for details and provide only a short summary of the main results in Appendix 1.

2 Field methods and statistical analysis

2.1 Choice and location of study sites

The rationale of the project was that different bird species prefer different foraging habitats. Thus, it was attempted to situate the study sites in such a way that each site covered a maximum diversity of habitats and that the combination of sites sufficiently covered all major habitats. For this selection procedure we had to rely on the MOVE1996 map, which distinguishes different habitats (or ecotopes as they are called in the legend of the map) on the basis of a suite of environmental characteristics (Withagen 2003). Given the dynamic nature of the Westerschelde, the map was rather old, which meant that the actual location of habitats could have changed considerably. We therefore also relied on visual inspection of the study site and the proposed study plots, to decide on the actual location of the study plots. Visual inspection was also necessary to decide if the selected study plots could be clearly seen from the central point. It turned out that ridges blocked the view of some plots on the Plaat van Baarland and high vegetation blocked the view of some plots on Paulinaschor. In both cases the location of the plots was changed. The project budget allowed for four study sites, whose general location is shown in Figure 2-1.

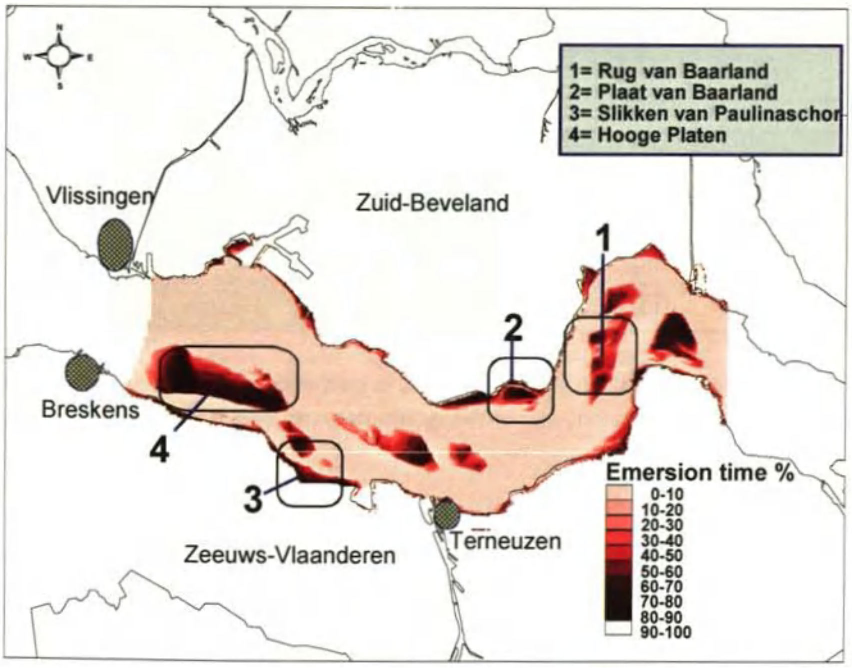

Figure 2-1. General location of the four study sites in the Westerschelde

In Figure 2-2 the location of the study plots within each site is also visualized. Based on personal experience with this type of study in other areas, we aimed for study plots measuring 50 x 50 m. This is a compromise between increasing the size of the plots, so that they contain more birds, and decreasing the size of the plots, so that they are more homogeneous with regard to the habitat variables under study. After an updated habitat map became available, it became clear that some important habitats were underrepresented in the original study plots. We therefore added four study plots at the "Rug van Baarland" site (see chapter 2.1.1) and another four study plots at the "Hooge Platen" study site (see chapter 2.1.4) in March 2004.

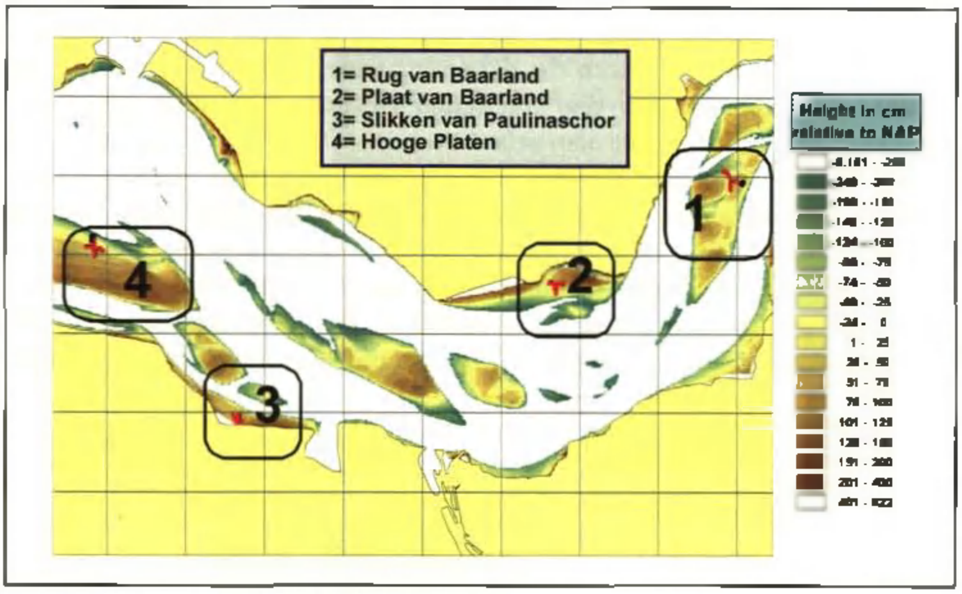

Figure 2-2. Location of the four study sites, including the actual location of the study plots in each site, in the Westerschelde.

2.1.1 Rug van Baarland

The study plots situated on the Rug van Baarland have emersion times ranging from 25% to 60% (Figure 2-3). Compared to the other sites, current velocities are high and it is therefore not surprising that the silt content of many plots is low. This is especially the case for the H-plots, which contain hardly any mud at all. The dynamic nature of these sites is also exemplified by megaripples, which occur there and are generally considered to be characteristic of highly dynamic areas. The plots K6, K7, K8 and K9 were added in March 2004, to increase the number of sites with short emersion times. These sites turned out to be muddier and bird densities were rather high. Photographs of the study site are shown in Figure 2-4.

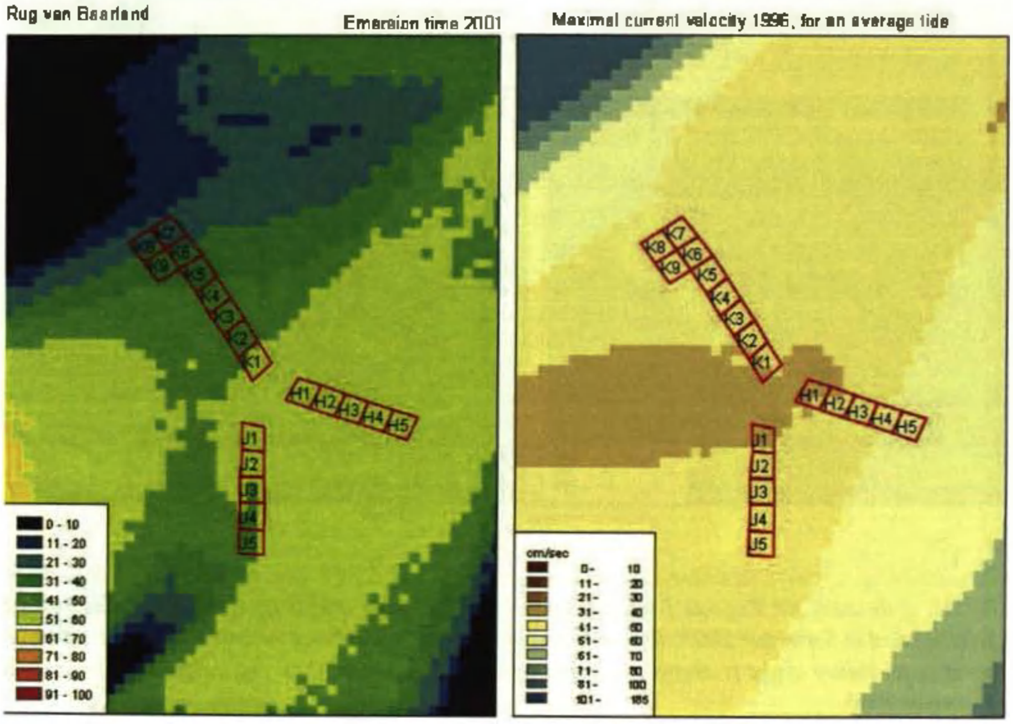

Figure 2-3. Location of the study plots at the study site Rug van Baarland with respect to (a) emersion time, and (b) maximum current velocity during an average tide.

Fig. 2.4c

Fig. 2.4b

Fig. 24c

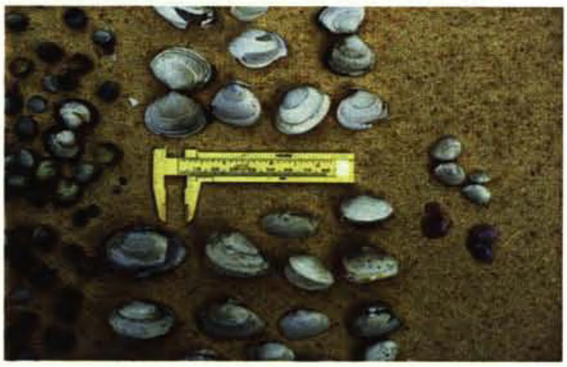

Fig. 2.4d

Figure 2-4. Pictures of the study site Rug van Baarland, taken by Fred Twisk. (a) Study plots designated H1 to H5 shortly after being exposed in September 2003. (b) Study plot H1 having been exposed for several hours on September 2003. (c) Close-up of the bottom of plot J1 shortly after being exposed in September 2003. (d) Shellfish remains collected in J-plots in September 2003.

2.1.2 Plaat van Baarland

With respect to silt and current velocity, the study plots on the Plaat van Baarland are intermediate between the Hooge Platen and Paulinaschor (Figure 2-5). Some of the plots are rather muddy, but other plots are sandier. Many little creeks run through the area. See also the photographs in Figure 2-6.

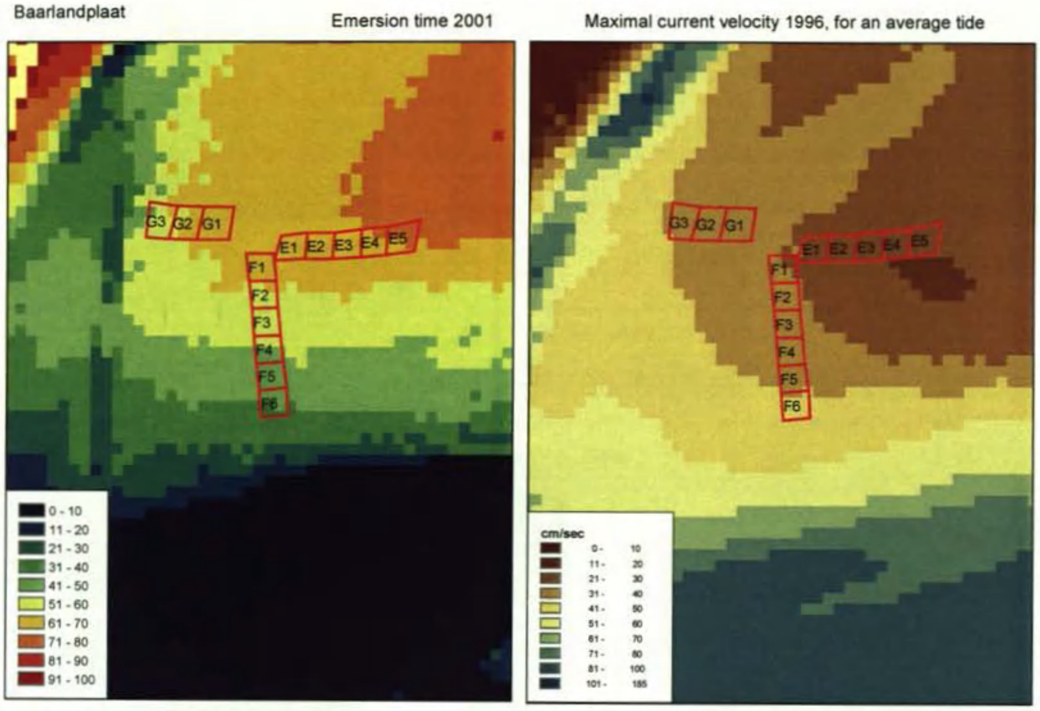

Figure 2-5. Location of the study plots at the study site Plaat van Baarland with respect to (a) emersion time, and (b) maximum current velocity during an average tide.

Fig. 2.6a

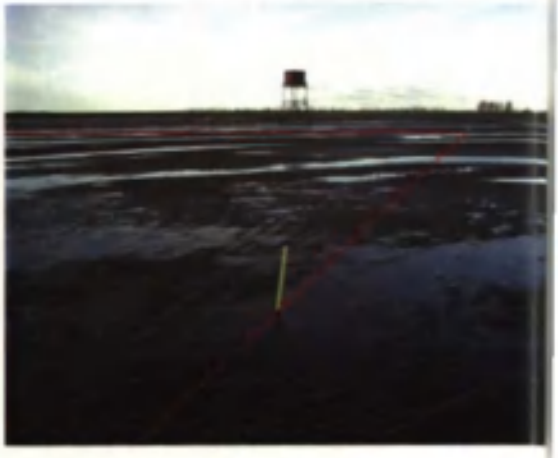

Fig. 2.6b

Fig. 2.6c

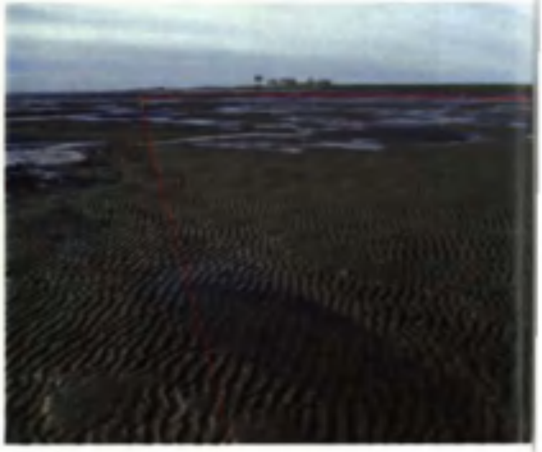

Fig. 2.6d

Figure 2-6. Pictures of the study site Plaat van Baarland taken by Fred Twisk. (a) Study plot F1 in September 2003. (b) Study plot F1 in November 2004. (c) Study plot G1 in September 2003. (d) Study plot E in November 2004.

2.1.3 Paulinaschor

The study plots on Paulinaschor include the sites with the longest exposure time, ranging from 60% to 70% (Figure 2-7). These plots are also very muddy and the higher plots border the saltmarsh (Figure 2-8).

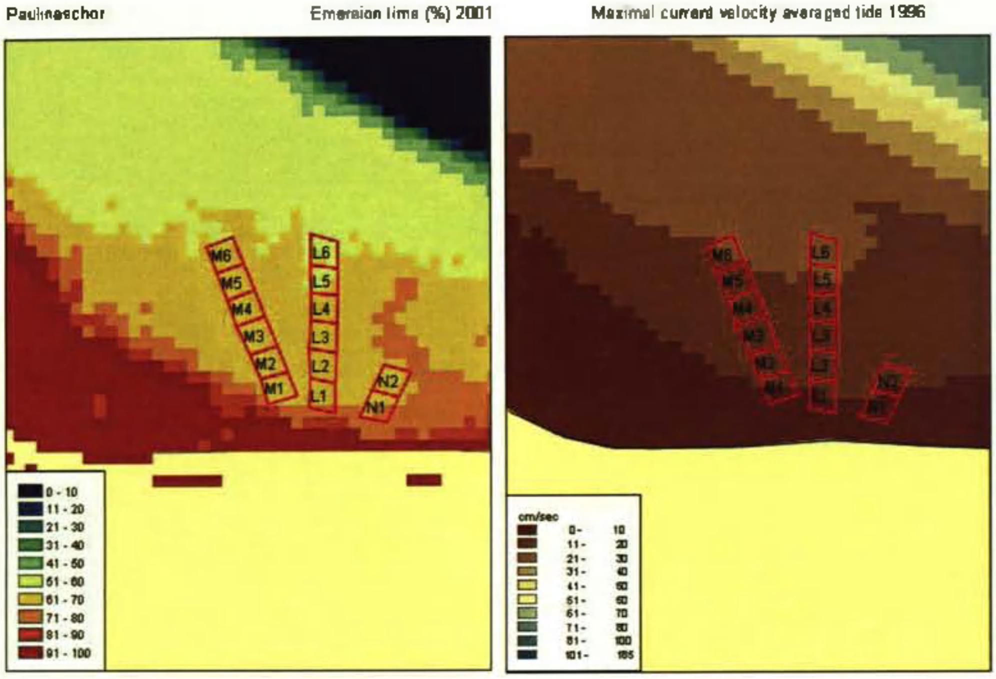

Figure 2-7. Location of the study plots at the study site Paulinaschor with respect to (a) emersion time, and (b) maximum current velocity during an average tide.

Fig. 2.8a

Fig. 2.8b

Fig. 2.8c

Fig. 2.8d

Figure 2-8. Pictures of the study site Paulinaschor taken by Fred Twisk. (a) M-plots in November 2004. (b) M-plots in November 2004. (c) L-plots in November 2004. (d) N-plots in November 2004.

2.1.4 Hooge Platen

Compared to the Rug van Baarland, the study plots on the Hooge Platen (Figure 2-9) cover the same range of depth, emersion times, median grain size and silt content, but current velocities tend to be lower. To increase the number of plots with short emersion time, the plots D6, D7, D8 and D9 were added in early 2004. These plots turned out to be very sandy and very few birds occurred there. Figure 2-10 shows some pictures of the study plots on the Hooge Platen.

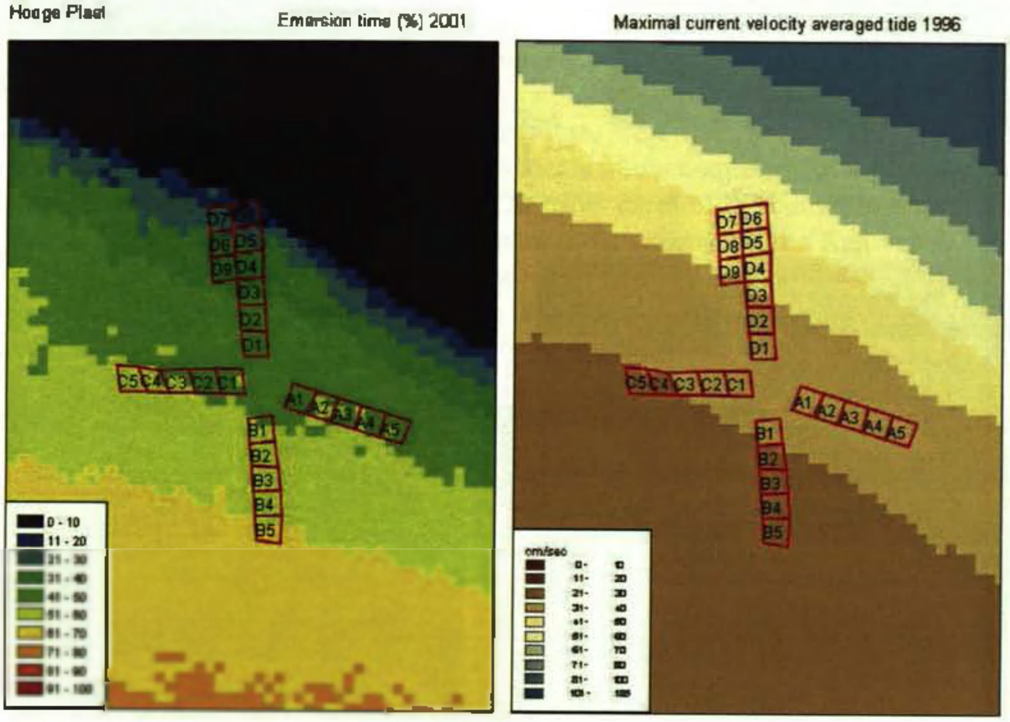

Figure 2-9. Location of the study plots at the study site Hooge Platen with respect to (a) emersion time, and (b) maximum current velocity during an average tide.

Fig. 2.10a

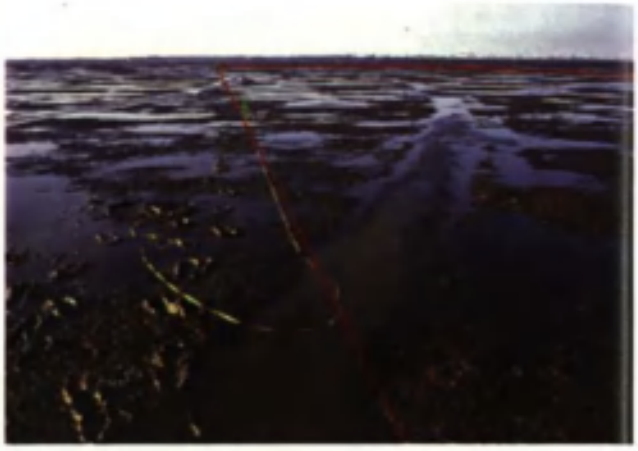

Fig. 2.10b

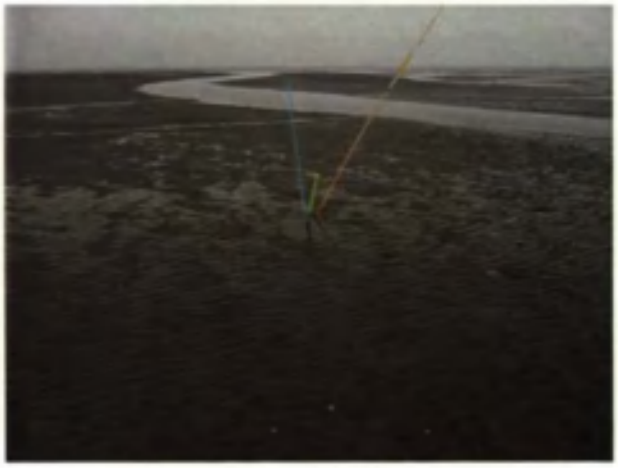

Fig. 2.10c

Fig. 2.10d

Figure 2-10. Pictures of the study site Hooge Platen taken by Fred Twisk. (a) Plot A4 in November 2004. (b) Plots B1, B2 and B3 in September 2003. Traces left by mechanized cockle boats are visible, but this was the only occasion where suction dredging may have affected some study plots. (c) Plot C5 in November 2004. (d) Plot D6 in November 2004.

2.2 Bird counts

At the Hooge Platen and the Rug van Baarland, bird counts were conducted from a boat which moored in the centre of the study site at the ebbing tide. This boat had a specially designed hide (3 m) that could be erected once the flat-bottomed boat was no longer rocked by the waves (Figure 2-11). The plots at the Plaat van Baarland were counted from a fixed hide (6 m) (Figure 2-12). The plots of Paulinaschor were counted from a car on the dike. Counts started when the first plot in a site exposed and ended when the last plot was covered again by the tide. In this way no birds were disturbed. The boat, which was only present on counting days, may have caused some disturbance, but we consider this unlikely.

The corners of the plots (measuring 50 by 50 m) were marked with plastic poles and with some experience it was possible to allocate all feeding birds to a particular plot. The plots were counted each half hour. The exact dates of the counts are listed in Table 2-1. The sites were counted on seven days, except for the Rug van Baarland, where unfavourable weather conditions prevented counts in both January and February 2004. The new plots D6 thru D9 and K6 thru K9 were counted from March 2004 onwards.

Figure 2-11. Photograph of the hide on top of the flat-bottomed boat that was used to count the study plots on the Hooge Platen and the Rug van Baarland. Picture taken by Marcel Kersten.

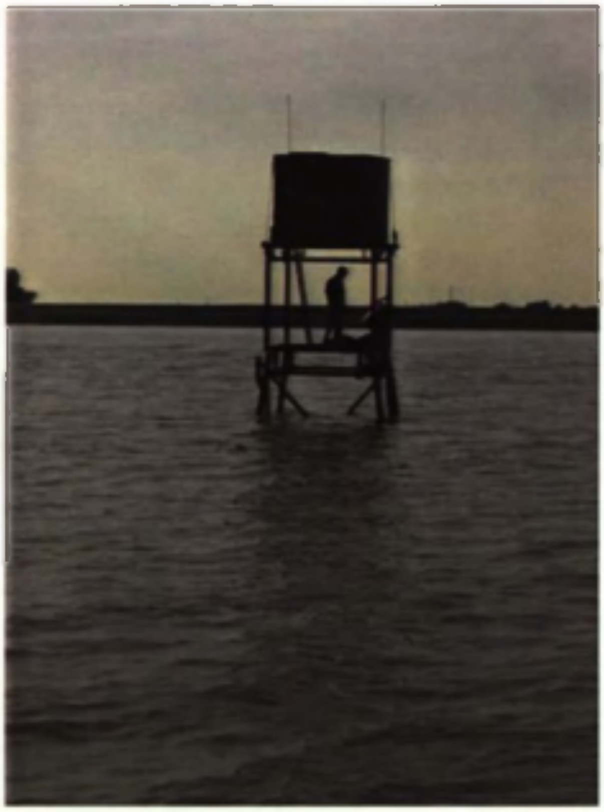

Figure 2-12. Photograph of the hide on the Plaat van Baarland. Picture taken by Bruno Ens.

Table 2-1. Dates on which the various sites were counted.

Year	Month	Hooge Platen	Paulina-schor	Plaat van Baarland	Rug van Baarland
2003	September	3	3	2	2
	November	14	13	12	13
2004	January		27	26	
	February	12			
	March	25	24	25	24
	April	23	23	22	22
	May	19	11	10	10
	September	3	3	2	2

2.3 Abiotic data

For each of the study plots, data on abiotic variables were either obtained from GIS maps, or from direct measurements in the plots. Table 2-2 summarizes the names with which the abiotic variables are designated throughout this report, the units in which they were measured, the source and a short description. As described in section 3.1, many of these variables are highly correlated. In section 3.1 we also discuss our arguments for including or excluding particular abiotic variables in our statistical modelling. Below, we will provide more detailed information on each of the abiotic variables.

Table 2-2. Description of abiotic variables that were used in this study. The data were either derived from direct measurements in the individual study plots (measured) or from geographically linking information in GIS maps to the plots (map).

Name	Data type	Unit	Description
Hmin	map	cm	Minimal depth (height) relative to NAP. Values taken from 20x20 m gridded map based on measurements in 2002
Hmax	map	cm	Maximal depth (height) relative to NAP. Values taken from 20x20 m gridded map based on measurements in 2002
Hmean	map	cm	Mean depth (height) relative to NAP. Values taken from 20x20 m gridded map based on measurements in 2002
Emin	map	% time	Minimum emersion time. Values taken from 20x20 m gridded map based on measurements in 2001
Emax	map	% time	Maximum emersion time. Values taken from 20x20 m grid gridded map based on measurements in 2001
Emean	map	% time	Mean emersion time. Values taken from 20x20 m gridded map based on measurements in 2001
Eclass	map	% time	Emersion time class of the centre of the plot. A value of 35 corresponds to an emersion time of 25-35%, 45 = 35-45% etc.
Salt	map	Psu	Salt content of the water at the centre of the plot. Values derived from map by RWS RIKZ on annual means around high water in 1992.
Dyn	map	(-)	Whether or not the plot should be classified as highly dynamic (value 1) or not (value 0) according to MOVE2001 habitat classification
M0	measured	µm	Mean median grain size. Samples were lumped per study plot and without pre-treatment analyzed with the Malvern Particle sizer 2000
S63	measured	% weight	Percentage of the sediment with a grain size <63µm. Samples were lumped per study plot and without pre-treatment analyzed with the Malvern Particle sizer 2000.
Sand	measured	µm	Mean mode of the grain size of the sand fraction.
Sfloat	map	% weight	Mean silt content (%<63 µ) according to the sediment map of the Westerschelde by Stelzer (2003), based on a combination of satellite pictures and data on 300 sediment samples
Vmean	map	cm/s	Mean current velocity during an average tide. Values taken from 20x20 m gridded map based on calculations for tides in 1996
Vspring	map	cm/s	Mean current velocity during spring tide. Values taken from 20x20 m gridded map based on calculations for tides in 1996

2.3.1 Sediment composition

When the 63 study plots were staked out in August 2003, four sediment samples to a depth of 5 cm were taken in each plot. The eight additional plots were sampled similarly when they were staked out in March 2004. For each plot the four samples were mixed and analyzed by RWS RIKZ according to the McLaren method with the Malvern particle sizer of the RWS RIKZ in Middelburg. The samples were not pre-treated (i.e. neither organic material nor calcareous material was removed). This will affect the resulting size distribution that is measured (Zwarts *et al.* 2004). To characterize this size distribution in a single variable, we used the median grain size (measured in µm) and the silt content (measured as % weight comprised by particles with a diameter less than 63 µm).

We also used silt content (measured as % weight comprised by particles with a diameter less than 63 µm) derived from a map produced by Stelzer (2003); see Figure 2-13. This silt content was determined from a combination of satellite pictures and

300 sediment samples. These samples were taken and analyzed in the same way as the samples from our study plots. The signal on the satellite picture only applies to the top millimetre or so of the sediment, so it is conceivable that there is only a weak correlation between this signal and the measured silt content of the top 5 cm of the sediment. the map probably depicts the composition of this thin top layer. The composition of the thin top layer is also quite variable on a short time scale.

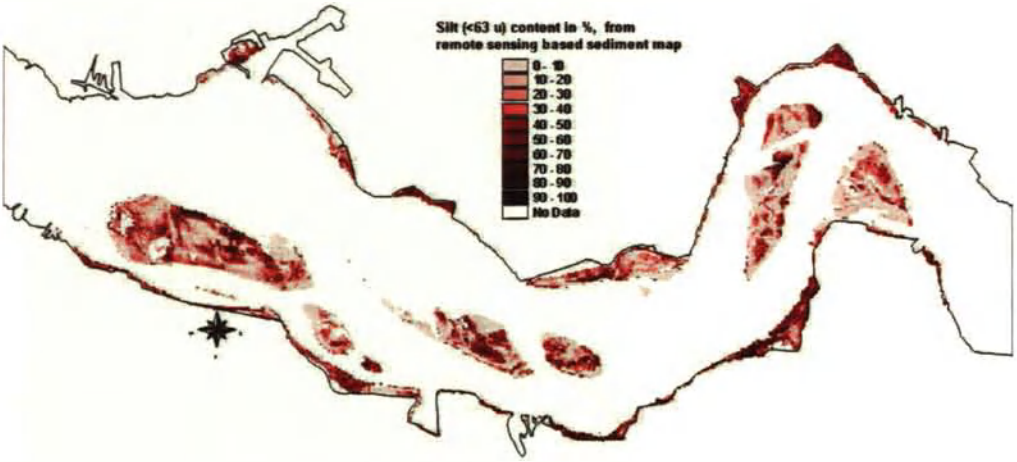

Figure 2-13. Silt content (measured as % weight comprised by particles with a diameter less than 63 µm) of the top layer of the sediment according to Stelzer (2003).

2.3.2 Height (depth) and emersion time

Both height and emersion time were derived from GIS maps. Height is regularly measured from ships by RWS. Via interpolation these measurements are transformed into a GIS map covering the entire area (Figure 2-14). From the map based on the measurements in 2002 we derived several variables for each of the counting plots: minimal height (maximal depth), maximal height (minimal depth) and mean height (mean depth). Emersion time is derived from the height map assuming an average tide (Figure 2-15). For each plot we determined the maximal emersion time (i.e. the emersion time of the part of the plot exposed longest), the minimal emersion time and the average emersion time.

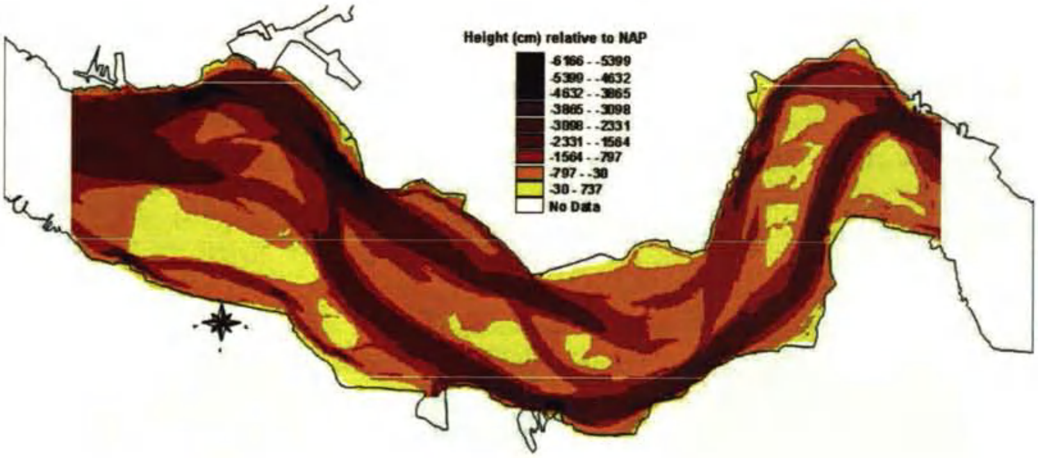

Figure 2-14. Height in cm relative to NAP. Source: RWS RIKZ.

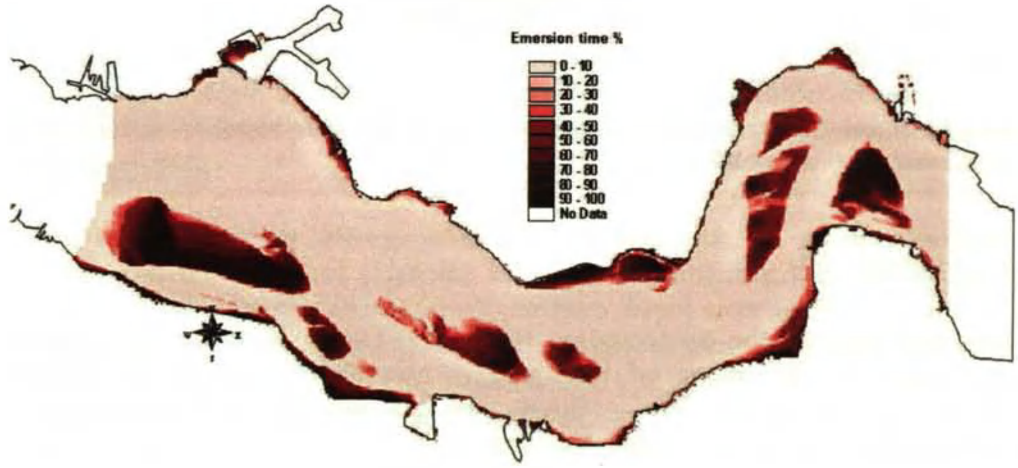

Figure 2-15. Emersion time (in % time). Source: RWS RIKZ.

2.3.3 Current velocity

The current velocity was calculated with the hydrological model SCALDIS100 (Lievense 1994). The depth-averaged maximal current velocity was calculated for an average tide in 1996 and a spring tide in 1996 by RWS RIKZ and the results were supplied as a GIS-map (Figure 2-16). We derived a value for each study plot by averaging the value of all grid cells (measuring 20 x 20 m) within the study plot.

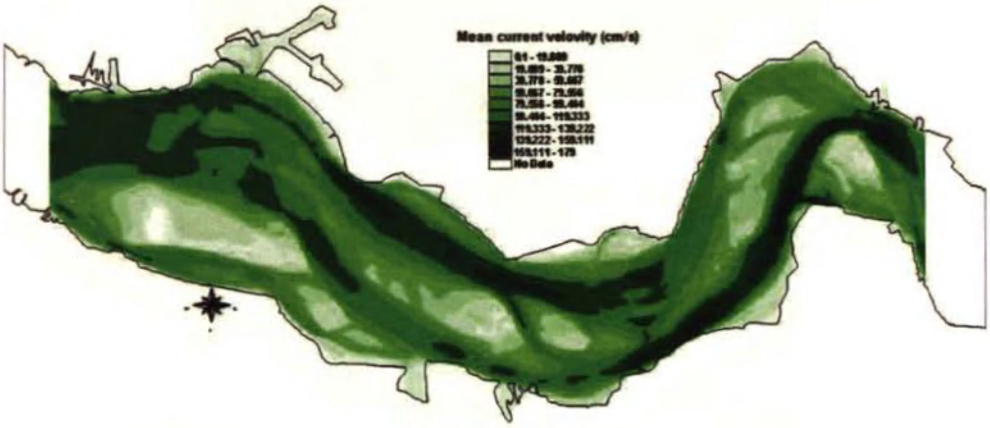

Figure 2-16. Maximal current velocity (cm/s) on an average tide in 1996 as calculated with the SCALDIS100 model (Lievense 1994). Source: RWS RIKZ.

2.3.4 Salinity

Salinity is defined as the concentration salt in seawater (g/kg in ‰). Measurement has changed in the course of time and is nowadays based on the electrical conductivity of a sample. Within limits, the unit psu (practical salinity unit) is interchangeable with the older ‰ indication. Salinity was derived from a combination of measurements in the Westerschelde and extrapolations with the model SCALDIS400 (van der Meulen & Silean 1997). We used annual means for the year 1992, being a year with an average river discharge.

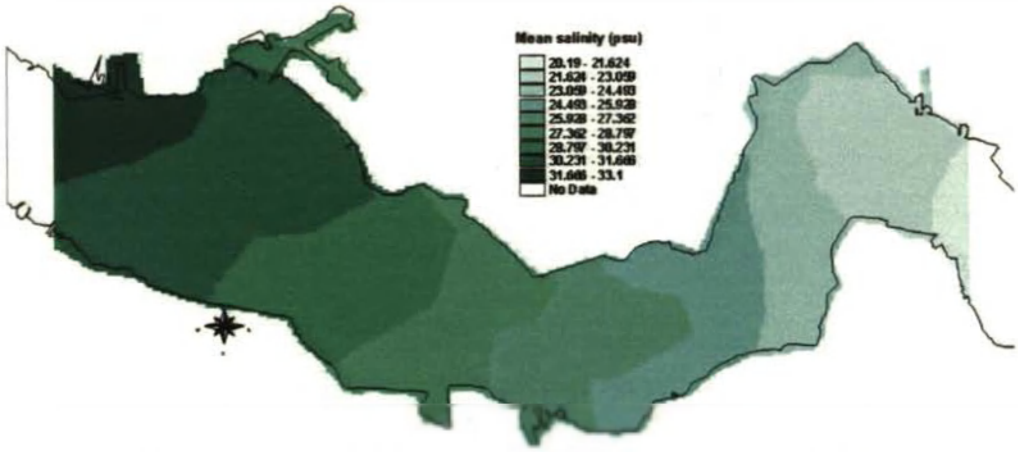

Figure 2-17. Average salinity (in psu) in 1992 according to measurements and extrapolations with the SCALDIS400 model (van der Meulen & Silean 1997). Source: RWS RIKZ.

2.4 Data on benthos

2.4.1 *Predicted maximal densities*

Ysebaert & Herman (2002) studied the relationship between the occurrence of benthic animals and abiotic variables in the Westerschelde and derived predictive models. RWS RIKZ applied these models to the available abiotic information and supplied us for each of the study plots with predicted maximal densities of the following benthic animals: *Aphelochaeta marioni, Heteromastus filiformis, Hydrobia ulvae, Nereis diversicolor, Pygospio elegans, Macoma balthica, Cerastoderma edule, Bathyporeia pilosa* and *Corophium volutator.* These predicted densities are the maximal densities, because they refer to autumn, when benthos densities are maximal.

2.4.2 Measured biomass densities

Between 29 October and 15 November 2003 samples of the benthos were collected in the 63 field plots established at that time by employees of AquaSense, Amsterdam. The data were made available by RWS RIKZ. Within each plot ten small samples (core diameter 4.5 cm, sample depth 20 cm) and five larger samples (core diameter 15 cm, sample depth 30 cm) were taken at random. Small samples were sieved on a 1 mm sieve and merged per plot. Larger samples were sieved on a 3 mm sieve and also merged per plot.

In the analysis bivalves (*Macoma balthica, Cerastoderma edule, Scrobicularia plana* and *Mya arenaria*) and the Mudsnail (*Hydrobia ulvae*) were distinguished at the species level. Bivalves of different size classes (small, medium, large) were analysed separately. For the different species borders between the size classes were as follows: *Macoma* 1 and 1.5 cm, *Cerastoderma* 1 and 2 cm, *Scrobicularia* 1 and 3 cm, *Mya* 2 cm (due to small numbers only two classes: small and large).

Polychaetes were split into five groups: a group consisting of *Eteone longa* and *Phyllodoce maculata* ('long and thin worms'), *Nereis* species (Ragworms, small and large individuals distinguished (width below or above 3 mm)), *Arenicola marina* (Lugworm, small and large individuals distinguished (width below or above 4 mm)), *Lanice conchilega* (Sand mason) and a group mainly consisting of *Aphaelochaeta marioni, Heteromastus filiformis, Pygospio elegans,* Capitellidae and the dominant species in numbers *Tubificoides benedii* ('other worms'). Crustaceans were split into *Corophium* species, Gammaridae, *Crangon crangon, Carcinus maenas* and *Cyathura carinata.*

Depending on the size of the organisms, density and biomass were calculated from the small samples only, the larger samples only or from both the sample types. The fact that more reliable estimates come from larger sampled areas was taken into account, as was the fact that too much effort can be put into analysing all individuals of smaller sized and numerous species.

2.5 Statistical analysis

2.5.1 Nomenclature

We applied multivariate regression analysis, mostly with non-linear models. Table 2-3 summarizes the many models that we investigated as part of this study. The table includes a nomenclature to which we will adhere throughout this report. Below, we will describe these models in more detail.

Table 2-3. Summary of the various statistical models that were investigated as part of this study, including the code by which they are referred to in this report and in Brinkman et al. (2005).

Variable				Description of the models	Code	Remark
Abiotic	Month	Site	Benthos			
All	NO	NO	NO	Monthly model	MOV	All species, 7 months
3	YES	NO	NO	Annual model (3-var)	Y3VM	All species, annual model
2	YES	YES	NO	Annual model (2-var)	Y2VMP	All species, annual model
0	NO	NO	YES	Benthos	BY	All species, annual model
0	YES	NO	YES	Benthos+month	BYM	All species, annual model
3	YES	NO	YES	3-variables+benthos	BY3VM	All species, annual model
2	YES	NO	YES	2-variables+benthos	BY2VM	Only Oystercatcher, Bar-tailed Godwit and Redshank; annual model
2	YES	NO	NO	Grouped data (sum), 2-variables	GSY2VM	All species, grouping of data, Sum foraging hours; annual model
2	YES	NO	NO	Grouped data (mean), 2-variables	GMY2VM	All species, grouping of data, mean foraging hours; annual model

2.5.2 Generalized Linear Modelling

In a number of standard cases, Generalized Linear Modelling techniques (GLM) can be used to find the appropriate parameters in non-linear models (McCullagh & Nelder 1989; Dobson 2002).

The dependent variable is the observed number of foraging hours summed over a tide in a plot (H). In GLM, the error variance need not be normally distributed and for a variable like foraging hours, it seems natural to assume a Poisson distribution. The aim is to construct a model F(X) that depends on a linear combination of the predictor variables $(X_1, X_1^2, X_2 \ldots)$

$$F(X) = a + bX_1 + cX_1^2 + dX_2 \ldots \qquad (1)$$

In this equation (1), a, b, c, d … are the fitted constants. The function F(X) is also called the Linear Predictor. We need a link function to transform the linear predictor into the fitted value, i.e. expected value E(H) of the dependent variable. We have chosen a logarithmic link function, so that it is possible to obtain an optimum curve with respect to a particular predictor variable:

$$\text{Ln}\,(E(H)) = F(X) \qquad (2)$$

Combining equations (1) and (2) we obtain:

$$E(H) = \exp\,(a + bX_1 + cX_1^{\,2} + dX_2 \ldots) \qquad (3)$$

The above model always yields curves that are "symmetrical" or show a maximum at low or high values of X_i. It is possible to obtain asymmetrical curves by introducing higher powers or plot roots of X_i, but that possibility was not explored. The shapes of the curves depend on the values of the parameters. All possible shapes for equation (3) with only one predictor variable and its' plotted value are depicted in Figure 2-18. The graphs on the left indicate an exponential increase for low values of the abiotic predictor variable, an exponential increase for high values of the abiotic predictor variable, or a U-shaped curve with an exponential increase of bird usage with both low and high values of the abiotic predictor variable. The graphs on the right indicate a true optimum curve, or an optimum curve which is truncated at either low or high values of the abiotic predictor variable. On the basis of ecological considerations we expect to find an optimum or a truncated optimum curve: we expect highest numbers in the best habitats, but we do not expect numbers to increase indefinitely at an accelerating rate, as happens in an exponential increase. A model with exponentially increasing numbers also leads to statistical problems when the model is used to make predictions outside the range of measurement of the abiotic predictor variables. Thus, the preferred shape from a statistical as well as an ecological point of view is an optimum, or a truncated optimum.

The analysis consisted of finding the set of predictor variables (X_1, $X_1^{\,2}$,X_2....), and the associated values for the parameters (a, b, c, d ...), that best explained the variation in foraging hours (H) with the least number of parameters. To this end we used a combined backward-forward approach in the statistical package Genstat (Lawes Agricultural Trust 2003). In the forward approach, the predictor variable that best explains the variation in foraging hours is chosen first. Subsequently, the next best predictor variable is entered in the equation, until new variables do not significantly improve the model. In the backward approach, all predictor variables are entered into the equation in the first step and variables are dropped from the model until no more variables can be dropped without significantly reducing the explanatory power of the model. Both procedures have the disadvantage that promising combinations of variables are sometimes overlooked. The combined backward-forward approach ingeniously avoids this drawback and finds the best model.

As a measure of the fit of the model we used the deviance, which is based on the ratio of the likelihood of observed distribution of foraging hours if the model were true, divided by the likelihood of the observed distribution of foraging hours if the fully saturated model (which contains all predictor variables) were true. The deviance does not depend on the underlying probability distribution and equals the residual sum of squares in case of a normal distribution. Thus, the percentage deviance explained can be compared to the percentage variance explained in a multiple regression assuming normally distributed errors. However, the fit of the model is not the only thing that matters, because an easy way to improve the fit is to increase the number of predictor variables, but this will decrease the predictive power of the model. A compromise is needed between the fit of the model and the number of parameters. We used the Akaike information criterion (AIC) to find the optimal compromise:

$$AIC = Dev/f + 2p \qquad (4)$$

In this equation, Dev is the deviance, p is the number of parameters in the model and f is the dispersion parameter. In a Poisson distribution, the variance equals the mean, but in many actual data sets, the variance is much higher than the mean. The scaling factor f indicates how much higher the variance is than expected under a Poisson distribution (which is the probability distribution assumed to underlie the data).

More details on the statistical analysis are provided by Brinkman *et al.* (2005). Below we will describe the different models that we tested and the nomenclature that we employ in this report to distinguish among these models.

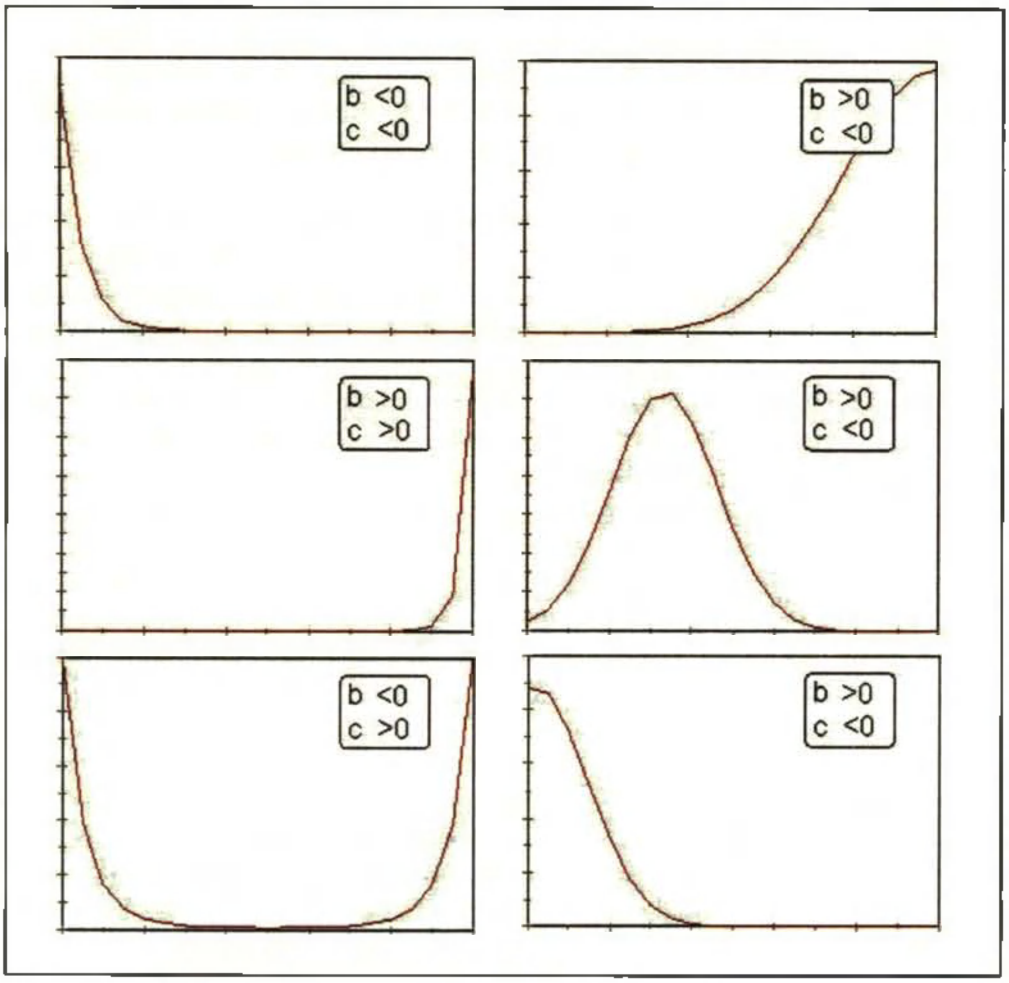

Figure 2-18. All possible shapes of the function $E(H) = \exp(a + bX_1 + cX_1^2)$. The value for E(H) is plotted on the Y-axis as a function of the value of X_1.

2.5.2.1 Monthly models

The first models that we investigated included the "maximal" set of abiotic variables. The word maximal is in parentheses because we did not include all the abiotic variables, since many were highly correlated. This is discussed in chapter 3.1 where we also explain how we arrived at the "maximal" set of variables that we used in the analysis. We derived a model for each of the seven individual counts. For this reason, we refer to these models as **monthly models**. The model code name is **MOV**. The fully saturated monthly model for a particular month had the following equation:

$$E(H) = \exp(a + b\ \text{Emean} + c\ \text{Emean}^2 + d\ \text{Vmean} + e\ \text{Vmean}^2 + f\ \text{Salt} + g\ \text{Salt}^2) \quad (5)$$

2.5.2.2 Annual models

The high explained deviances that we found when fitting the monthly models, could be due to overparameterization. Perhaps we had too many parameters and too few sites to produce meaningful models for a single count. We therefore assumed that the densities of the birds varied in the course of the season, but that this did not affect the basic relationship between bird usage and the abiotic predictor variables. Seasonal variation was incorporated in the model as follows:

$$E(H) = \exp(a + b\ \text{Emean} + c\ \text{Emean}^2 + d\ \text{Vmean} + e\ \text{Vmean}^2 + f\ \text{Salt} + g\ \text{Salt}^2 + h\ \text{Sep} + i\ \text{Nov} + j\ \text{Jan} + k\ \text{Mar} + l\ \text{Apr}) \quad (6)$$

The month variables, like Sep, take the value 1 if the count was in that month (in this case September) and 0 if the count was in another month, and h, i, j, k and l are the parameters that need to be estimated. Counts were made in six different months, but we included only five month variables, because these implicitly define the sixth month. We chose May as the sixth month, so May = 1 – Sep – Nov – Jan – Mar – Apr, and the bird usage in May is then the baseline against which the other months can be compared. As is clear from this equation, the month effect consists of multiplying the response predicted by the abiotic predictor variables with a factor exp(c) where c is the parameter for that particular month. The code name for this model is **Y3VM**.

We studied two variants of the **annual model**. The first variant includes salt and we refer to it as the **full annual model**. It is described in equation (6). This model was used for the first validation of the model predictions.

One idea behind this model is that the variable Salt may either capture a biological meaningful relationship, or it may primarily distinguish between sites and thus capture differences between sites that might be related to differences in the actual food supply for instance. To investigate the latter possibility, we included location variables in the model, instead of Salt, leading to the following model (an **annual model with location**):

$$E(H) = \exp(a + b\ \text{Emean} + c\ \text{Emean}^2 + d\ \text{Vmean} + e\ \text{Vmean}^2 + f\ \text{East} + g\ \text{West} + h\ \text{Eastmid} + i\ \text{Sep} + j\ \text{Nov} + k\ \text{Jan} + l\ \text{Mar} + m\ \text{Apr}) \quad (7)$$

In this equation, the location variables East, West and Eastmid are treated the same way as the month variables, i.e. they take the value 1 if the plots are in the particular location and the value 0 if the plots are not in that location. Similarly, we included three location variables in the model, instead of four, since Westmid = 1 – East – West – Eastmid. The code name for this model is **Y2VMP**.

To investigate if location and Salt could be regarded as interchangeable, we compared for each species the predictions from equation (6) to the predictions from equation (7).

2.5.2.3 Grouping data

The validations with the **full annual model (Y3VM)** were rather disappointing and revealed a major problem with these models. For some abiotic predictor variables, the predicted bird hours steeply increased for either very low or very high values of the predictor variable. Thus, very high bird usage was predicted for relatively rare habitats where we did not have measurements.

Ideally, we should have returned to the field and collect additional information on these relatively rare habitats. Clearly, this was not possible. Closer inspection of the curves and the data suggested that in many cases a few extreme values (i.e. a count with a lot of birds) had a big impact on the curves. We tested if grouping the data might reduce the impact of such extreme values.

The abiotic predictor variables emersion time and current velocity were each divided in 10 categories, leading to 100 different habitat classes. The variable salinity was not included, as this would have led to too many categories. Next, we added for each class the foraging hours of all plots belonging to that class. Clearly, categories with many plots will have more foraging hours, all else being equal. In type I of the **grouped variable model (GSY2VM)**, we divided the total number of foraging hours by the maximum value. In type II of the **grouped variable model (GMY2VM)**, we divided the total number of foraging hours by the number of study plots in the category. In both cases the model can be represented by the following equation:

$$E(H) = (p\ \text{Sep} + q\ \text{Nov} + r\ \text{Jan} + s\ \text{Mar} + t\ \text{Apr}) \exp(a + b\ \text{Emean} + c\ \text{Emean}^2 + d\ \text{Vmean} + e\ \text{Vmean}^2) \quad (8)$$

This equation bears a close resemblance to equation (6), except that the variable Salt is not included and that the monthly variation is incorporated in a slightly different way. First, we estimated the exponential part of the equation using GLM, without distinguishing between months. Next, we estimated for each month the monthly parameter using least squares minimization, comparing the values predicted with the GLM with the actual counts in that month. For more details, see Brinkman *et al.* (2005).

2.5.3 Models with benthic data

The important question that we wanted to answer was whether benthos data could significantly improve our predictive models after abiotic variables had been taken into account. For this exercise, we could use either the densities of benthos that were predicted from abiotic variables (see chapter 2.4.1), or the biomass densities that were actually measured in the study plots (see chapter 2.4.2).

We put more effort in investigating the effect of actual benthos data on bird numbers, even though this was not part of the original research question. As described in section 2.4, measurements on benthos were obtained in September 2003. Several benthos species occurred in such low densities that it was neither meaningful nor statistically possible to include them as a separate variable in the analysis. One option would have been to simply exclude these rare species from the analysis. Instead, several of such scarce species were lumped into a single variable using a principal component analysis (Brinkman *et al.* 2005). The logic behind the principal component analysis was to find a common factor describing these rare species. In the end, 14 "meaningful" variables remained, consisting of the densities (measured in g AFDW / m^2) of: Cockles of three different size classes, *Scrobicularia plana* of three different size classes, Ragworms of two size classes, Lugworms of two size classes, *Lanice conchilega*, a lumped variable of all thin and long polychaetes, a lumped variable of all *Macoma balthica* + remaining worms and a lumped variable of all crustaceans, all gastropods and *Mya arenaria*[2]. As the dependent variable, we used the number of foraging hours of a particular bird species in a particular plot during a particular count. The first model that we investigated was a linear regression relating the number of foraging hours (H) to the (meaningful) benthos densities:

$$H = a_0 + \sum_{i=1}^{n} a_i B_i \qquad (9)$$

In this equation, *n* is the total number of benthic variables (i.e. 14), a_0, a_1, .., a_{14} are the fitted constants and B_1, B_2, ..., B_{14} represent the benthic variables. The code name for this model is **BJ**.

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[2] Since some of the lumped variables contained benthic species that differed considerably in ecology, the added benefit of including such lumped variables in the analysis, instead of simply deleting all rare benthic species from the analysis may be questioned. In only one analysis did we observe a significant correlation involving a lumped variable. Foraging hours of Redshank showed a significant negative correlation with the lumped variable containing all crustaceans, all gastropods and the bivalve *Mya arenaria*. This variable includes *Corophium*, which is a preferred prey of Redshank (Goss-Custard 1977). However, in the study of Goss-Custard (1977) *Corophium* densities of up to 8000 per m^2 were measured, whereas in this study the maximal density in the few study plots where it occurred, was only 57 per m^2.

The above equation does not take into account that bird densities vary considerably in the course of the season. Thus, our next model (coded with the name **BJM**) included the variable month as nominal variable:

$$H = a_0 + \sum_{i=1}^{n} a_i B_i + \sum_{j=1}^{m-1} c_j M_j \qquad (10)$$

In this equation, m is the total number of different months in which we did observations (i.e. 6), M_j refers to the month in which observations were done and takes the values 1 if the observations were in month M_j and 0 if the observations were in a different month. Finally, c_1, c_2, .., c_5 represent the fitted constants for the seasonal variation. It should be noted that this way of incorporating seasonal differences in density is different from equations (6) and (7) where month occurs as an argument in an exponential function.

To examine whether the actual benthos data significantly improved our predictive models after abiotic variables had been taken into account, we first fitted the abiotic model according to equation (5). Next, we investigated if adding benthic variables significantly improved the model. Thus, the fitted model (coded with the name **BY3VM**) is described by a combination of equations (6) and (10):

$$E(H) = \exp(a + b\ \mathrm{Emean} + c\ \mathrm{Emean}^2 + d\ \mathrm{Vmean} + e\ \mathrm{Vmean}^2 + f\ \mathrm{Salt} + g\ \mathrm{Salt}^2 + h\ \mathrm{Sep} + i\ \mathrm{Nov} + j\ \mathrm{Jan} + k\ \mathrm{Mar} + l\ \mathrm{Apr}) + \sum_{i=1}^{n} a_i B_i \qquad (11)$$

The abiotic part was always included in the model, so the exercise amounted to investigating if adding benthic variables significantly reduced the residual variance.

In equation (11) the variable *Salt* might act as a proxy for location and associated variations in benthic food supply. Thus, we also investigated the contribution of benthos data to an abiotic model without *Salt*:

$$E(H) = \exp(a + b\ \mathrm{Emean} + c\ \mathrm{Emean}^2 + d\ \mathrm{Vmean} + e\ \mathrm{Vmean}^2 + h\ \mathrm{Sep} + i\ \mathrm{Nov} + j\ \mathrm{Jan} + k\ \mathrm{Mar} + l\ \mathrm{Apr}) + \sum_{i=1}^{n} a_i B_i \qquad (12)$$

The code name for this model was **BY2VM**.

2.6 Validation

To validate the regression models two approaches were considered. First, foraging hours 'observed' and predicted in additional intertidal plots were compared. Second, a comparison was made between predicted numbers of foraging hours in intertidal regions (converted to number of birds) with number of birds counted at associated high tide roosts. While the first approach concerns observations and predictions for the same geographical areas, the second approach is based on assumptions about the relations between foraging areas (low tide situation) and high tide roosts (high tide situation).

To execute both kinds of validation, two types of information were available: bird counts in intertidal plots during low tide ('low tide counts') and bird counts at high tide roosts ('high tide counts'). Taking into account the conversion of number of foraging hours to number of birds it was possible to compare predictions and actual counts for each species for the corresponding month. For this conversion we assumed that birds of a given species needed a fixed number of foraging hours to satisfy their energy needs (Table 2-4). We divided the total number of foraging hours by this species-specific number to obtain the number of birds.

We used both validation approaches on the **full annual model (Y3VM)**. To validate the **grouped variable model (GMY2VM)**, we only used the high tide counts.

Table 2-4. Number of foraging hours per individual bird. as used to convert foraging hours to number of birds.

Species	Number of foraging hours per individual
Ringed Plover	8.25
Shelduck	6.00
Dunlin	8.25
Bar-tailed Godwit	5.00
Oystercatcher	5.00
Redshank	8.25
Curlew	5.00
Grey Plover	8.25

2.6.1 Low tide counts

Additional low tide counts of foraging birds were performed in 41 different plots (0.3 to 6.1 ha each, average size 2.8 ha) distributed over seven sites in the western part of the Westerschelde (Figure 2-19). Because 24 plots were counted twice, a total of 65 counts are available. At four sites counts were made during the entire low tide period while at the other sites only counts from high water to low water were made. All counts were made at 15 minute intervals and converted to foraging hours by multiplying the total number of birds by 0.25 (one quarter of an hour). When only ebb tide counts were available, this figure was multiplied by two to arrive at an estimate of total foraging hours per low tide period.

Low tide counts were made in November 2003 (sites Hooge Platen, Schelphoek, Baarland), April and May 2004 (sites Zuidgors and Terneuzen), in September and November 2004 (site Schorerpolder/Sloehaven) and in October and December 2004 (site Nijs- & Hooglandpolder). The counts are documented in Aquasense (2004), Boudewijn & Vonk (2004), Hoekstein & Boudewijn (2004), Boudewijn *et al.* (2005a), Boudewijn *et al.* (2005b) and Boudewijn *et al.* (2005c). Because no models for October and December are available, the results for Nijs- & Hooglandpolder were compared with model predictions for September and December respectively.

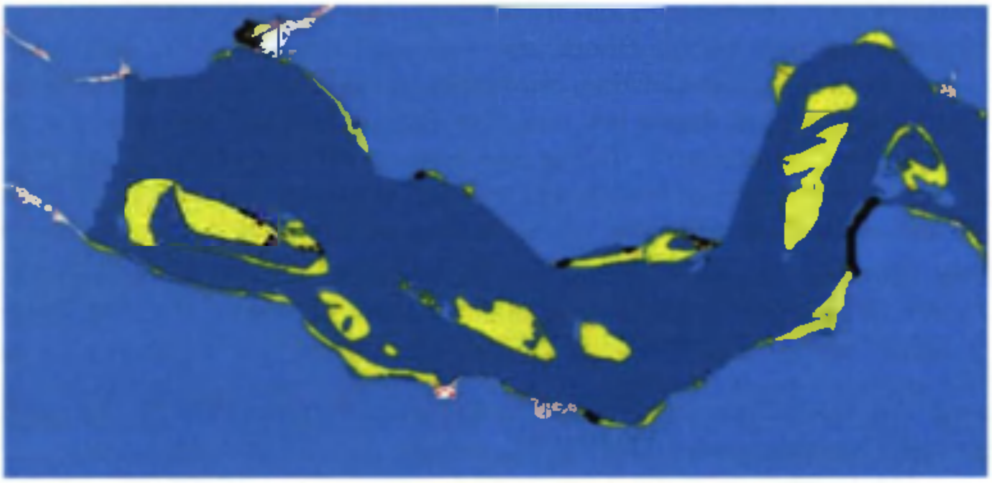


Figure 2-19. Location (in black) of plots where low tide counts were performed for validation. Source: RWS RIKZ.

2.6.2 High tide counts

Monthly counts of birds roosting at high tide along the shores of the Westerschelde are part of the national monitoring programme organised by the National Institute for Coastal and Marine Management/*RWS RIKZ*. Data from this programme are used for the validation with high tide counts. Depending on the species, some of the counts were incomplete or unreliable because high tide roosts could not be visited by the observer or were for some reason disturbed. In such cases all counts for that particular month were left out of the analysis. Otherwise for each month the average of counts in the period July 1999 to June 2004 was used. Based on knowledge of movements of birds between individual roosts, counts were aggregated for five geographical regions (sectors) with little or no exchange of birds (pers. comm. Cor Berrevoets, RWS RIKZ).

2.6.3 Predicted distributions

The regression models were combined with maps of environmental variables to produce the predicted number of foraging hours for every possible point in the intertidal in the western part of the Westerschelde. Areas with emersion times exceeding 85% were excluded from the maps. These areas, which are all situated above high tide level at neap tides, are covered with vegetation or are otherwise regarded as insignificant foraging areas for waders and Shelduck (pers. comm. Dick de Jong, RWS RIKZ).

From these maps, total number of foraging hours for individual plots were calculated (low tide counts). In the area relations between high tide roosts and low tide foraging areas are poorly known. Mostert *et al.* (1990) documented what was known at that time about flight directions of waders visiting certain high tide roosts.

Generally speaking the high tide roosts closest to the foraging areas are used. Peter Meininger and Cor Berrevoets (RWS RIKZ) advised on splitting up the intertidal area into regions that best correspond with the sectors distinguished in the high tide counts. Some additional information about bird movements between tidal flats and the high tide roosts was obtained by Marcel Kersten (Altenburg & Wymenga) and Fred Twisk (RWS RIKZ) during this project. For the validation based on high tide counts, the maps with predicted foraging hours were split into seven regions (Figure 2-20).

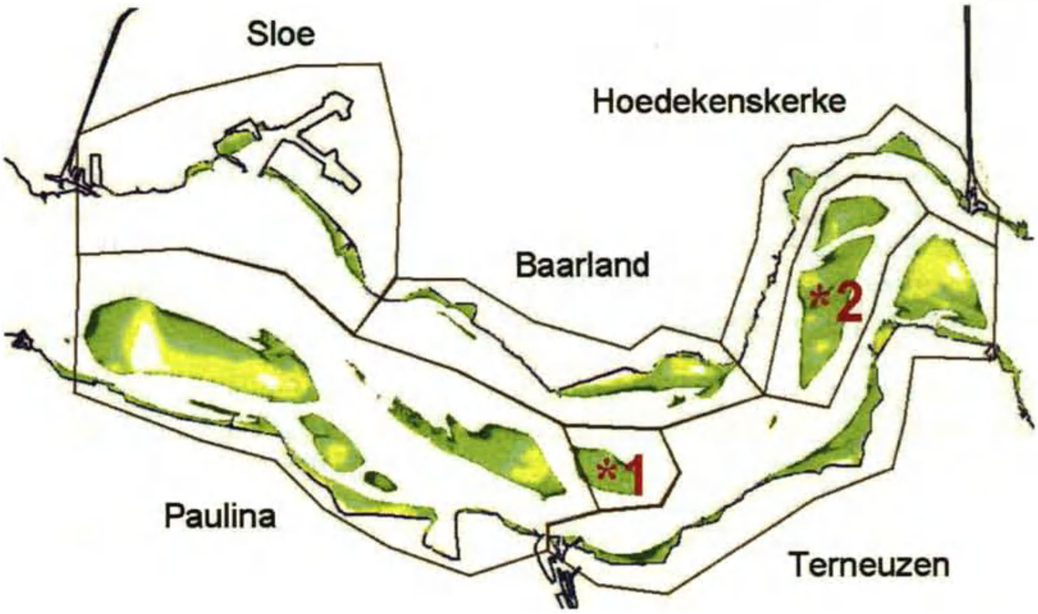


*Figure 2-20. Map of the regions distinguished for the validation on the basis of the high tide counts. Low tide regions and associated high tide sectors (Paulina, Sloe, Baarland, Hoedekenskerke, and Terneuzen) are indicated. Data from low tide regions marked with a star were used as follows: *1 was joined with data from Paulina and *2 with data from Hoedekenskerke for Shelduck and with Terneuzen for all other species. Source:* RWS RIKZ.

2.6.4 Comparison between predictions and observations

For the low tide counts number of foraging hours predicted and 'observed' could be compared directly. A positive linear relation was expected to exist between the number of hours predicted and observed.

To be able to compare number of birds (high tide counts) with model predictions (foraging hours) the number of foraging hours from the maps was divided by the estimated number of foraging hours per individual as given by Boudewijn *et al.* (2005a), see Table 2-4. These are 'mean' values taken from the literature and concern the entire low tide period, as observed in daytime situations and without taking into account seasonal differences.

For the high tide counts, two aspects were considered: 1) the number of birds predicted (as calculated from the number of foraging hours predicted) and observed for the entire study area (absolute comparison, season 2003/2004 only) and 2) the *proportion* of the total number of birds counted (high tide counts) and of the total number of foraging hours predicted (maps) for corresponding high tide sectors and low tide regions (relative comparison, average situation seasons 1999/2000 to 2003/2004). This way, a correct conversion of number of foraging hours predicted to number of birds in the area is important for the absolute comparison, but not for the relative comparison. The choice of associated high tide sectors and low tide regions is important for the relative comparison, but not for the absolute comparison.

Depending on the species, for each of the five high tide sectors the number of birds was compared with the number calculated for one or more of the seven low tide regions. The low tide region marked with '*1' in Figure 2-20 was supposed to be associated with high tide sector Paulina, the region marked with '*2' in Figure 2-20 was supposed to be associated with high tide sector Hoedekenskerke (Shelduck only) or Terneuzen (all other species).

For each species except Sanderling and Knot (models with low explained variance) one month with high numbers was chosen to compare model results with high tide counts.

3 Results

3.1 Abiotic variables

Several of the abiotic variables appeared to be highly correlated. Not surprisingly, emersion time showed a strong positive correlation with height (Figure 3-1a) and silt content showed a strong negative correlation with median grain size (Figure 3-1b). Current velocity showed a negative correlation with silt content (Figure 3-1c) and a positive correlation with median grain size (Figure 3-1d).

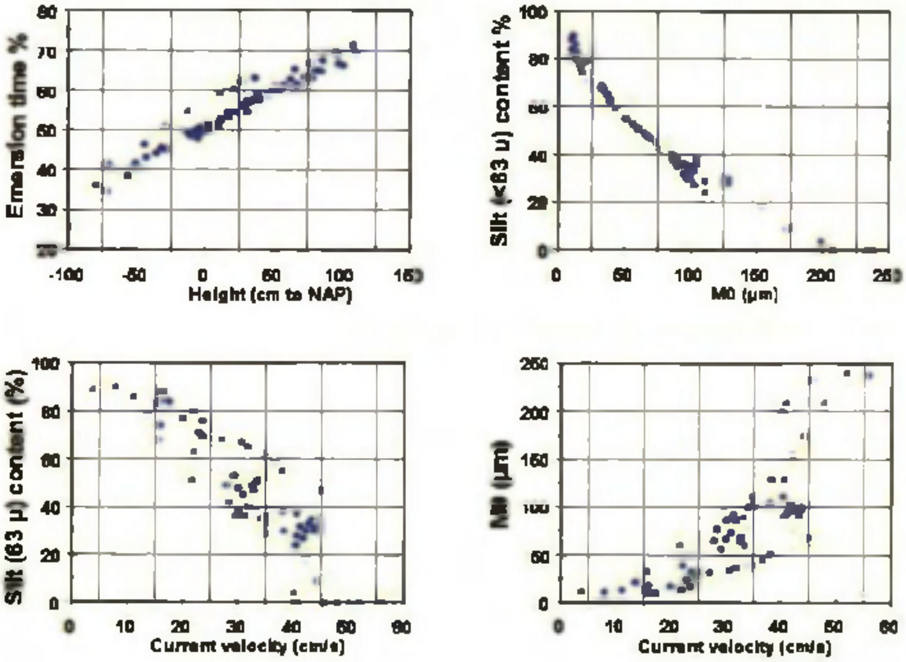


Figure 3-1. Correlation between abiotic variables measured in the study plots (silt content and median grain size), or predicted from GIS-maps (emersion time, depth and current velocity). (a) Emersion time (% time) plotted against depth (cm). (b) Silt content (% mass > 63 µm) plotted against median grain size (µm). (c) Silt content (% mass > 63 µm) plotted against average current velocity (cm/s). (d) Median grain size (µm) plotted against average current velocity (cm/s).

Adding a new predictor variable (like silt content) to a regression equation that already includes a highly correlated predictor variable (like median grain size) will not improve the predictive power of the equation. Thus, a set of potential predictor variables without strong correlations is needed. In deciding on this set, non-statistical arguments may enter. We decided to include emersion time and exclude height, because emersion time directly relates to the feeding opportunities of the birds. Following the same argument we should have included silt content (or median grain size) and excluded current velocity. However, we made the opposite choice as the sediment variables have several problems. First, there are many different methods to measure the silt content and the methods employed considerably affect the results (Zwarts *et al.* 2004). Possibly as a result of this, the silt content as measured in this study, does not correlate well with the sediment map produced by Stelzer (2003) on the basis of satellite images and ground truth (Figure 3.2).

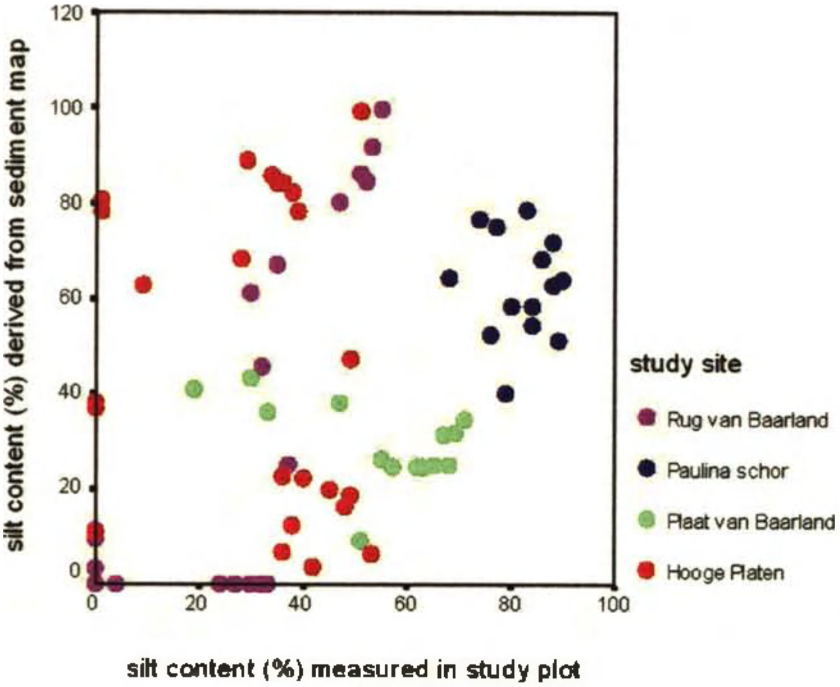


Figure 3-2. Correlation between silt content (% mass > 63 µm) measured in the study plots (see methods) and silt content (% mass > 63 µm) as derived for the study plots from the sediment map produced by Stelzer (2003).

A likely explanation is that the satellite image only reflects the composition of the thin top layer of a few mm, whereas our samples apply to the top 5 cm of the sediment. The thin top layer is probably quite variable on a short time scale as a result of periods with strong wave action (which removes fine sediments) or growth of diatoms (which capture fine sediments in a layer of mucus). Second, producing sediment maps is not part of a regular monitoring scheme and it is difficult to predict how sediment composition will change as a result of human activities. Thus, sediment composition is of limited value as a predictor variable in the models that we develop and we therefore decided to use current velocity.

In the end, we used at maximum three different abiotic predictor variables (and their quadratic terms) in our modelling: salinity (which did not show strong correlations with the other predictor variables), emersion time and current velocity. It turned out that emersion time and current velocity were negatively correlated. This was especially clear within study sites, except for the Rug van Baarland, but also apparent in the Westerschelde estuary as a whole (Figure 3-3). The four study sites were characterized by different combinations of emersion time and current velocity and covered the most common combinations of these two variables in the estuary as a whole (Figure 3-3). However, it is clear that we did not have study plots in the less common combinations.

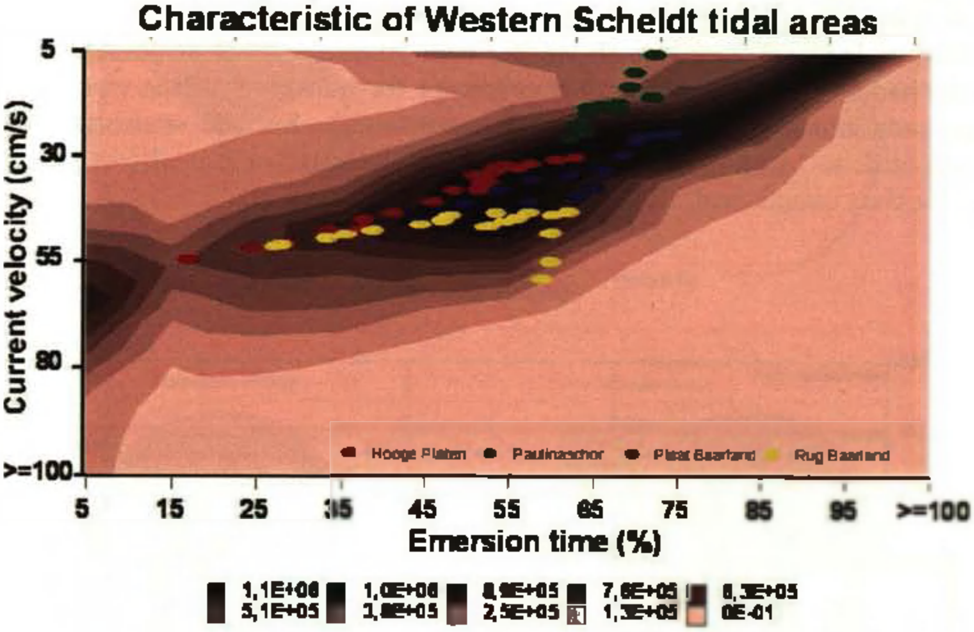


Figure 3-3. Relationship between current velocity (cm/s) and emersion time (%) for the study plots (each dot represents a plot and different study sites are indicated with different symbols) and for the Westerschelde as a whole (indicated with the contour diagram). The numbers next to the boxes indicate the total number of grid cells in each combined interval of 10% emersion time and 10 cm/s current velocity. The contour lines are derived from an interpolation of the scores and for this reason provide a false sense of accuracy.

3.2 Measurements on the food supply

The benthic biomass was smallest in the plots at Plaat van Baarland and highest in the plots at Hooge Platen (Figure 3-4). The biomass of crustaceans was very small compared to that of worms and especially bivalves at all sites. At Hooge Platen transect D had much lower biomasses on average than the other transects. At Rug van Baarland transect J had much higher biomasses than the other transects. At Paulinaschor the average biomass in transect N was much lower than in the other transects.

At Hooge Platen, Paulinaschor and Rug van Baarland Cockles (*Cerastoderma edule*) dominated the biomass, while the Baltic Tellin (*Macoma balthica*) was also present in relatively high biomasses (Figure 3-5). At Plaat van Baarland, Cockles were almost absent and the Baltic Tellin dominated the biomass. Here 'other worms' had a large contribution to the biomass too, consisting almost exclusively of *Heteromastus filiformis* and Capitellidae in equal densities. At Hooge Platen the densities of 'other worms' were dominated by *Aphelochaeta marioni* (49%), *Heteromastus filiformis* (32%) and Capitellidae (15%). At Rug van Baarland *Heteromastus filiformis* (54%) and Capitellidae (42%) dominated this group of worms, while at Paulina they determined 71% and 18% of densities of the 'other worms' respectively.

Averaged over all four study sites, animals smaller than 9 mm dominated the population of Baltic Tellins, and animals smaller than 15 mm dominated the Cockle population. In *Scrobicularia* animals smaller than 10 mm were most numerous, while all *Mya* had shell lengths above 17 mm (except for transect J at Rug van Baarland, where only animals smaller than 9 mm were found). For the statistical analyses relating birds to benthos, only biomass data per size class were used (see paragraph 2.4.2 for class boundaries).

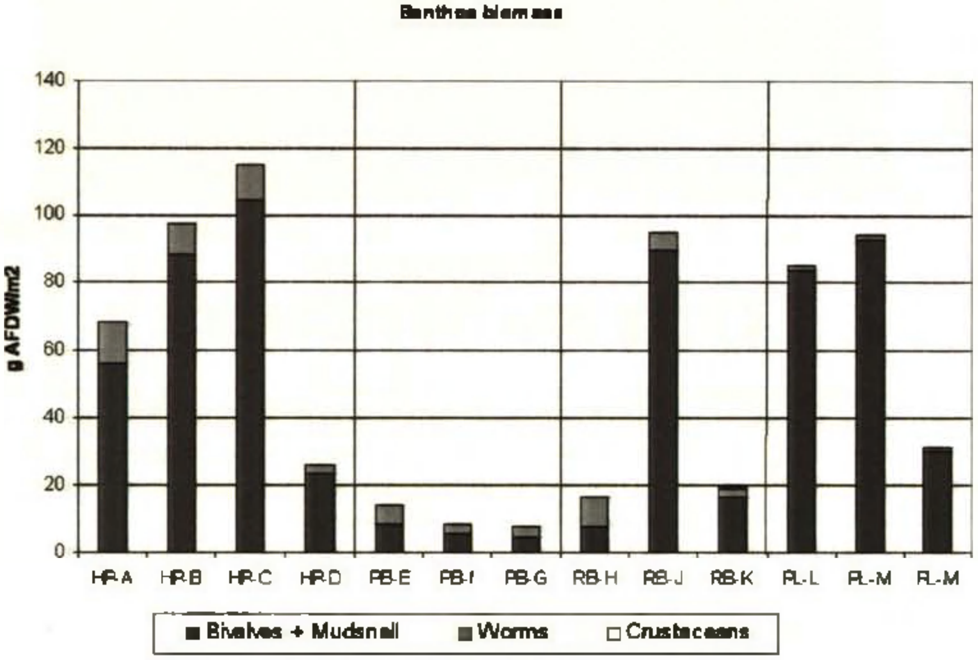


Figure 3-4. Average biomass per plot in the transects at Hooge Platen (HP), Plaat van Baarland (PB), Rug van Baarland (RB) and Paulinaschor (PL) as determined in autumn 2003. Source: RWS RIKZ.

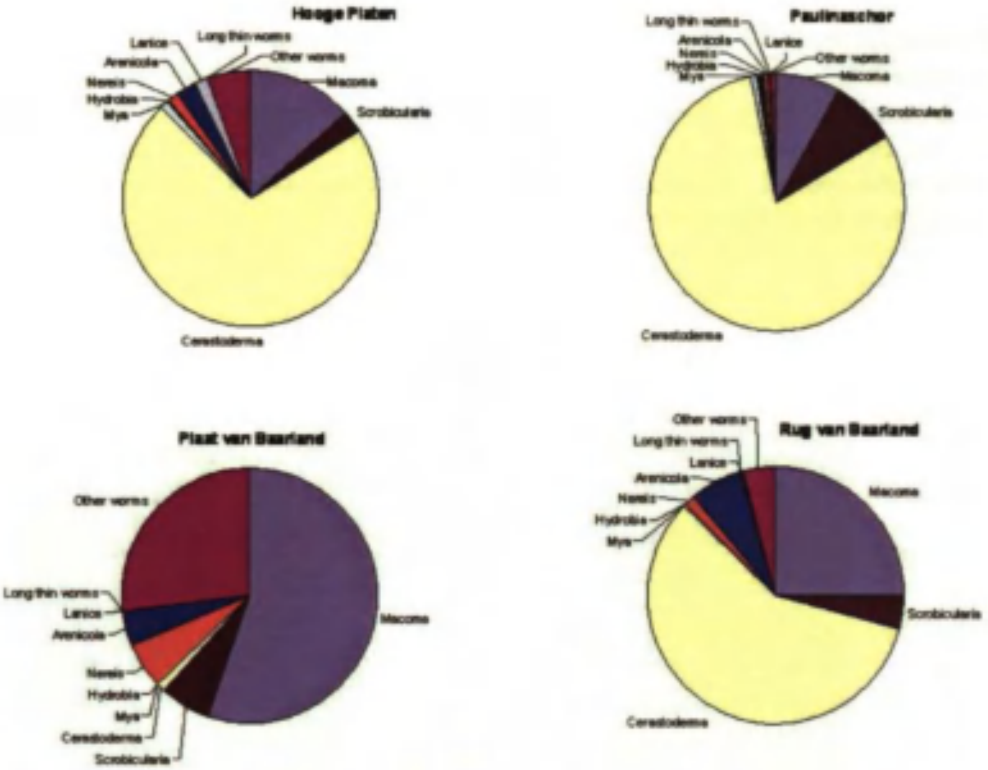


Figure 3-5. The relative contribution of the different species and species groups to the total biomass in autumn 2003 at (a) Hooge Platen, (b) Plaat van Baarland, (c) Rug van Baarland, (d) Paulinaschor. Source: RWS RIKZ.

3.3 Results per bird species

3.3.1 Shelduck

3.3.1.1 Prey choice

According to the review of Leopold *et al.* (2004) Shelduck feed on all small prey on or just below the surface of the mud. The Mud Snail *Hydrobia* is often an important prey item. A detailed study of food choice of Shelduck in the Delta area (Meininger & Snoek 1992) shows that Mud Snails are the most important prey in the saline areas. In the brackish eastern part of the Westerschelde, bivalves and *Hydrobia* are absent, and the birds feed mainly on diatoms. Shelduck no only feed on the exposed tidal flats, but also in shallow water. We have one direct observation of a Shelduck taking a small Cockle.

3.3.1.2 Phenology

Shelduck numbers typically peak in June/July and many birds stay to moult in August-September (Berrevoets *et al.* 2003). After that numbers decline steadily to very low numbers in the period November-January. From March to May numbers slowly increase. Figure 3-6 indicates that we did not collect counts during the period when maximal numbers of Shelduck are present in the Westerschelde. Moulting Shelduck tend to keep swimming and only visit the edges of the tidal flats (Meininger, pers. comm.). The low numbers in November 2003 and January 2004 conform to the general pattern, but this is not true for the fact that the count in May 2004 exceeds both counts in September.

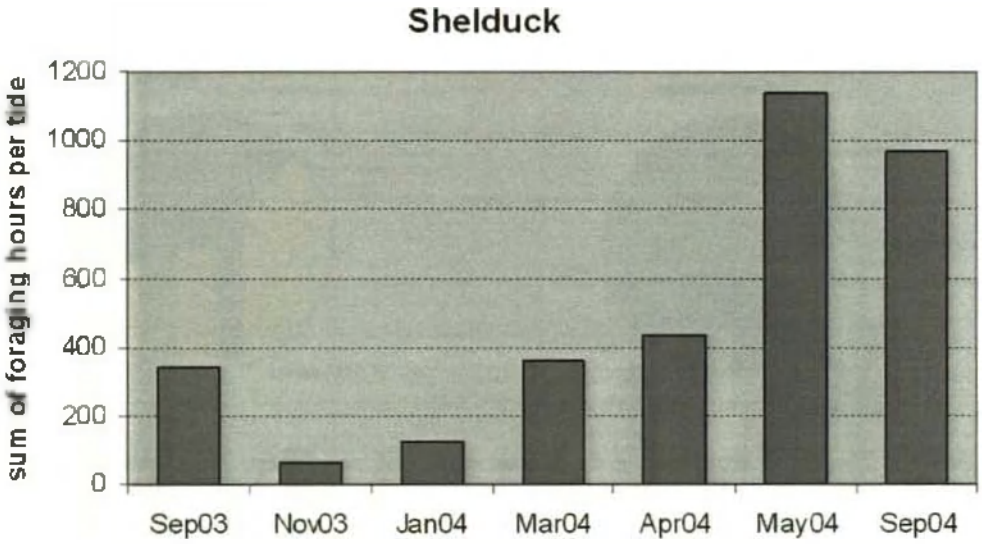


Figure 3-6. The total number of foraging hours of Shelduck during each of the observation periods. Note that the number of sites counted increased from 63 to 71 during the study. In January/February 2004 not all sites could be counted due to bad weather conditions.

3.3.1.3 Distribution

Emersion time, current velocity and salinity significantly influenced the distribution of Shelduck in the five counts for which it proved possible to build a distribution model (Table 3-1). The same variables were also included in the full annual model (Table 3-2). The amount of deviance that was explained by the monthly models varied between 42% and 64% (Table 3-1). The parameter estimates indicate that the shape of the curves varied qualitatively between months, so it is no surprise that the explained deviance of the full annual model is below this range.

When the parameter estimates are examined in more detail we find that only in a minority of cases an optimum, or a truncated optimum is indicated (Table 3-1). For the monthly models, this is the case for salinity in January/February 2004 and for emersion time in April and May 2004. Numbers were low during the count in January/February 2004, so the optimum for salinity is probably a statistical fluke. For the other months the relationship with salinity corresponds to the results of (van

Kleunen 1999) and (Stuart *et al.* 1990), who found more Shelduck in the more saline mouth of the Westerschelde than in the central part. (van Kleunen 1999) also reports many Shelduck in the brackish eastern part, but we did not study this area.

*Table 3-1. Monthly distribution models (**MOV**; see methods for details) for the Shelduck. No models could be fitted for the data in September 2003 and November 2003. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

	Jan/Feb04	Mar04	Apr04	May04	Sep04
constant	-673	21.93	9.1	23.63	251.4
Emean	0.427	-0.0555	0.3	0.2552	0
Emean^2	0	0	-0.00383	-0.00387	-0.00167
Vmean	0	-0.2619	-0.3649	-0.32	0
Vmean^2	0.00881	0.00284	0.004138	0.00241	-0.00415
Salt	45.6	-0.479	0	-0.601	-17.61
Salt^2	-0.807	0	-0.00748	0	0.3196
Deviance explained	57%	40%	48%	64%	42%

Figure 3-7 suggests that Shelduck occur in a wide range of habitats and are only absent in areas with very short emersion times, which was also noted by Van Kleunen (1999). The observations also suggest that areas which have both a long emersion time and a high current velocity are also unattractive. Van Kleunen (1999) reports highest densities in very muddy areas, but we did not observe a very strong preference for areas with low current velocities.

Since the full annual model (Table 3-2) does not contain optimum curves for any of the variables, predicted numbers of foraging hours are maximal outside the combined range of emersion time and current velocity for which we collected data (Figure 3-8). Very high numbers of foraging hours are predicted for areas with short emersion times and low current velocities (Figure 3-8). This is probably a statistical artefact.

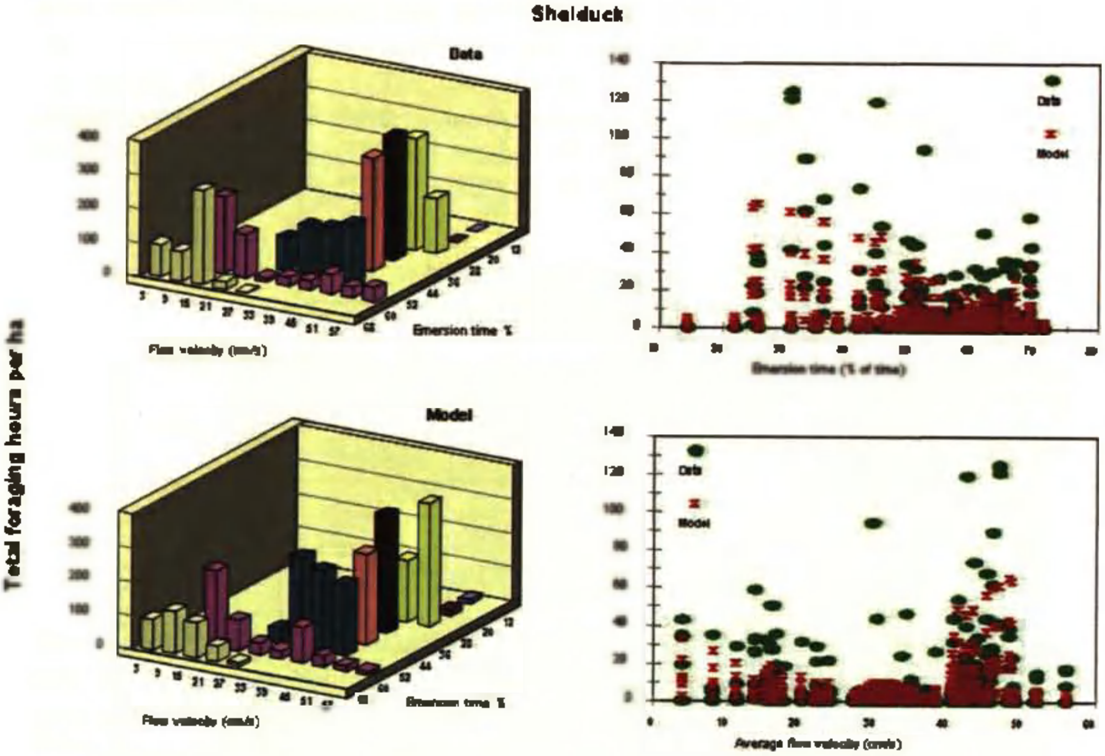


Figure 3-7. Distribution of Shelduck with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). (a) Foraging hours as a function of both variables as observed. (b) Foraging hours as a function of both variables as predicted. (c) Foraging hours as a function of emersion time, comparing observations and model predictions. (d) Foraging hours as a function of current velocity, comparing observations and model predictions.

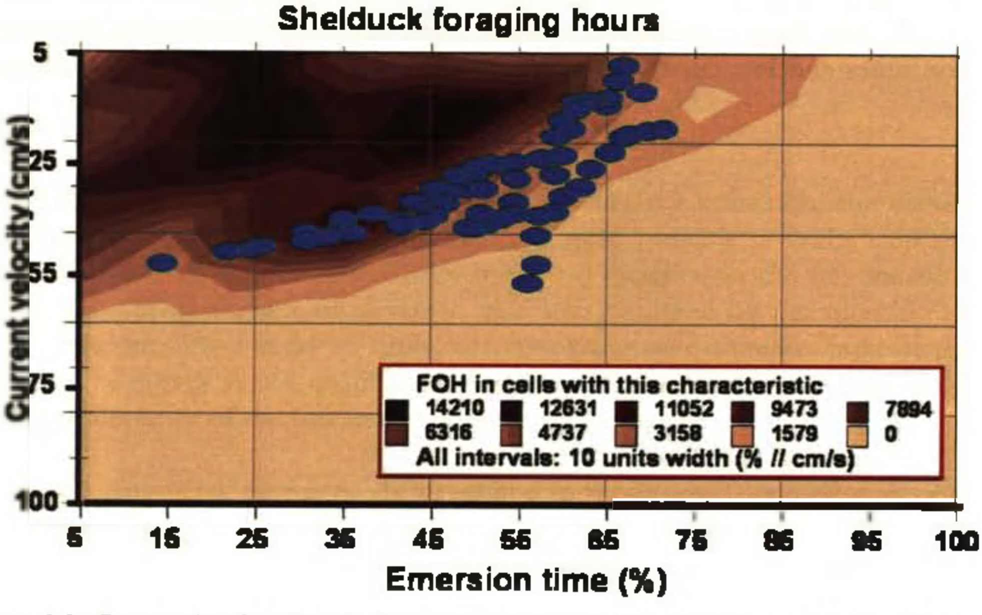


*Figure 3-8. Contour plot of predicted foraging hours of Shelduck with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). Predictions are based on the full annual model (**Y3VM**). Dots indicate the study plots. The numbers next to the boxes indicate the total number of foraging hours in each combined interval of 10% emersion time and 10 cm/s current velocity. The contour lines are derived from an interpolation of the scores and for this reason provide a false sense of accuracy*

*Table 3-2. Parameter estimates of the full annual distribution model (**Y3VM**) for the Shelduck. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

constant	112
Emean	0
$Emean^2$	-0.000936
Vmean	-0.147
$Vmean^2$	0
Salt	-7.310
$Salt^2$	0.129
Sep	-0.430
Nov	-2.600
Jan	-1.330
Mar	-1.150
Apr	-0.969
May	0
Explained	36.5%

3.3.2 Oystercatcher

3.3.2.1 Prey choice

Oystercatchers are among the best studied waders. Reviews of their diet can be found in Hulscher (1996), Zwarts *et al.* (1996a) and Zwarts *et al.* (1996b). The most recent review is provided by Bult *et al.* (2004), who include studies that appeared since 1996 (Table 3-3). During winter, Oystercatchers feed nearly exclusively on shellfish, especially Cockles and Mussels, but other shellfish like *Mya arenaria*, *Macoma balthica* and *Scrobicularia plana* are also taken.

The prey choice observed in this study (Table 3-4) conforms to the general pattern described in Table 3-3. Since there are no mussel beds on the flats of the Westerschelde, we expect Cockles to be the most important prey item in winter and this is indeed the case.

Table 3-3. Summary of the importance of different prey to Oystercatchers in summer and winter. From Bult et al. (2004)

English name	Scientific name	Importance as food source during summer	Importance as food source during winter
Mussel	*Mytilus edulis*	Important staple food for coastal breeders	Very important staple food: always accessible
Cockle	*Cerastoderma edule*	Important staple food for coastal breeders	Very important staple food: always accessible
Sand Gaper	*Mya arenaria*	Moderately important for coastal breeders	In some years important alternative food source: only small animals are within reach and only every now and then there is a strong year class
Peppered Furrow Shell	*Scrobicularia plana*	Limited importance for coastal breeders	Of limited importance: only every now and then there is a strong year class and burrows deeper in winter so that it becomes inaccessible
Baltic Tellin	*Macoma balthica*	Important staple food for coastal breeders	Dependable, but less attractive alternative prey: burrows deeper in winter and therefore less profitable than in summer; less variable between years compared to other prey
American Razor Clam	*Ensis directis*	Limited importance for coastal breeders: probably only taken by a few specialists	Very limited importance: probably only taken by a few specialists
Shorecrab	*Carcinus maenas*	Limited importance to coastal breeders	Unimportant: Oystercatchers take only large crabs and these large crabs spend the winter in gullies out of reach of the birds
Ragworm	*Nereis diversicolor*	Important staple food for coastal breeders	Unimportant: burrows deeper in winter and is less active, so the birds cannot catch them
Lugworm	*Arenicola marina*	Limited importance to coastal breeders	Unimportant due to strongly reduced activity in winter
Earthworm	*Lumbricus, Allolobophora etc. sp.*	Important staple food for inland breeders	Important alternative prey, especially after rainfall; less dependable than prey from mud flats, because meadows freeze earlier than mud flats
Tipulid	*Tipula sp.*	Important staple food for inland breeders	Important alternative prey, especially after rainfall; less dependable than prey from mud flats, because meadows freeze earlier than mud flats

Table 3-4. Observations of prey species taken by Oystercatchers feeding in the study sites. For each site the number of individuals seen to take a particular prey species was recorded.

	Plaat van Baarland	Hooge Platen	Paulina schor	Rug van Baarland	Total	%
Cerastoderma edule	0	104	1	132	237	79%
unknown shellfish	1	0	4	0	5	2%
Macoma balthica	0	19	1	22	42	14%
Nereis diversicolor	0	0	5	7	12	4%
Carcinus maenas	0	0	1	0	1	0%
unknown prey	1	0	1	0	2	1%

3.3.2.2 Phenology

Highest numbers of Oystercatchers habitually occur in the Westerschelde in late summer, early autumn (Berrevoets *et al.* 2003). Thereafter numbers decline until minimum numbers are reached in the period March-June. This pattern is also reflected in the number of birds counted during low tide in the study sites (Figure 3-9), except for the rather low numbers counted in January/February 2004, which might be related to the fact that not all sites were counted.

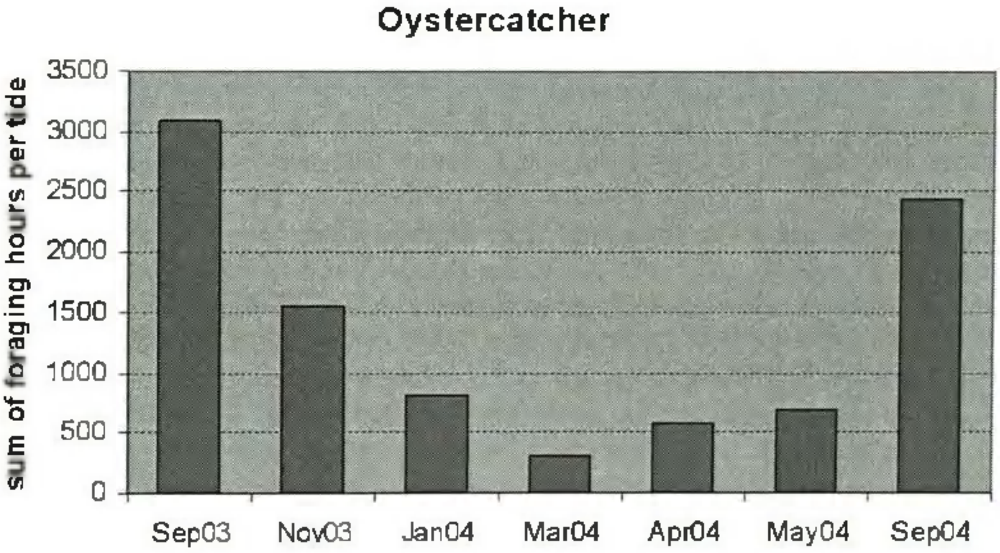


Figure 3-9. The total number of foraging hours of Oystercatchers during each of the observation periods. Note that the number of sites counted increased from 63 to 71 from March 2004 onwards. In January/February 2004 only 48 sites could be counted due to bad weather conditions.

3.3.2.3 Distribution

The Oystercatcher is among the more abundant of the species that we investigated. Due to its abundance, it proved possible to construct a distribution model for each of the counts (Table 3-5). In almost all cases, emersion time, current velocity and salinity had a significant effect. In the case of emersion time, this was often an optimum curve, but in the case of salinity we obtained a U-shaped function in the majority of cases. This was also the shape we obtained in the full annual model (Table 3-6). This is probably a statistical artefact and not in line with the observations of Van Kleunen (1999) and Stuart *et al.* (1990), who both observed that the density of Oystercatchers increased from low values in the brackish eastern part of the Westerschelde, to high values in the saline western part.

*Table 3-5. Monthly distribution models (**MOV**; see methods for details) for the Oystercatcher. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

	Sep03	Nov03	Jan/Feb04	Mar04	Apr04	May04	Sep04
constant	35.2	-12.61	-942	160.7	160.4	284.1	165.1
Emean	1.534	0.757	1.724	-0.3701	-0.546	0.885	0
Emean^2	-0.01364	-0.00758	-0.01432	0	0	-0.00846	0
Vmean	-0.205	-0.0802	0.2381	0	0.339	0.269	0
Vmean^2	0.002301	0	0	-0.00745	-0.01758	-0.01134	0
Salt	-5.3	0	62.1	-9.41	-8.46	-22.01	-12.08
Salt^2	0.0993	0	-1.084	0.1649	0.1448	0.3973	0.2224
Deviance explained	57.5%	31.0%	80.7%	70.1%	64.9%	59.1%	40.8%

Oystercatchers occurred over a wide range of current velocities and emersion times (Figure 3-10). Because not a single variable showed an optimum curve in the full annual model (Table 3-6), maximal densities of Oystercatchers were predicted outside the range of emersion times and current velocities over which we obtained data (Figure 3-11). Highest densities were predicted for low current velocities and long emersion times. This is probably a statistical artefact.

*Table 3-6. Parameter estimates of the full annual distribution model (**Y3VM**) for the Oystercatcher. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

constant	85
Emean	0
Emean^2	-0.00026
Vmean	-0.0727
Vmean^2	0
Salt	-5.90
Salt^2	0.108
Sep	1.52
Nov	1.01
Jan	0.679
Mar	-0.723
Apr	0
May	0
% Explained	27.6

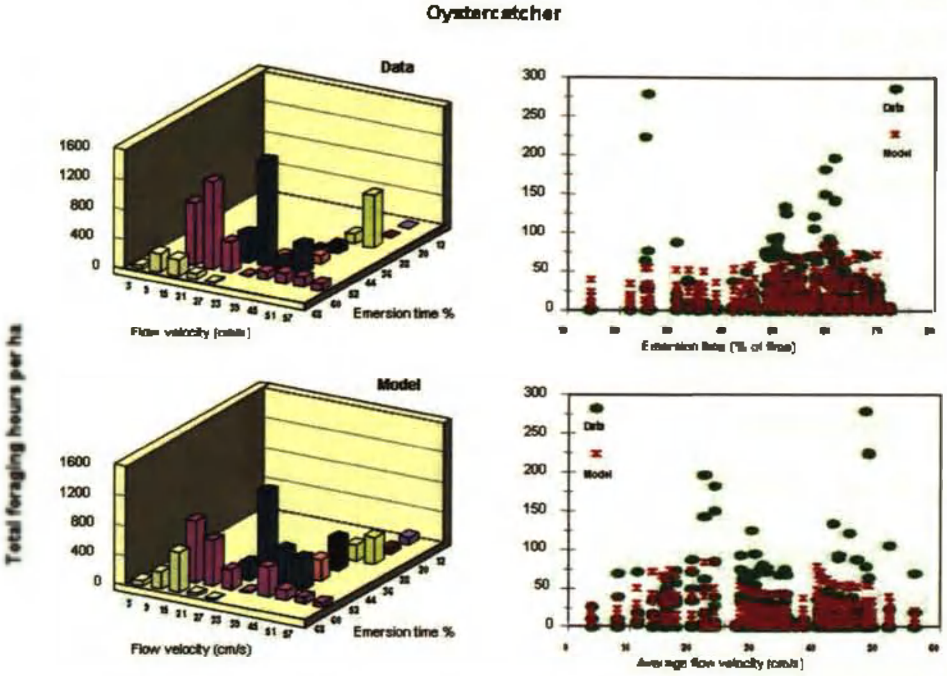


Figure 3-10. Distribution of Oystercatchers with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). (a) Foraging hours as a function of both variables as observed. (b) Foraging hours as a function of both variables as predicted. (c) Foraging hours as a function of emersion time, comparing observations and model predictions. (d) Foraging hours as a function of current velocity, comparing observations and model predictions.

As will be shown later, the Oystercatcher is the only species where actual measurements on the prey offer a better explanation of the distribution of the birds than models with abiotic data only. Since the benthic data were collected in the autumn of 2003, we averaged the bird count data for the counts of September 2003, November 2003 and January/February 2004. We restricted the analysis to prey known to be taken by Oystercatchers (Table 3-3). As was to be expected, large Cockles always showed a strong positive correlation to the foraging hours of Oystercatchers. Among the simple correlations, the highest correlation was with total biomass density of Cockles ($r=0.53$, $N=63$, $P<0.001$), followed by Cockles greater than 2 cm ($r=0.46$, $N=63$, $P<0.001$), Cockles between 1 and 2 cm ($r=0.33$, $N=63$, $P<0.01$). All other correlation coefficients were less than 0.3, but included significant correlations for *Macoma* 1-1.5 cm, *Macoma* >1.5 cm, total *Macoma*, *Scrobicularia* 1-3 cm, Lugworm with a width > 4 mm and total biomass density of Lugworm. Multiple regression with forward inclusion of terms, with prey separated by size class and species lead to a model with large Cockles, intermediate sized *Scrobicularia* and large Lugworms (Table 3-7). When prey were lumped per species, backward elimination of terms retained, apart from biomass density of Cockles, also the biomass density of *Scrobicularia* and Lugworms. However, forward inclusion of terms only lead to biomass density of Cockles being included in the model. This relationship is plotted in Figure 3-12, where each dot represents a plot, and Figure 3-13 where data are averaged per study site. It is clear that the absence of Oystercatchers from the study site Plaat van Baarland is due to the absence of Cockles. A striking absence of Cockles from the Plaat van Baarland was also noted by Duiker & Bos (1996) in 1996 and also according to the RIVO surveys Cockle densities were generally low at this site in the period 1992-2003 (Steenbergen *et al.* 2004). Earlier research showed that the particular morphological conditions of the site are unfavourable for Cockles (Bouma *et al.* 2001).

Table 3-7. Terms included in a linear regression model predicting the foraging hours per tide per ha of Oystercatchers (in the autumn and winter of 2003/2004) from biomass densities of their prey measured in the autumn of 2003.

	Unstandardized Coefficients		Standardized Coefficients	t	P
	B	SE	Beta		
(Constant)	12.614	4.875		2.587	.012
Cockles length > 2 cm	.305	.082	.394	3.712	.000
Scrobicularia length 1-3 cm	5.136	1.528	.365	3.362	.001
Lugworm width > 4 mm	3.170	1.467	.233	2.160	.035

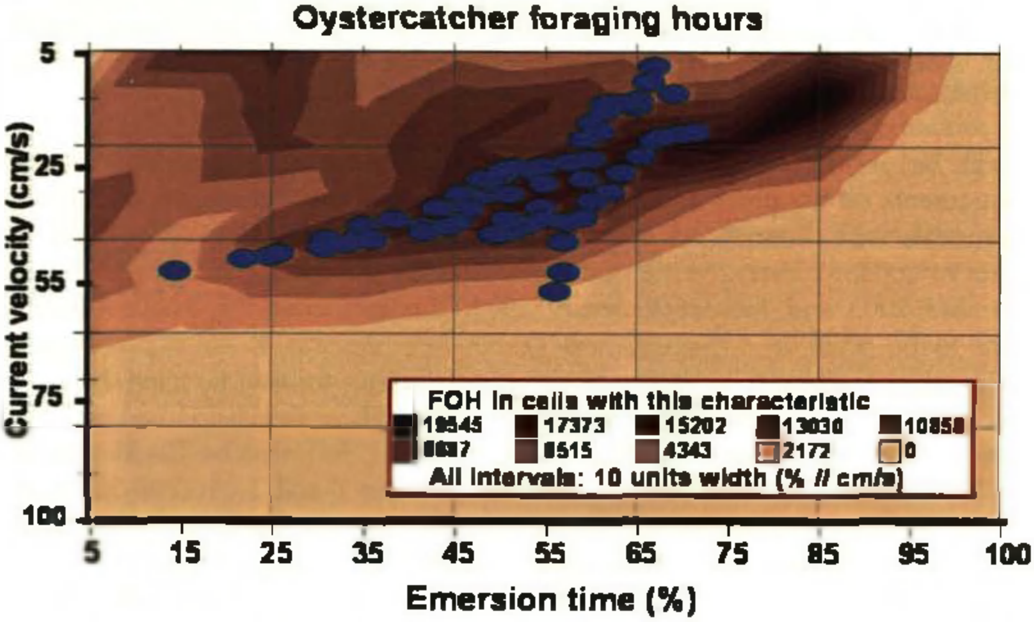


*Figure 3-11. Contour plot of predicted foraging hours of Oystercatcher with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). Predictions are based on the full annual model (**Y3VM**). Dots indicate the study plots. The numbers next to the boxes indicate the total number of foraging hours in each combined interval of 10% emersion time and 10 cm/s current velocity. The contour lines are derived from an interpolation of the scores and for this reason provide a false sense of accuracy.*

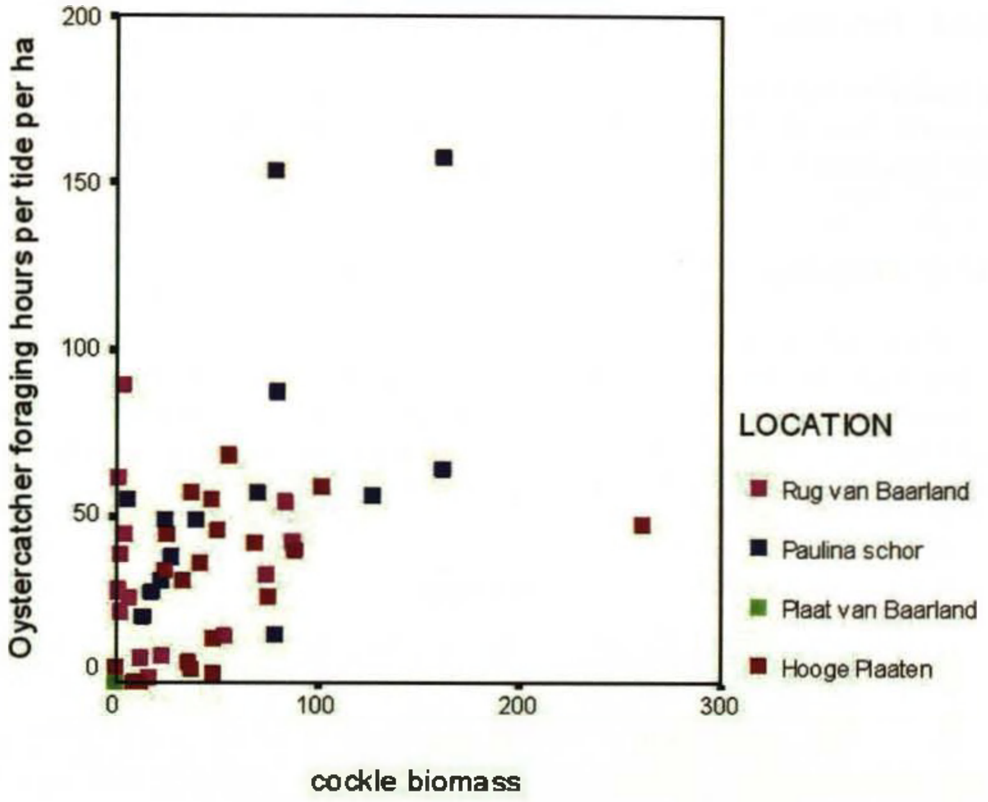


Figure 3-12. Total foraging hours of Oystercatchers per tide per ha plotted against the biomass density of Cockles. Each dot represents a study plot and plots of different sites are distinguished with separate symbols.

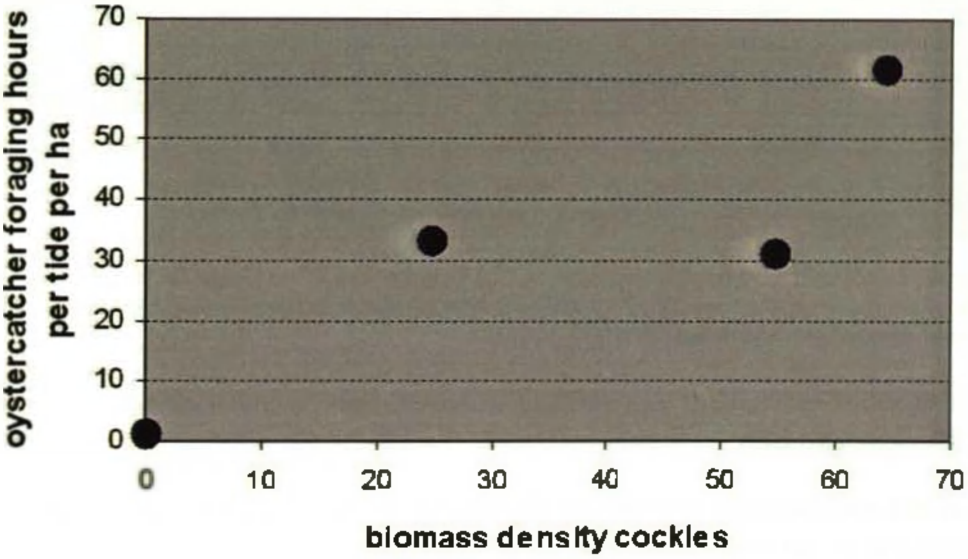


Figure 3-13. Total foraging hours of Oystercatchers per tide per ha plotted against the biomass density of Cockles. Each dot represents a study site.

3.3.3 Avocet

3.3.3.1 Prey choice

According to the review by Leopold *et al.* (2004) Avocet preferentially feed on the Ragworm *Nereis diversicolor*. Avocets also regularly feed in shallow water. We have no direct observations on the prey choice of the Avocet.

3.3.3.2 Phenology

Avocet numbers tend to peak in late autumn and a lower peak occurs in early spring. Numbers are low during winter and summer (Tulp *et al.* 2001). During most counts, we observed hardly any Avocets in our study plots, but a peak number occurred in November 2003 (Figure 3-14). This is in line with the general pattern, except that the variation in numbers is more extreme than in the general pattern.

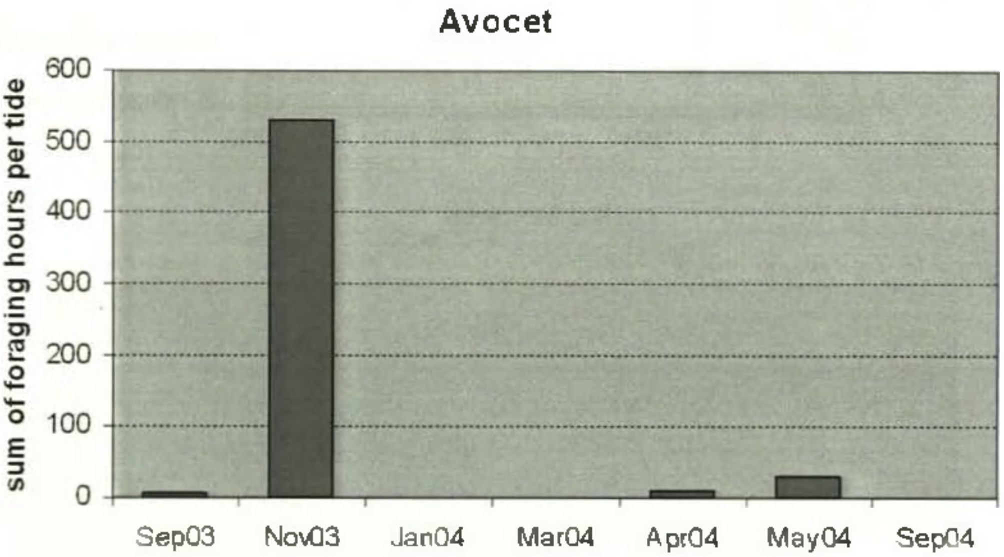


Figure 3-14. The total number of foraging hours of Avocet during each of the observation periods. Note that the number of sites counted increased from 63 to 71 from March 2004 onwards. In January/February 2004 only 48 sites could be counted due to bad weather conditions.

3.3.3.3 Distribution

We could not construct distribution models for Avocets, because they occurred too infrequently in our study sites.

3.3.4 Ringed Plover

3.3.4.1 Prey choice

According to the review by Leopold *et al.* (2004) Ringed Plover usually take small worms; they found no records of Ringed Plover taking bivalves.

We have only a few direct observations on the prey choice of the Ringed Plover, but they are in line with the general picture described above. On the Hooge Platen we observed 10 birds taking Ragworms. On the Plaat van Baarland we observed 3 birds taking Ragworms and 2 birds taking small unidentified worms.

3.3.4.2 Phenology

Ringed Plover reach peak numbers during autumn migration in August and September, whereas numbers are very low during other times of the year, with the exception of a small peak in May during spring migration (Berrevoets *et al.* 2002). Our counts are in line with this general pattern, except that we observed rather few birds in May (Figure 3-15).

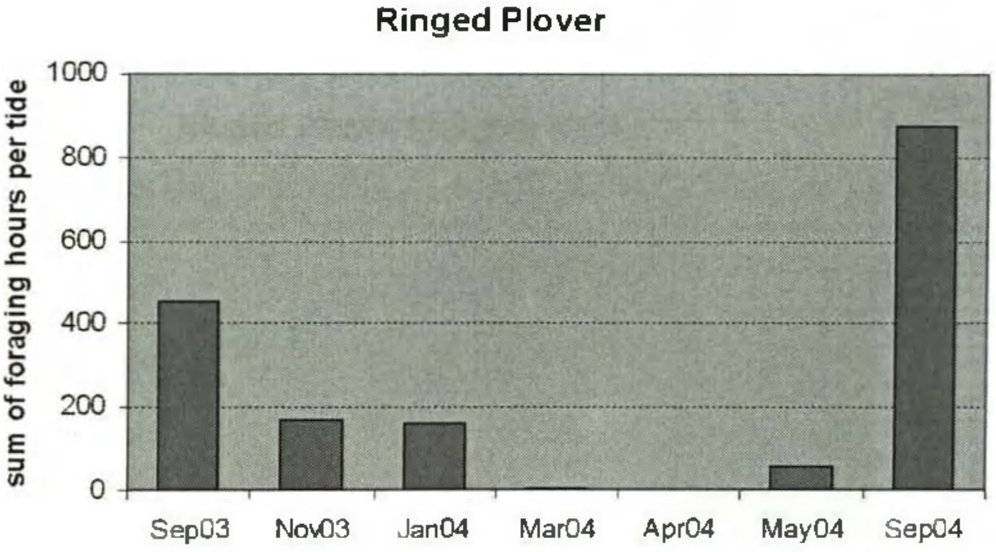


Figure 3-15. The total number of foraging hours of Ringed Plover during each of the observation periods. Note that the number of sites counted increased from 63 to 71 during the study. In January/February 2004 not all sites could be counted due to bad weather conditions.

3.3.4.3 Distribution

For the counts for which we could construct a distribution model, emersion time, current velocity and salinity significantly affected the distribution of Ringed Plover in the majority of cases (Table 3-8). The deviance that was explained was sometimes very high. However, it is possible that this is a statistical artefact resulting from a few counts with high numbers. The outliers in Figure 3-16 support this view.

The full annual model includes emersion time, current velocity and salinity and for all three variables the parameter values indicate an optimum curve (Table 3-9). The summary graph suggests that Ringed Plover have a quite narrow distribution and occur only in areas with rather long emersion times and intermediate current velocities(Figure 3-16). The contour plot also indicates an optimum, but this optimum is outside the combined range of emersion time and current velocity in which we did our measurements on the birds (Figure 3-17).

*Table 3-8. Monthly distribution models (**MOV**: see methods for details) for the Ringed Plover. We could not construct models for March, April and May 2004. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

	Sep03	Nov03	Jan/Feb04	Sep04
constant	-12.82	-12531	-22	-222.3
Emean	0	0	[illegible]	0.3082
$Emean^2$	0.000516	0	-0.02898	0
Vmean	0.875	2.642	0.546	1.521
$Vmean^2$	-0.01366	-0.03769	0	-0.01787
Salt	0	932.1	-4.19	12.54
$Salt^2$	0	-17.34	0	-0.2189
Deviance explained	43.4%	98.9%	97.4%	66.3%

*Table 3-9. Parameter estimates of the full annual distribution model (**Y3VM**) for the Ringed Plover. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

constant	-181.5
Emean	0.580
$Emean^2$	-0.003
Vmean	1.047
$Vmean^2$	-0.012
Salt	9.810
$Salt^2$	-0.172
Sep	2.417
Nov	1.069
Jan	1.042
Mar	-2.320
Apr	-6.390
May	0
Deviance Explained	63.7%

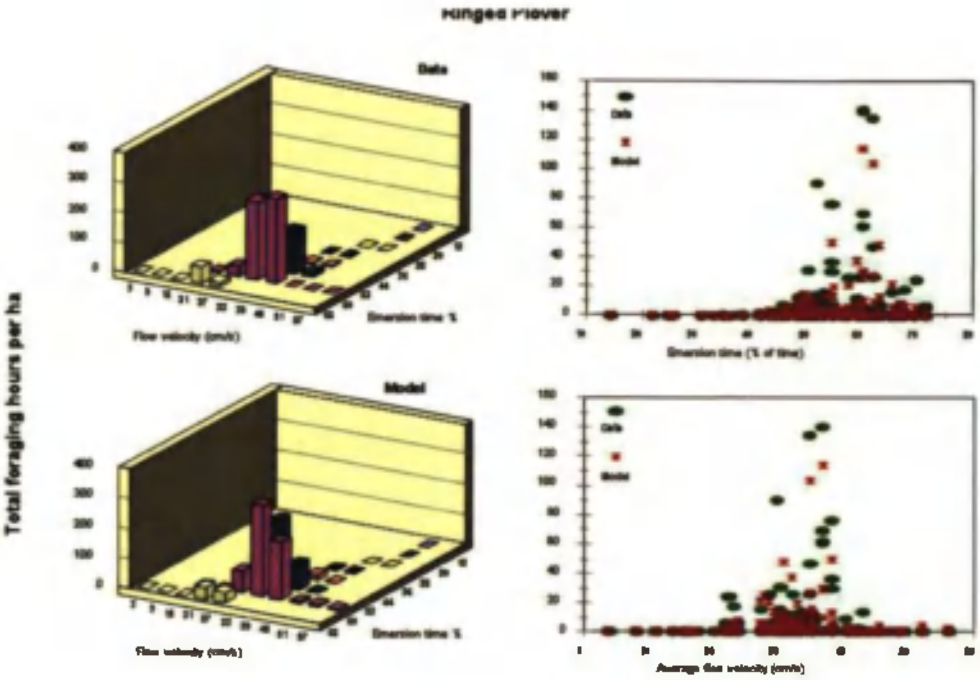


Figure 3-16. Distribution of Ringed Plover with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). (a) Foraging hours as a function of both variables as observed. (b) Foraging hours as a function of both variables as predicted. (c) Foraging hours as a function of emersion time, comparing observations and model predictions. (d) Foraging hours as a function of current velocity, comparing observations and model predictions.

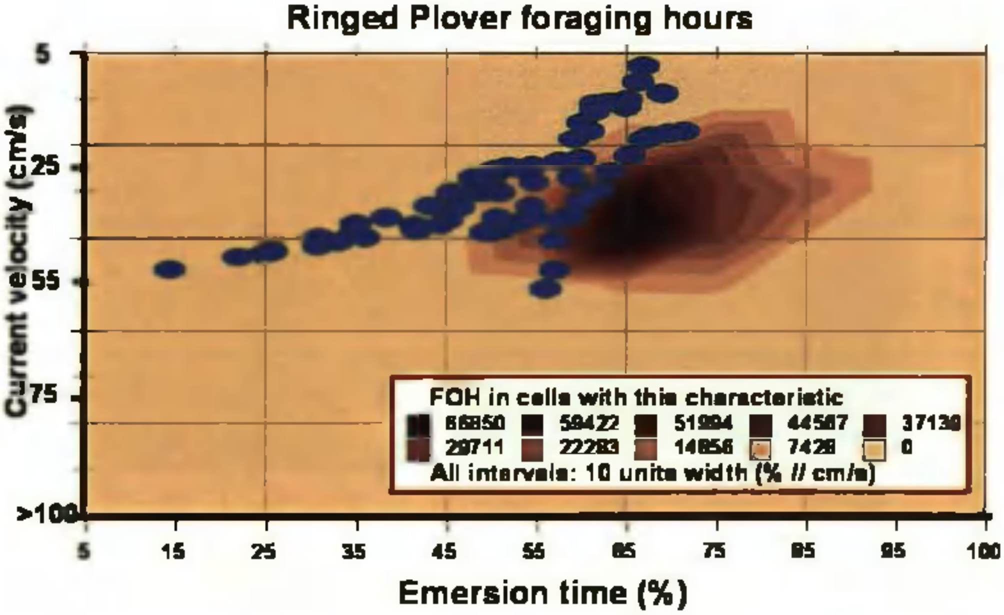


*Figure 3-17. Contour plot of predicted foraging hours of Ringed Plover with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). Predictions are based on the full annual model (**Y3VM**). Dots indicate the study plots. The numbers next to the boxes indicate the total number of foraging hours in each combined interval of 10% emersion time and 10 cm/s current velocity. The contour lines are derived from an interpolation of the scores and for this reason provide a false sense of accuracy.*

3.3.5 Grey Plover

3.3.5.1 Prey choice

According to the review by Leopold *et al.* (2004) Grey Plover preferentially prey on large worms, especially Ragworms, but also take bivalves and small worms. They rarely take crustaceans.

We have only a few direct observations on the prey choice of Grey Plover, but they fit the general pattern described above. On the Hooge Platen 8 birds were observed to take Ragworms. On the Plaat van Baarland, 1 bird was observed to take Ragworms and 3 birds took unknown worms.

3.3.5.2 Phenology

Grey Plover are virtually absent from the Westerschelde in June and July. Peak numbers occur during spring migration in May and during autumn migration in September. Numbers are somewhat lower during late autumn, winter and early spring (Berrevoets *et al.* 2002). In our counts, high numbers in September 2003 and May 2004 are in line with this pattern, but low numbers in September 2004 and especially the peak count in March 2004 are not (Figure 3-18).

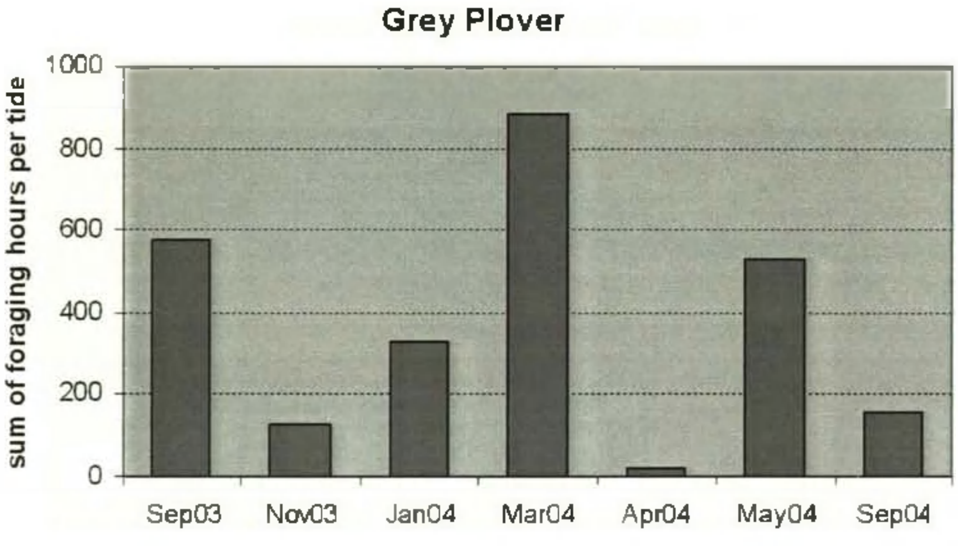


Figure 3-18. The total number of foraging hours of Grey Plover during each of the observation periods. Note that the number of sites counted increased from 63 to 71 from March 2004 onwards. In January/February 2004 only 48 sites could be counted due to bad weather conditions.

3.3.5.3 Distribution

Grey Plover were sufficiently abundant in the study plots to construct models for each of the counts (Table 3-10). Nearly always, emersion time, current velocity and salinity had a significant effect, but the shape of the curves differed between months. As a result, the full annual model, which also included all three variables (Table 3-11), explained much less of the deviance than many of the models for a particular month. According to previous studies, Grey Plover occur throughout the estuary in spring and summer, but are confined to the saline western part in winter (Stuart *et al.* 1990; van Kleunen 1999). Thus, a change in distribution pattern could be real, but the relationship with salinity that we observed in January is very likely a statistical artefact.

Grey Plover did not occur in areas with short emersion times and high current velocities (Figure 3-19). Van Kleunen (1999) did not observe a clear relationship with emersion time, but his data suggested a strong preference for muddy areas. The full annual model indicated optimal values for intermediate emersion times and low current velocities, corresponding to high silt content (Table 3-11, Figure 3-20). These values are within the combined range of emersion time and current velocity over which we collected data.

*Table 3-10. Monthly distribution models (**MOV**; see methods for details) for the Grey Plover. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

	Sep03	Nov03	Jan/Feb04	Mar04	Apr04	May04	Sep04
constant	-63.6	-45.4	3011	-277.2	-4737	-149.2	-37.2
Emean	0.3652	1.814	3.629	0.584	0	0	0.1624
Emean^2	0	-0.01757	-0.02893	-0.00379	-0.00632	-0.0008	0
Vmean	1.106	0	0	0	0	0.176	0.958
Vmean^2	-0.01246	0	0.01291	0.00208	-0.01096	-0.00366	-0.01024
Salt	0.832	0	-227.2	18	323	11.47	0.33
Salt^2	0	0	4.08	-0.313	-5.48	-0.2143	0
Deviance explained	63.7%	28.1%	68.7%	63.4%	44.0%	32.6%	28.5%

*Table 3-11. Parameter estimates of the full annual distribution model (**Y3VM**) for the Grey Plover. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

constant	-111
Emean	0.427
Emean^2	-0.003
Vmean	0.074
Vmean^2	0.000
Salt	6.870
Salt^2	-0.121
Sep	0.000
Nov	-1.180
Jan	0.000
Mar	0.782
Apr	-2.930
May	0
Deviance Explained	27.6%

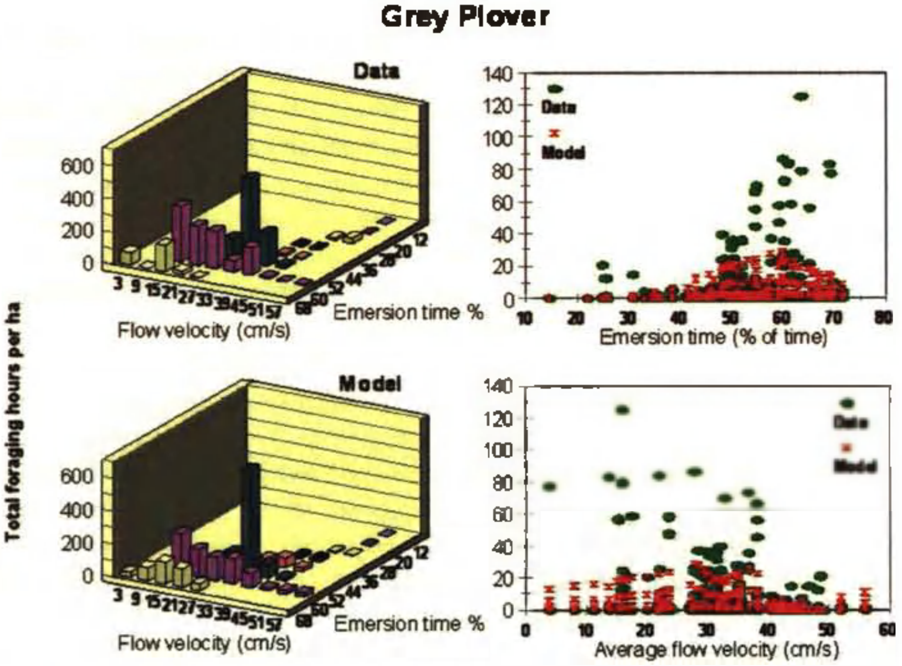


Figure 3-19. Distribution of Grey Plover with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). (a) Foraging hours as a function of both variables as observed. (b) Foraging hours as a function of both variables as predicted. (c) Foraging hours as a function of emersion time, comparing observations and model predictions. (d) Foraging hours as a function of current velocity, comparing observations and model predictions.

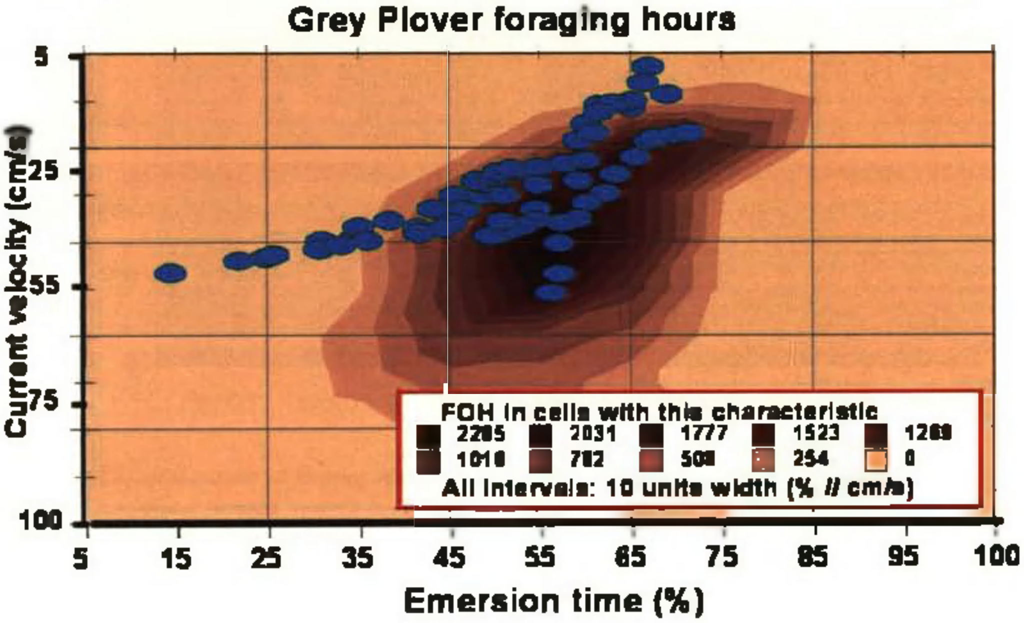


*Figure 3-20. Contour plot of predicted foraging hours of Grey Plover with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). Predictions are based on the full annual model (**Y3VM**). Dots indicate the study plots. The numbers next to the boxes indicate the total number of foraging hours in each combined interval of 10% emersion time and 10 cm/s current velocity. The contour lines are derived from an interpolation of the scores and for this reason provide a false sense of accuracy.*

3.3.6 Knot

3.3.6.1 Prey choice

Knot usually prey on bivalves and the relatively thin-shelled Baltic Tellin are preferred, but the birds can also feed on small Cockles and Mussels (Leopold *et al.* 2004). Knots are unique in that they hardly ever prey on worms.

We have no direct observations on the prey choice of Knot.

3.3.6.2 Phenology

High numbers of Knot occur in the Delta between October and March (Berrevoets *et al.* 2002). This pattern is not observed in our counts, where we had a massive influx of Knots in our study sites in November 2003 and observed only a few birds, or no birds at all, during the other counts (Figure 3-21). In the western Wadden Sea, and probably in the Delta area as well, Knots feed in large flocks that roam over large distances (Piersma *et al.* 1993). Whether or not a flock lands to feed in a particular area is partly a matter of chance.

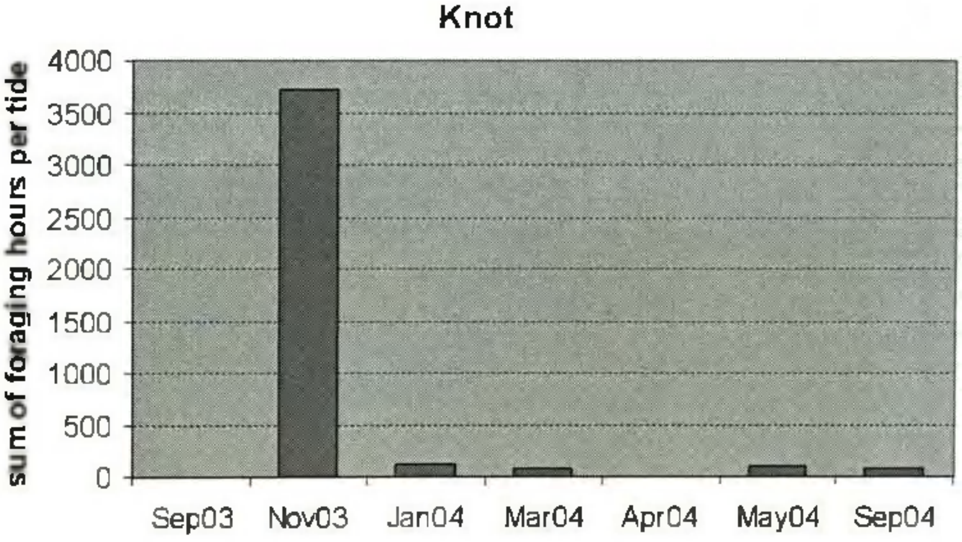


Figure 3-21. The total number of foraging hours of Knot during each of the observation periods. Note that the number of sites counted increased from 63 to 71 from March 2004 onwards. In January/February 2004 only 48 sites could be counted due to bad weather conditions.

3.3.6.3 Distribution

Emersion time, current velocity and salinity significantly influenced the distribution of Knot in the six counts for which it proved possible to build a distribution model (Table 3-12). The same variables were also included in the full annual model (Table

3-13). The amount of deviance that was explained by the monthly models varied between 28% and 83%.

When the parameter estimates are examined in more detail we find that only in a minority of cases an optimum, or a truncated optimum is indicated (Table 3-12). Stuart *et al.* (1990) only observed Knots in the mouth of the Westerschelde, so it is surprising that we find an optimum, instead of a monotonic increase in numbers with salinity.

Figure 3-22 suggests that Knot occur in a rather narrow range of habitats with intermediate emersion times and intermediate current velocities. Figure 3-22 also shows that there are a few extreme data points and these probably caused models that did not predict optimum curves inside the narrow range that visual inspection of the data suggests. The extreme data points are probably also responsible for the fact that the full annual model predicted maximal densities outside the combined range of emersion time and current velocity over which we collected data (Figure 3-23).

*Table 3-12. Monthly distribution models (**MOV**; see methods for details) for the Knot. We could not construct a model for April 2004. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

	Sep03	Nov03	Jan/Feb04	Mar04	May04	Sep04
constant	-192.3	583	-40487	-734	-235.1	-37.2
Emean	0	-0.3071	0	8.68	0.08	0
Emean^2	0	0	-0.01371	-0.0745	0	0.001776
Vmean	0	0	35.5	0.442	0.2429	1.294
Vmean^2	-0.01385	-0.0088	-0.553	0	0	-0.01857
Salt	0	-41	2475	33.45	15.55	0.364
Salt^2	0.219	0.747	-55.1	-0.589	-0.282	0
Deviance explained	68.5%	50.0%	83.2%	61.9%	28.2%	40.0%

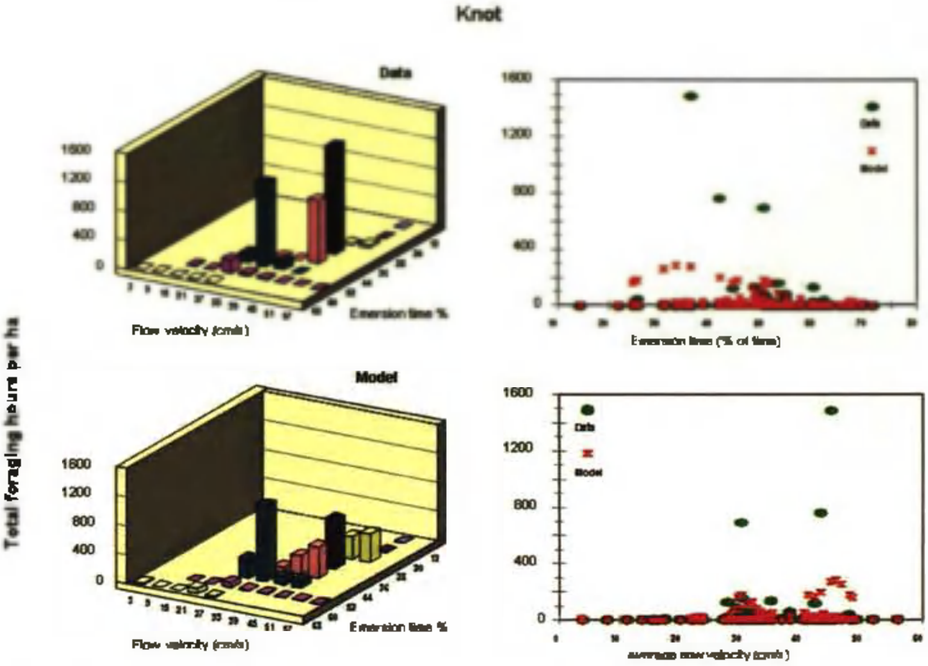


Figure 3-22. Distribution of Knot with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). (a) Foraging hours as a function of both variables as observed. (b) Foraging hours as a function of both variables as predicted. (c) Foraging hours as a function of emersion time, comparing observations and model predictions. (d) Foraging hours as a function of current velocity, comparing observations and model predictions. Ivonne

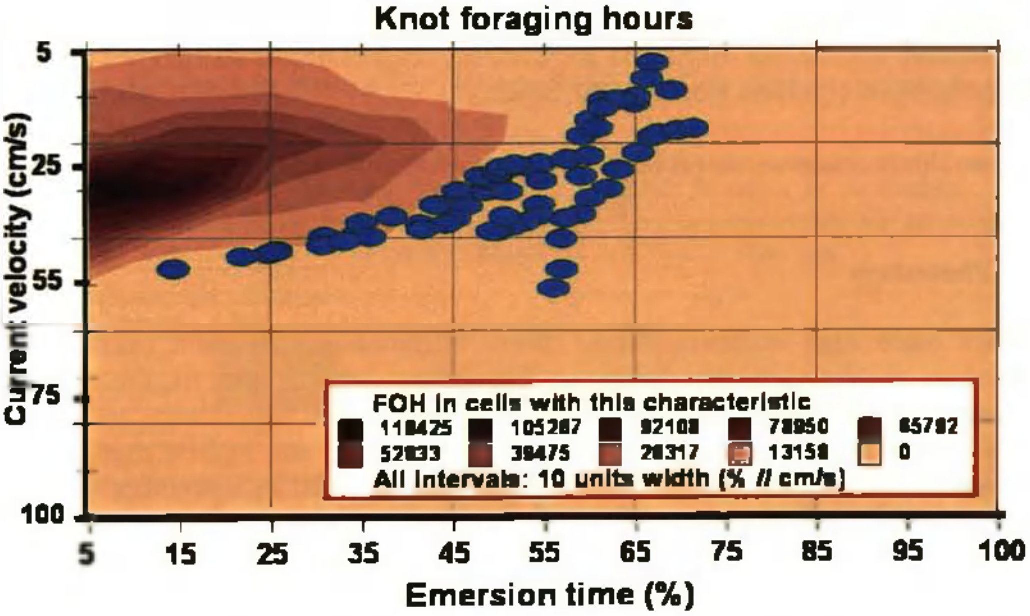


*Figure 3-23. Contour plot of predicted foraging hours of Knot with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). Predictions are based on the full annual model (**Y3VM**). Dots indicate the study plots. The numbers next to the boxes indicate the total number of foraging hours in each combined interval of 10% emersion time and 10 cm/s current velocity. The contour lines are derived from an interpolation of the scores and for this reason provide a false sense of accuracy.*

*Table 3-13. Parameter estimates of the full annual distribution model (**Y3VM**) for the Knot. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

constant	183
Emean	-0.205
Emean^2	0
Vmean	0.52
Vmean^2	-0.0125
Salt	-12.7
Salt^2	0.228
Sep	0
Nov	3.69
Jan	1.14
Mar	0
Apr	-2.48
May	0
Deviance Explained	52.9%

3.3.7 Sanderling

3.3.7.1 Prey choice

The Sanderling is a rather opportunistic species that feeds on anything edible washed on the beach. According to Leopold *et al.* (2004) the worm (*Scololepis squamata*) is often mentioned as prey, but they could not trace the original observation, other than that this is the most common worm on the beach.

We have no direct observations on the prey choice of the Sanderling.

3.3.7.2 Phenology

Sanderlings reach high numbers during spring migration in May and occur in relatively low numbers in the Westerschelde during other times of the year (Berrevoets *et al.* 2002). Our counts in the plots bear some resemblance to this pattern. In many months, we did not count any Sanderlings and highest numbers were counted in May (Figure 3-24). However, numbers counted in November were similar to numbers counted in May.

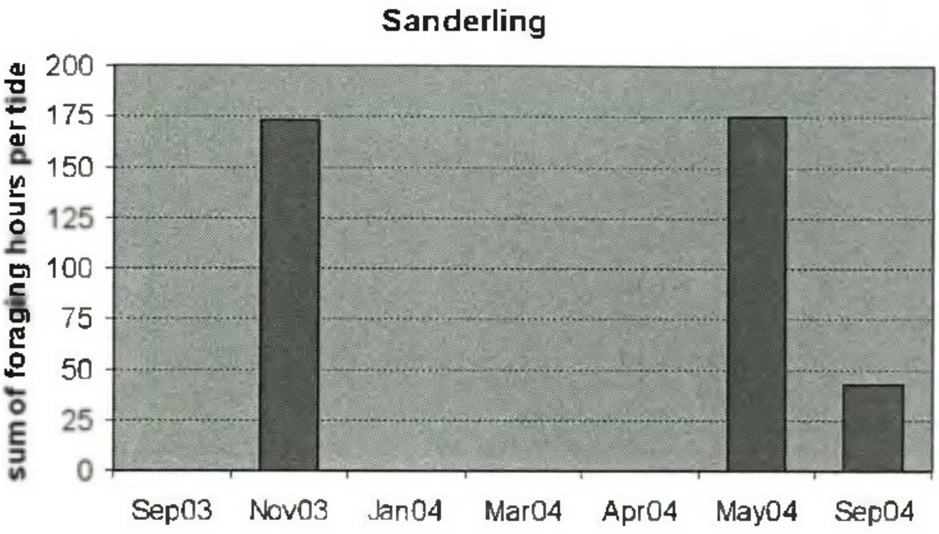


Figure 3-24. The total number of foraging hours of Sanderling during each of the observation periods. Note that the number of sites counted increased from 63 to 71 from March 2004 onwards. In January/February 2004 only 48 sites could be counted due to bad weather conditions.

3.3.7.3 Distribution

For Sanderling we could only construct a model for September 2004 (Table 3-14), which included emersion time, current velocity and salinity. The full annual model did incorporate data of other months and differed qualitatively from the model for September 2004 (Table 3-15). Stuart *et al.* (1990) did not observe Sanderlings in the brackish eastern part of the Westerschelde, but no clear preference for either the central or western part of the area.

*Table 3-14. Monthly distribution models (**MOV**; see methods for details) for the Sanderling. We could only construct a model for September 2004. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

	Sep04
Constant	968
Emean	5.5
Emean^2	-0.0566
Vmean	-1.277
Vmean^2	0
Salt	-78
Salt^2	1.418
Deviance explained	63.7%

*Table 3-15. Parameter estimates of the full annual distribution model (**Y3VM**) for the Sanderling. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

constant	1300
Emean	0.361
Emean^2	-0.00175
Vmean	0.623
Vmean^2	-0.00493
Salt	-101.0
Salt^2	1.89
Sep	-2.11
Nov	0.00
Jan	-9.50
Mar	-10.40
Apr	-10.40
May	-0.032
Deviance Explained	63.4%

3.3.8 Dunlin

3.3.8.1 Prey choice

Dunlin feed mostly on small worms, i.e. small individuals of species like *Nereis* and *Lanice*, but can also take small bivalves and crustaceans (Leopold *et al.* 2004). We have no direct observations of the prey choice of Dunlin.

3.3.8.2 Phenology

Dunlin are virtually absent from the Westerschelde in the period June-September and then increase to high numbers in late autumn/early winter after which numbers decline again (Berrevoets *et al.* 2003). This seasonal pattern is also reflected in observations in the study plots (Figure 3-25).

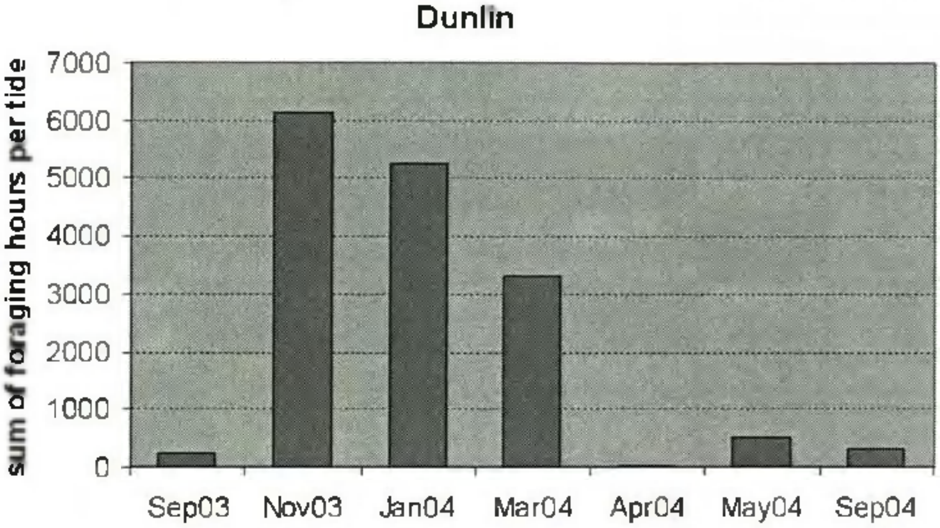


Figure 3-25. The total number of foraging hours of Dunlin during each of the observation periods. Note that the number of sites counted increased from 63 to 71 from March 2004 onwards. In January/February 2004 only 48 sites could be counted due to bad weather conditions.

3.3.8.3 Distribution

Emersion time, current velocity and salinity significantly influenced the distribution of Dunlin in the six counts for which it proved possible to build a distribution model (Table 3-16). The same variables were also included in the full annual model (Table 3-17). The amount of deviance that was explained by the monthly models varied between 37% and 94%. In slightly more than half the cases, the parameter values indicated an optimum curve (Table 3-16) and in the full annual model, an optimum curve was implicated for all three variables (Table 3-17).

Stuart *et al.* (1990) only observed Dunlin in the saline western part of the Westerschelde, but Van Kleunen (1999) also observed Dunlin in the central part. With regard to emersion time and current velocity (a proxy for silt content), our results (Figure 3-26) are slightly different from those of Van Kleunen (1999), who observed maximal densities in areas with emersion times exceeding 60% and silt contents exceeding 50%.

The contour plot indicates that maximal numbers of foraging hours are predicted within the combined range of emersion time and current velocity over which we collected data (Figure 3-27).

*Table 3-16. Monthly distribution models (**MOV**; see methods for details) for the Dunlin. It was not possible to construct a model for April 2004. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

	Sep03	Nov03	Jan/Feb04	Mar04	May04	Sep04
Constant	-78.49	-251	-23.4	-306.1	-257.5	-40.8
Emean	0.619	2.556	1.244	0.776	1.656	0.2117
Emean²	0	-0.02153	-0.0117	-0.00554	-0.00916	0
Vmean	0.962	0	0	0.541	0.1169	1.39
Vmean²	-0.00944	0.001871	0	-0.00806	0	-0.01791
Salt	0	13.59	-0.1478	19.45	16.61	0
Salt²	0.02899	-0.2411	0	-0.341	-0.301	0.00674
Deviance explained	94.3%	51.9%	37.5%	64.3%	36.9%	36.9%

*Table 3-17. Parameter estimates of the full annual distribution model (**Y3VM**) for the Dunlin. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

Constant	-169
Emean	1.180
Emean²	-0.0104
Vmean	0.152
Vmean²	-0.00125
Salt	9.68
Salt²	-0.1[illegible]
Sep	-0.649
Nov	2.25
Jan	2.37
Mar	1.86
Apr	-2.67
May	0
Deviance Explained	57.8%

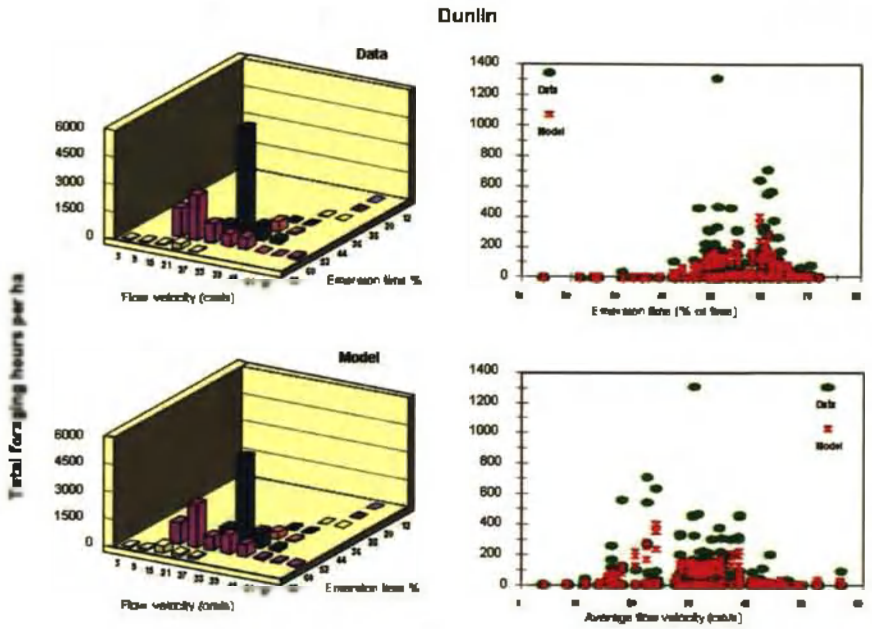


Figure 3-26. Distribution of Dunlin with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). (a) Foraging hours as a function of both variables as observed. (b) Foraging hours as a function of both variables as predicted. (c) Foraging hours as a function of emersion time, comparing observations and model predictions. (d) Foraging hours as a function of current velocity, comparing observations and model predictions.

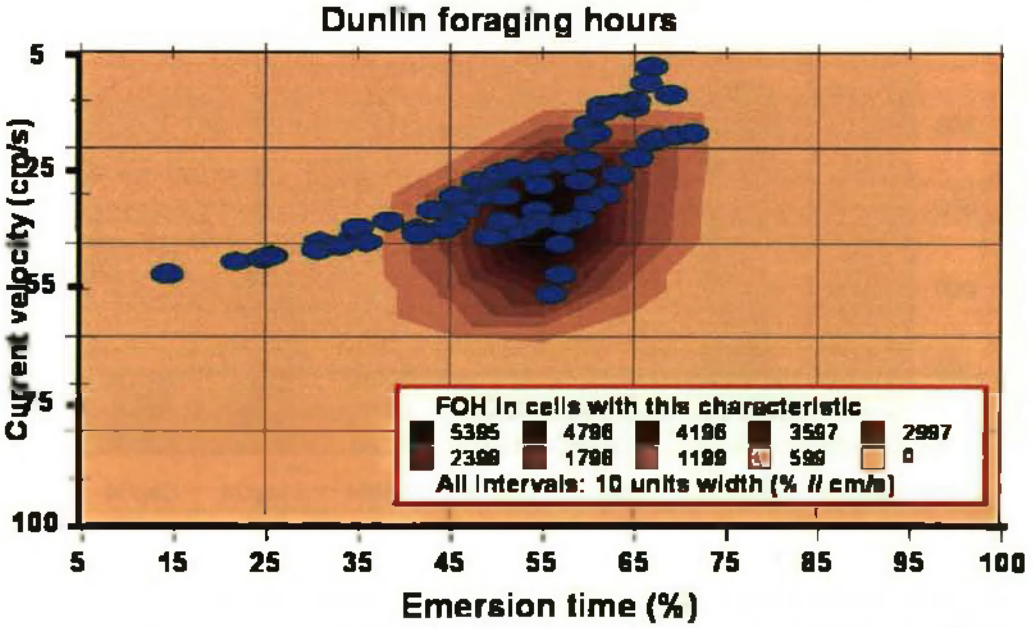


*Figure 3-27. Contour plot of predicted foraging hours of Dunlin with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). Predictions are based on the full annual model (**Y3VM**). Dots indicate the study plots. The numbers next to the boxes indicate the total number of foraging hours in each combined interval of 10% emersion time and 10 cm/s current velocity. The contour lines are derived from an interpolation of the scores and for this reason provide a false sense of accuracy.*

3.3.9 Bar-tailed Godwit

3.3.9.1 Prey choice

According to the review of Leopold *et al.* (2004) Bar-tailed Godwits can feed on a wide range of prey species. Usually, worms like *Nereis*, *Nephtys* and *Scoloplos* are the staple food; several species of bivalve are also regularly taken.

We have only a few direct observations on the prey choice of Bar-tailed Godwit, but they are in line with the above description of the diet. On the Rug van Baarland, 2 birds took Baltic Tellin. On the Hooge Platen, 4 birds took Baltic Tellin and 5 birds took Ragworm.

3.3.9.2 Phenology

The phenology of the Bar-tailed Godwit is very similar to the phenology of the Sanderling: high numbers in May during spring migration and low numbers during other times of the year (Berrevoets *et al.* 2002). As with the Sanderling, the pattern in our observations resembled this pattern, except for November when we also counted high numbers (Figure 3-28). In fact, the foraging hours that we observed in November 2003 were double the number that we observed in May 2004.

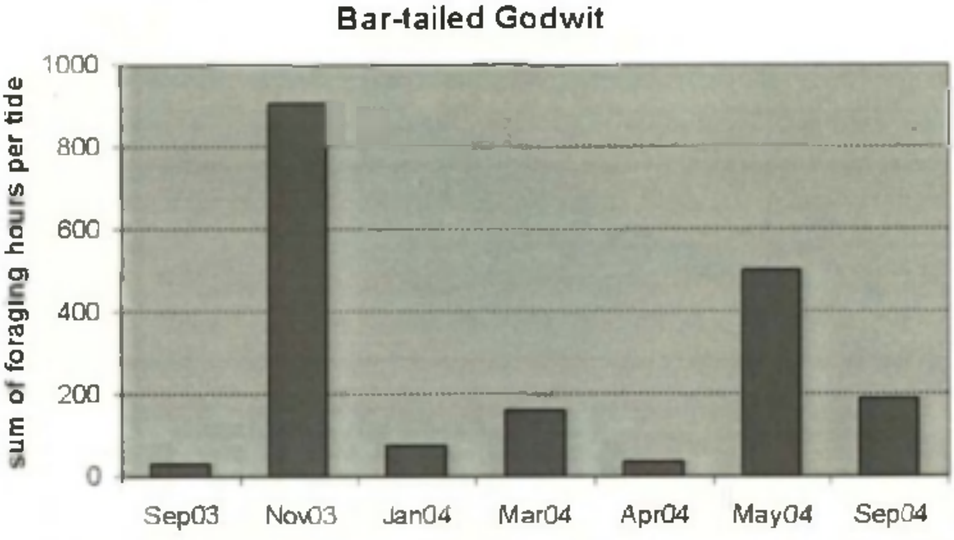


Figure 3-28. The total number of foraging hours of Bar-tailed Godwit during each of the observation periods. Note that the number of sites counted increased from 63 to 71 from March 2004 onwards. In January/February 2004 only 48 sites could be counted due to bad weather conditions.

3.3.9.3 Distribution

In most of the six months for which we could construct a distribution model, emersion time, current velocity and salinity had a significant effect (Table 3-18). In two of the monthly models, current velocity was not included, and it also fell out of the full annual model (Table 3-19).
Figure 3-29 suggests that Bar-tailed Godwits occur in a narrow range of intermediate current velocities and emersion times. Yet, in only slightly more than half of the cases did the monthly models predict an optimum curve for these variables.

Even though current velocity is not included in the full annual model, the contour plot suggests an optimum for current velocities between 15 and 50 cm/s (Figure 3-30). We suspect this is due to an underlying correlation between current velocity and salinity.

*Table 3-18. Monthly distribution models (**MOV**; see methods for details) for the Bar-tailed Godwit. We could not construct a model for April 2004. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

	Sep03	Nov03	Jan/Feb04	Mar04	May04	Sep04
constant	291	240	-660766	-43.4	134.5	-72.8
Emean	0	2.322	11.71	0	1.116	0.3667
Emean^2	0	-0.02295	-0.207	0.000012	-0.01044	0
Vmean	0.286	0	0	1.729	0	1.671
Vmean^2	-0.00895	0	0	-0.0351	-0.00277	-0.01669
Salt	-21.55	-23.1	43282	0.838	-12.05	0
Salt^2	0.394	0.442	-709	0	0.2249	0.02134
Deviance explained	28.4%	83.6%	96.0%	43.4%	57.4%	55.1%

*Table 3-19. Parameter estimates of the full annual distribution model (**Y3VM**) for the Bar-tailed Godwit. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

Constant	24.6
Emean	1.08
Emean^2	-0.01
Vmean	0
Vmean^2	0
Salt	-4.46
Salt^2	0.092
Sep	-1.51
Nov	0.592
Jan	-1.86
Mar	-1.15
Apr	-2.74
May	0
Deviance Explained	59.8%

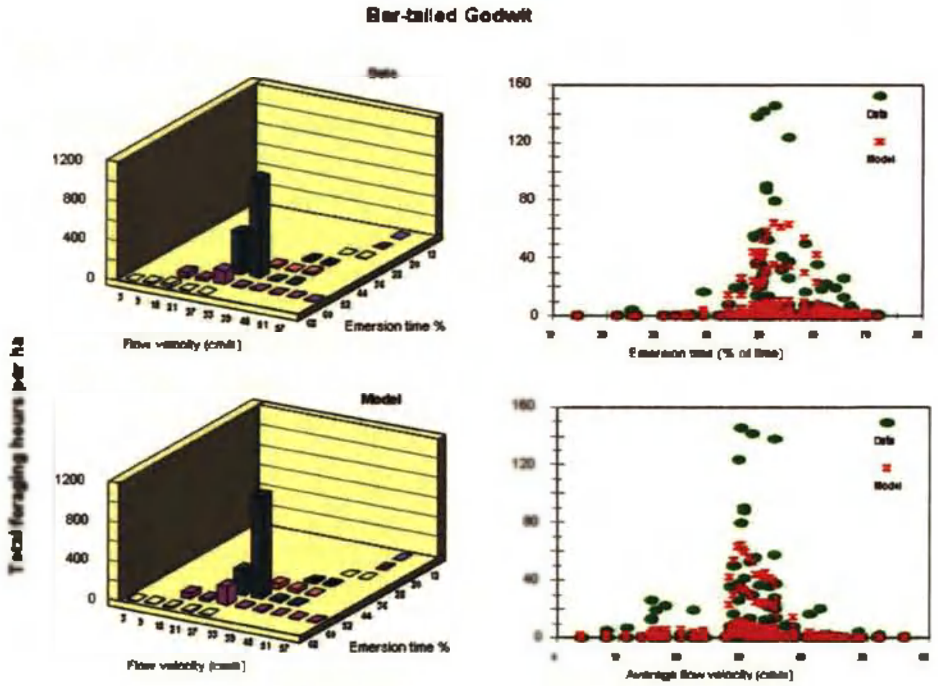


Figure 3-29. Distribution of Bar-tailed Godwit with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). (a) Foraging hours as a function of both variables as observed. (b) Foraging hours as a function of both variables as predicted. (c) Foraging hours as a function of emersion time, comparing observations and model predictions. (d) Foraging hours as a function of current velocity, comparing observations and model predictions.

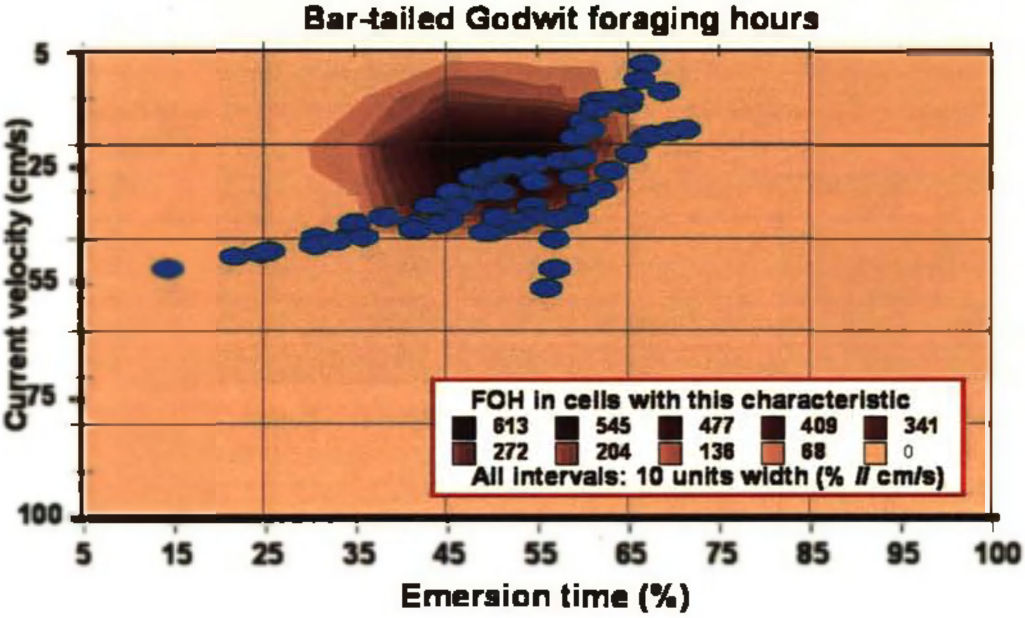


*Figure 3-30. Contour plot of predicted foraging hours of Bar-tailed Godwit with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). Predictions are based on the full annual model (**Y3VM**). Dots indicate the study plots. The numbers next to the boxes indicate the total number of foraging hours in each combined interval of 10% emersion time and 10 cm/s current velocity. The contour lines are derived from an interpolation of the scores and for this reason provide a false sense of accuracy.*

3.3.10 Curlew

3.3.10.1 Prey choice

The prey choice of Curlews has been extensively studied in the Netherlands. These studies included both muddy areas: the Frisian coast near Paesens Moddergat (Ens & Zwarts 1980; Ens & de Vries 1983; Zwarts & Wanink 1984), the Groningen coast (de Vlas 1970), the very muddy Dollard area (Esselink & van Belkum 1986), the muddy and brackish Ventjagersplaten (Zwarts 1974), as well as more sandy mud flats close to Vlieland (van der Baan et al. 1958), Schiermonnikoog (Voss & Koolhaas 1969; Roselaar 1970) and Ameland (Kersten & Piersma, in Smit & Wolff (1981)). Prey choice of Curlews has also been studied in Germany (Höfmann & Hoerschelmann 1969; Knief 1987; Petersen & Exo 1999), Denmark (Kiis 1986), and the United Kingdom (Goss-Custard & Jones 1976; Cramp & Simmons 1983; Evans *et al.* 1979), including a study by Goss-Custard & Jones (1976) on tidal flats with a high density of *Lanice* where 70% of the prey taken consisted of *Lanice*, and the remainder of the prey consisted of Shorecrabs. From this work, based on a large number of observations and analyses of pellets, faeces and stomachs, a very diverse diet emerges, consisting of a diversity of bivalves (with *Mya* being the most important species though), a variety of large worm species (mainly *Nereis* and to a lesser extent *Arenicola* and *Lanice*) and about 20% other prey, mainly Shorecrabs (a preferred prey in summer and early autumn) and occasionally shrimps. Curlews also regularly feed in meadows on earthworms and other meadow prey, especially when these meadows are wet as happens during stormy weather in autumn and spring. As long as the meadows do not freeze, they are a good alternative feeding place when the mud flats are not available for feeding. Being large, Curlews need large prey to survive, so they cannot survive on small worms or mud snails.

According to our own observations, Ragworms were the most important prey item in the Westerschelde, followed by Shorecrabs and bivalves (Table 3-20). These findings fit well with observations on the Ventjagersplaten, where almost no other prey than *Nereis* were taken (Zwarts 1974) and an analysis of Curlew faeces in the Westerschelde, indicating *Nereis* and Shorecrabs as the main prey (Ruiters 1992). When Curlews ingest shells of *Macoma* this is often as grit for their gizzard, so the observation of Ruiters (1992) of *Macoma* fragments should not lead us to believe that *Macoma* is an important prey item. The greater emphasis on worms compared to other studies could be due to the fact that the most abundant bivalve in the Westerschelde, the Cockle, is not a regular prey item of Curlews.

Table 3-20. Observations of prey species taken by Curlew feeding in the study sites. For each location the number of individuals seen to take a particular prey was recorded on several days.

	Plaat van Baarland	Hooge Platen	Paulina schor	Rug van Baarland	total	%
Mya arenaria	0	2	0	0	2	2%
Macoma balthica	0	0	1	0	1	1%
Scrobicularia plana	0	2	0	1	3	3%
Unknown bivalve	4	0	0	0	4	4%
Cerastoderma edule	0	0	0	4	4	4%
Carcinus maenas	1	17	2	2	22	20%
Arenicola marina	0	2	0	0	2	2%
Nereis diversicolor	2	26	3	32	63	57%
Unknown worm	3	0	0	0	3	3%
Small prey	1	0	0	5	6	5%

3.3.10.2 Phenology

The seasonal pattern in the number of Curlews in the Delta area hasn't changed during the last decades (Berrevoets *et al.* 2001): a few summering birds in May and June, highest numbers in late summer and early autumn, lower numbers in midwinter and a second peak in early spring, which is lower than the peak in autumn. This pattern is also reflected in the number of birds counted during low tide in the study sites, except for the rather low numbers counted in March 2004 (Figure 3-31).

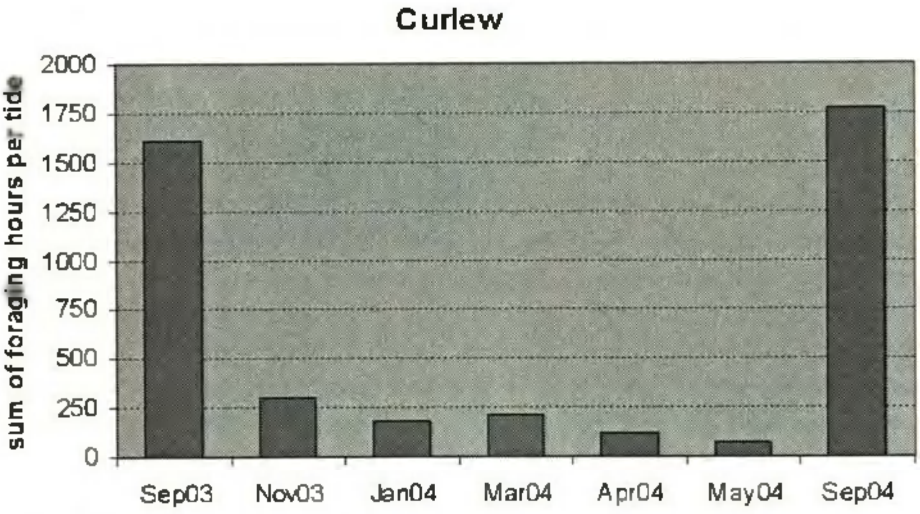


Figure 3-31. The total number of foraging hours of Curlews during each of the observation periods. Note that the number of sites counted increased from 63 to 71 from March 2004 onwards. In January/February 2004 only 48 sites could be counted due to bad weather conditions.

3.3.10.3 Distribution

For the Curlew, we could construct a monthly distribution model for six counts. Emersion time, current velocity and salinity were nearly always included (Table 3-21). All three variables were also included in the full annual model (Table 3-22). More often than not, the shape of the curves was not an optimum.

Figure 3-32 shows that Curlew occurred over a broad range of emersion times and current velocities. (van Kleunen 1999) also observed that this species occurred throughout the estuary with no strong relationships with either emersion time, silt content or salinity. The latter is also apparent from the data presented by (Stuart *et al.* 1990).

Since the full annual model includes a U-shaped function for emersion time, maximal densities are predicted for very low and very high values of emersion time, which are outside the range over which we collected information on bird densities (Figure 3-33).

*Table 3-21. Monthly distribution models (**MOV**; see methods for details) for the Curlew. We could not construct a model for March 2004. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

	Sep03	Nov03	Jan/Feb04	Apr04	May04	Sep04
constant	-11.46	2.491	-544	17.56	124.2	7.54
Emean	[illegible]	0	[illegible]	-0.097	0	-0.2323
Emean²	-0.00299	-0.00006	-0.01217	0.0004	-0.00028	0.002456
Vmean	0.267	0	0	-0.266	0	[illegible]
Vmean²	-0.00522	0	0.00325	0.00446	0	-0.00439
Salt	0	0	[illegible]	-0.4253	-9.11	0
Salt²	0	-0.00101	-0.623	0	0.1652	-0.0022
Deviance explained	53.5%	1.8%	74.8%	67.0%	36.3%	49.1%

*Table 3-22. Parameter estimates of the full annual distribution model (**Y3VM**) for the Curlew. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

constant	3.950
Emean	-0.157
Emean²	0.002
Vmean	0.122
Vmean²	-0.003
Salt	0
Salt²	-0.002
Sep	2.920
Nov	1.240
Jan	0.880
Mar	0 806
Apr	0
May	0
Deviance Explained	53.8%

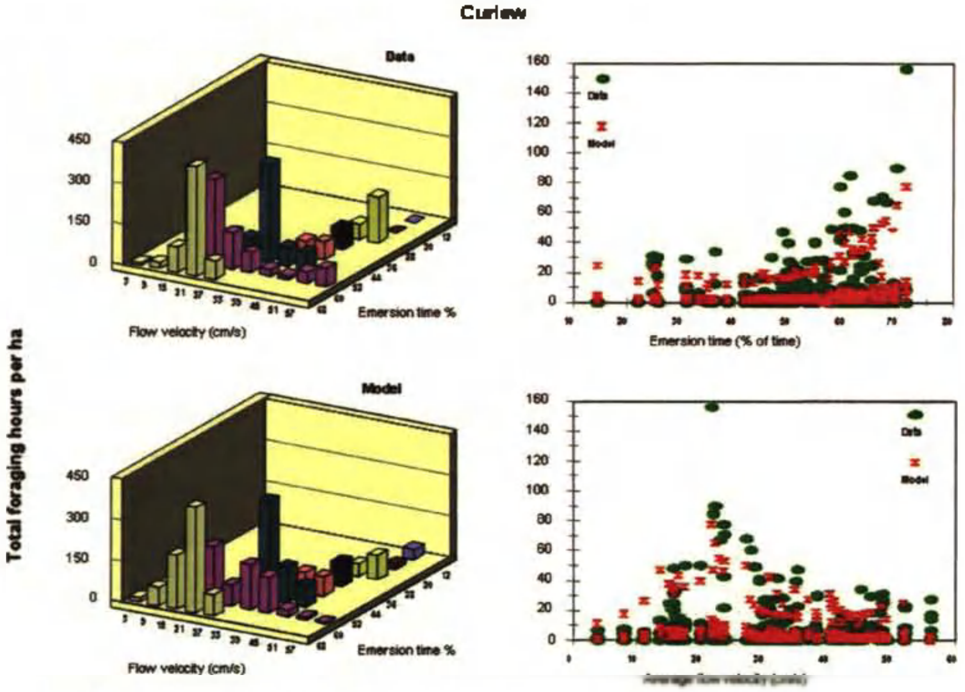


Figure 3-32. Distribution of Curlew with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). (a) Foraging hours as a function of both variables as observed. (b) Foraging hours as a function of both variables as predicted. (c) Foraging hours as a function of emersion time, comparing observations and model predictions. (d) Foraging hours as a function of current velocity, comparing observations and model predictions.

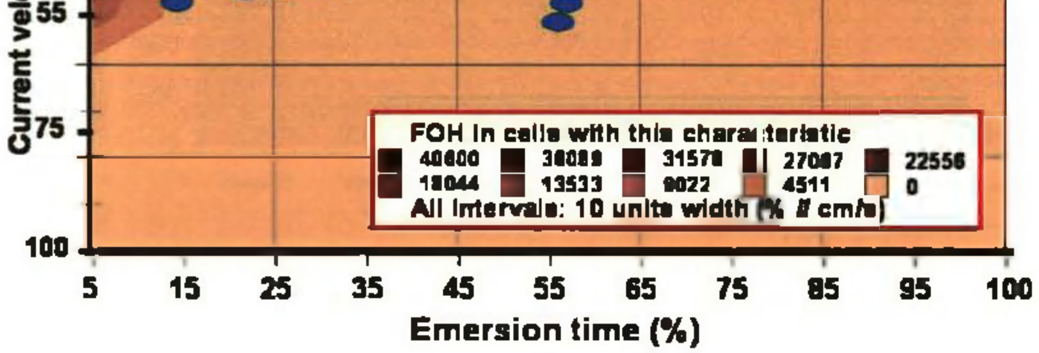


*Figure 3-33. Contour plot of predicted foraging hours of Curlew with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). Predictions are based on the full annual model (**Y3VM**). Dots indicate the study plots. The numbers next to the boxes indicate the total number of foraging hours in each combined interval of 10% emersion time and 10 cm/s current velocity. The contour lines are derived from an interpolation of the scores and for this reason provide a false sense of accuracy.*

3.3.11 Redshank

3.3.11.1 Prey choice

Redshank feed on the one hand on several worm species and on the other hand on several species of crustaceans (Leopold *et al.* 2004). We have no direct observations of the prey choice of Redshanks.

3.3.11.2 Phenology

From September to February the number of Redshanks in the Westerschelde is generally low. Numbers are higher from March to June and peak numbers are reached in July (Berrevoets *et al.* 2002). We did not count during the months that peak numbers are reached and for the months that we did count, the pattern is opposite to the trend described above. In several months during autumn and winter, especially January 2004, we counted more birds than during spring (Figure 3-34).

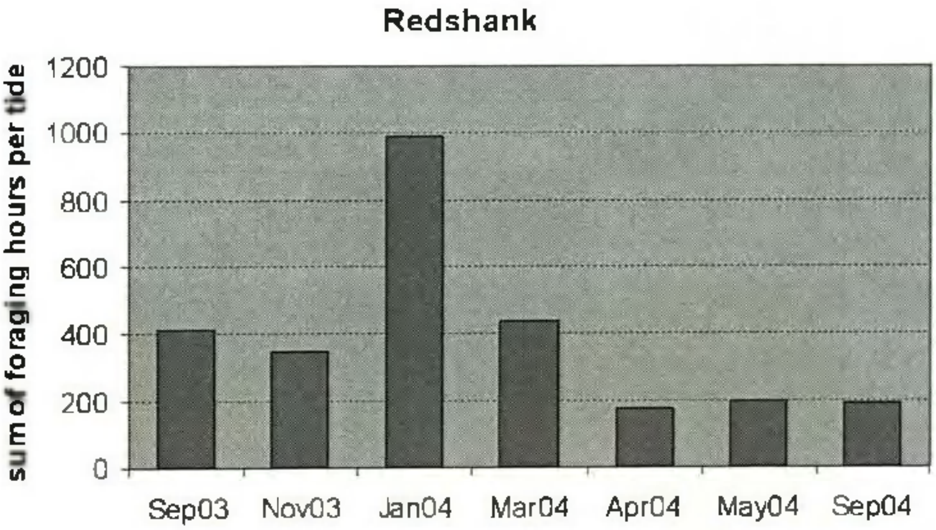


Figure 3-34. The total number of foraging hours of Redshank during each of the observation periods. Note that the number of sites counted increased from 63 to 71 from March 2004 onwards. In January/February 2004 only 48 sites could be counted due to bad weather conditions.

3.3.11.3 Distribution

The most striking aspect of the monthly models and the full annual models is the extremely high percentage of the deviance that these models explained (Table 3-23, Table 3-24). For the monthly models this varied between 55% and 92%, and the value for the full annual model was 74%. The cause of this is that the Redshank consistently occurred in areas with low current velocities (i.e. muddy areas) and long emersion times (Figure 3-35). In his text Van Kleunen (1999) concludes that Redshank are most common in muddy areas with a long emersion time, in line with our observations. However, his graph indicates a preference for short emersion times. With regard to salinity Van Kleunen (1999) concludes a preference for high salinities, but this is contradicted by Stuart *et al.* (1990) who found high numbers in the eastern brackish part and it is also not in line with our observations (the full annual model does not include salinity).

The full annual model does not include optimum curves, but increasing numbers of foraging hours with decreasing emersion times and especially with decreasing current velocities. As a result, maximal densities are predicted outside the combined range of emersion time and current velocity over which we collected data (Figure 3-36). We have no explanation for the discrepancy between the monthly models and the full annual model.

*Table 3-23. Monthly distribution models (**MOV**; see methods for details) for the Redshank. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

	Sep03	Nov03	Jan/Feb04	Mar04	Apr04	May04	Sep04
constant	-111.9	2.827	-7625	-309	228	129.8	7.5
Emean	3.97	0	12.01	0	0	1.244	0
Emean²	-0.03501	0	-0.0925	0.001051	-0.00368	-0.01276	-0.00088
Vmean	-0.2146	0.329	-0.0857	-0.0851	0	-0.3458	0
Vmean²	0	-0.01998	0	0	-0.01225	0	-0.00594
Salt	0	0	539	22.09	-14.15	-11.07	0
Salt²	0	0	-10	-0.394	0.241	0.204	0
Deviance explained	78.6%	83.3%	91.8%	86.8%	66.0%	55.0%	61.7%

*Table 3-24. Parameter estimates of the full annual distribution model (**Y3VM**) for the Redshank. A zero indicates that a particular variable was not included in the final model. When the parameter values indicate an optimum curve, they are shaded grey.*

constant	10.500
Emean	-0.101
Emean²	0
Vmean	0
Vmean²	-0.007
Salt	0
Salt²	0
Sep	0.478
Nov	0.620
Jan	1.660
Mar	0.854
Apr	0
May	0
Deviance Explained	74.4%

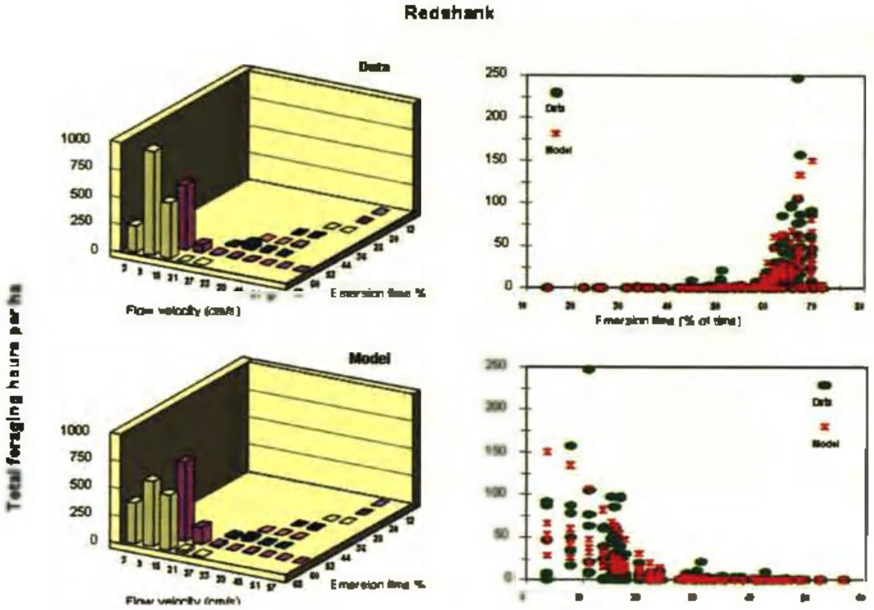


Figure 3-35. Distribution of Redshank with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). (a) Foraging hours as a function of both variables as observed. (b) Foraging hours as a function of both variables as predicted. (c) Foraging hours as a function of emersion time, comparing observations and model predictions. (d) Foraging hours as a function of current velocity, comparing observations and model predictions.

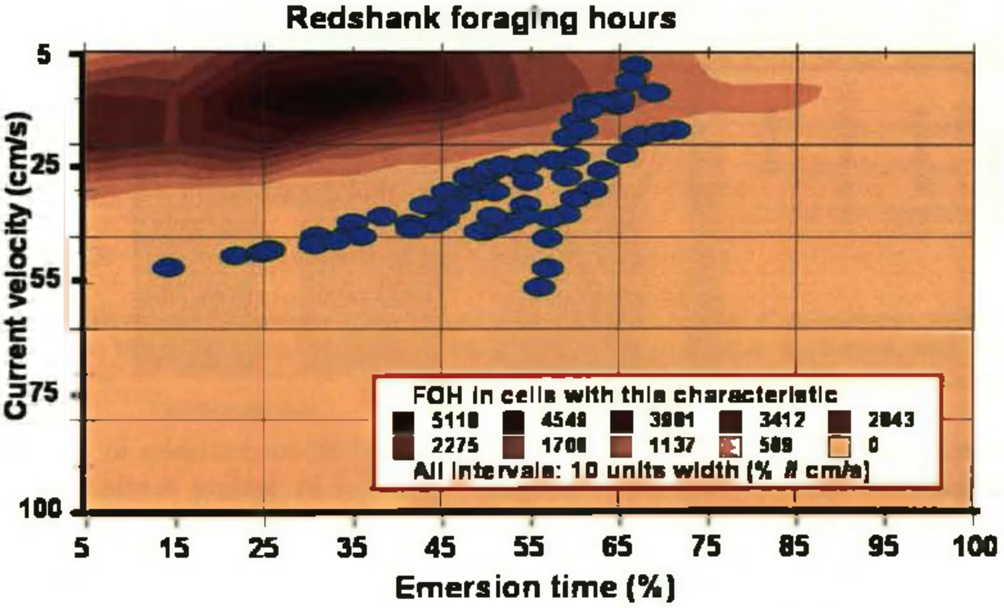


*Figure 3-36. Contour plot of predicted foraging hours of Redshank with respect to emersion time (% time) and maximal current velocity during an average tide (cm/s). Predictions are based on the full annual model (**Y3VM**). Dots indicate the study plots. The numbers next to the boxes indicate the total number of foraging hours in each combined interval of 10% emersion time and 10 cm/s current velocity. The contour lines are derived from an interpolation of the scores and for this reason provide a false sense of accuracy*

3.4 Linking bird distribution to prey or abiotic variables?

Preliminary investigations with models that included the predicted densities of several benthic organisms as predictor variables indicated that these predictor variables did not significantly improve the fit of the models (Brinkman *et al.* 2005). In addition, we saw no conceptual advantage in such models, as the benthic densities are in fact predicted from the same abiotic variables that were also used to predict bird densities directly (see also Appendix 1). For these reasons we abandoned investigating such models at an early stage in our investigations.

We put more effort in studying benthos variables derived from actual measurements on the benthos in the study plots. On their own, the benthos variables explained rather little of the variance in foraging hours per plot for the majority of bird species (Figure 3-37). Explicitly incorporating month as a nominal variable improved the models, but the variance that was explained by the models remained low. Only for Oystercatcher, Redshank and Curlew did the variance that was explained exceed 25%.

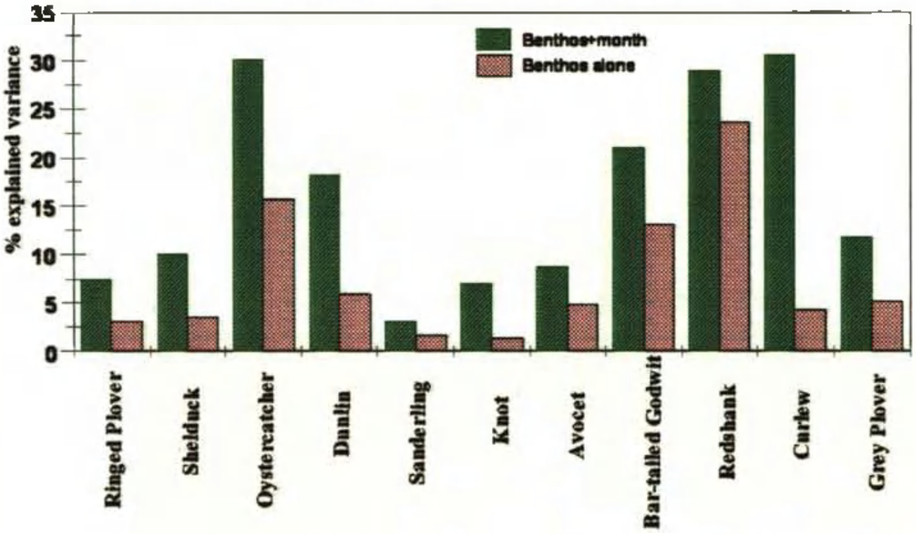


Figure 3-37. The success (measured as % variance explained) of benthos variables in explaining the foraging distribution (measured in foraging hours summed over a tide in a plot) of 11 bird species. Model ***BY*** *and model* ***BYM*** *(that explicitly incorporates month as a nominal variable) are compared.*

These percentages were hardly changed when we first introduced abiotic variables in the model and then investigated if the fit of the model could be improved by adding benthic variables (Figure 3-38).. Only for Oystercatchers did adding benthic variables substantially improve the model.

The abiotic model that we used in the above comparison (**Y3VM**) included salinity. It is possible that salinity was a proxy for site and that by including salinity, we captured all the variance that might possibly be explained by the differences in benthos between the sites. We therefore also did the analysis for an abiotic model with only current velocity and emersion time (**Y2VM**). We selected the three species where the benthic model (**BY**) explained a substantial part of the variation in foraging hours. As before, only for Oystercatchers did adding of benthic variables substantially improve the model (Figure 3-39).

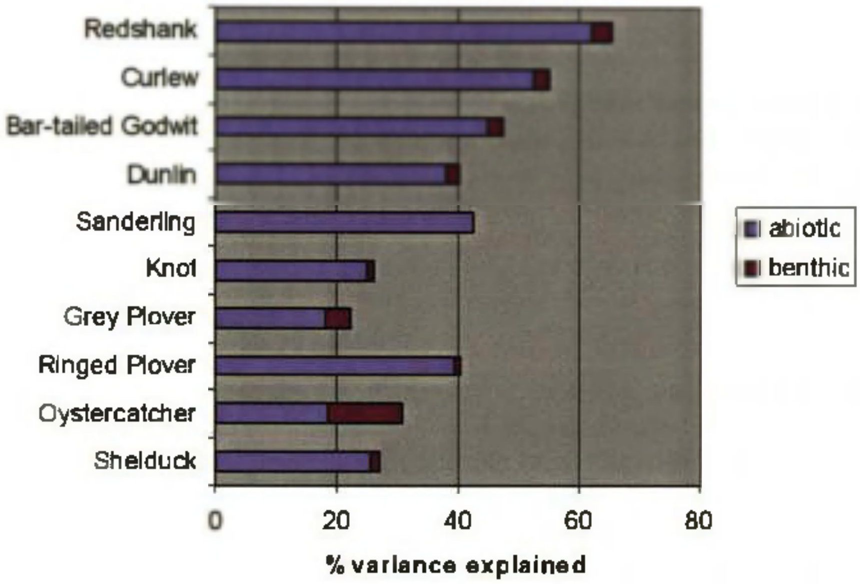


*Figure 3-38. The success (measured as % variance explained) of a model (**BY3VM**) incorporating both abiotic variables and benthos variables in explaining the foraging distribution (measured in foraging hours summed over a tide in a plot) of 11 bird species. The extra contribution of the benthic variables is indicated separately*

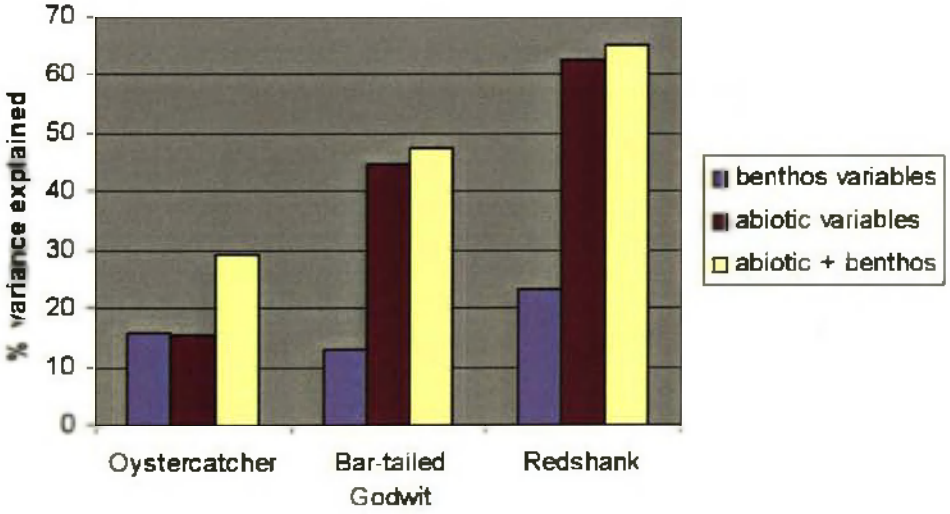


*Figure 3-39. Comparison of the success (measured as % variance explained) of an annual model with only 2 abiotic variables (**Y2VM**), of a model with only benthos variables (**BY**) and an annual model containing both abiotic and benthic variables (**BY2VM**) for three bird species: Oystercatcher, Bar-tailed Godwit and Redshank.*

4 Validation

In the following paragraphs the annual models with salinity, emersion time and current velocity as explaining variables are named 'full annual models' **(Y3VM)**, and models with the grouped variables emersion time and current velocity only are named 'grouped variables models' **(GSY2VM)**.

4.1 Low tide counts

Linear regression showed that for the Grey Plover the full annual model explained only 22% of the 'observed' number of foraging hours. The absolute number is strongly underestimated (Figure 4-1). For the other nine bird species less than 1% of the variation is explained by the full annual models. For these species the relation between predicted and observed numbers was dominated by the occurrence of two contrasting situations: in some plots observed numbers were much higher than predicted and in some others they were much lower (e.g. Figure 4-2). Selecting only those plots where counts were made during the entire low tide period, or only months with high numbers of birds did not improve the relations significantly. It is concluded that, at the small spatial and temporal scale employed here, the predictions could not be validated.

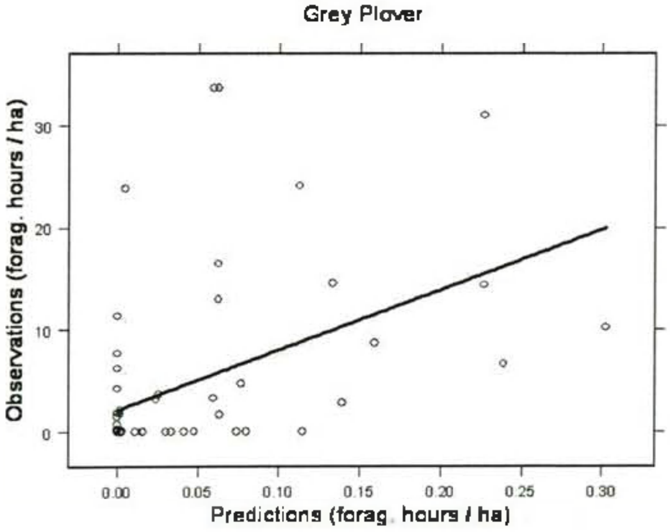


Figure 4-1. Grey Plover: number of foraging hours predicted and observed for low tide plots (all data). Source: RWS RIKZ.

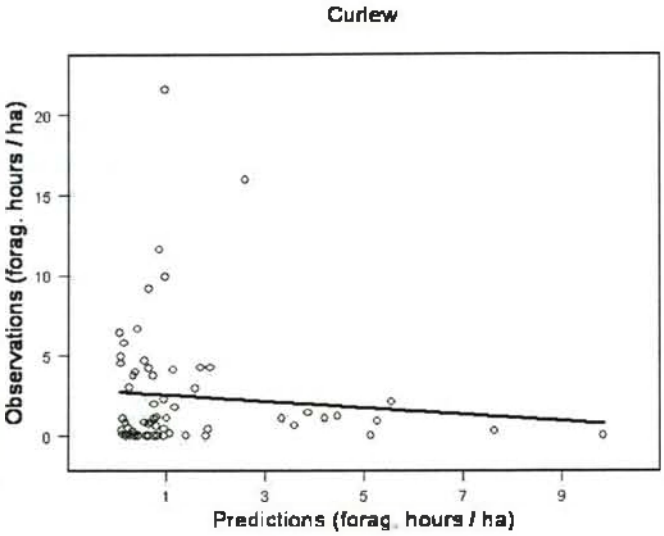


Figure 4-2. Curlew: example of predicted and observed number of foraging hours in low tide plots showing 'no relation' (all data).

4.2 High tide counts

For each species the relative distribution over the five high tide sectors, as observed in the seasons 1999/2000 through 2003/2004 is presented first. Next the results of the validation of both the full annual models and the grouped variables models are presented. The *relative* distribution over the five associated high tide sectors and low tide regions is presented graphically and discussed in the text. The *absolute* values of predicted and observed number of birds in the entire study area are presented in the text only.

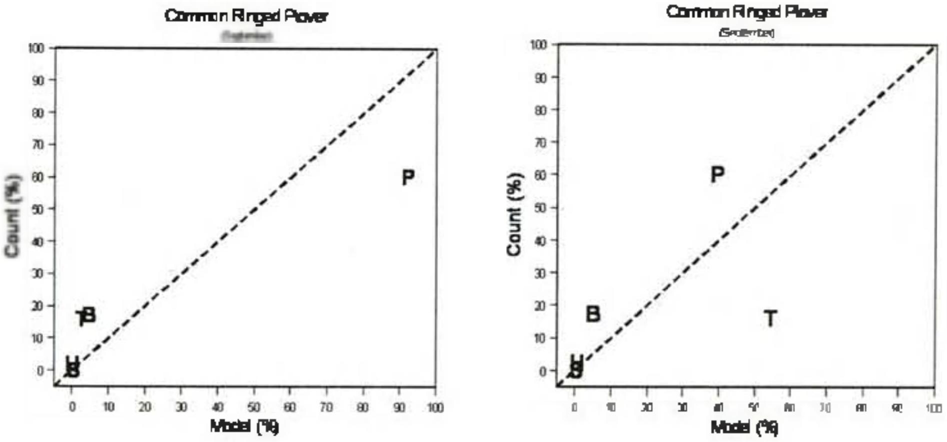
4.2.1 Ringed Plover (September)

The proportion of birds present in the five high tide sectors varied considerably from year to year. The smallest numbers were present in sectors Sloe (average 1 % (minimum 0, maximum 2 %) and Hoedekenskerke (3 % (0-8 %)). Sector Paulina contributed 61 % (19-84 %), Baarland 18 % (0-46 %) and Terneuzen 17 % (4-32 %).

For the full annual model the graph with proportions (Figure 4-3a) shows a dominance of sector Paulina in both the model (low tide regions) and counts (high tide sectors). The model overestimates the proportion that is related to sector Paulina and underestimates those related to sectors Baarland and Terneuzen. The number of birds in the entire area is about 45.000 according to the model and 1340 according to the counts, respectively. For conversions of foraging hours to number of birds a factor of 8.25 was used. As the number observed in the entire area in September

1999-2003 never exceeded 3000 birds it is clear that the model strongly overestimates the occurrence of Ringed Plovers at the scale of the entire area.

For the grouped variables model the graph with proportions (Figure 4-3b) shows large differences between the model predictions and observations for sectors Paulina and Terneuzen. This model overestimates the total number of birds in the entire area by a factor 11.



Full annual model

Grouped variables model

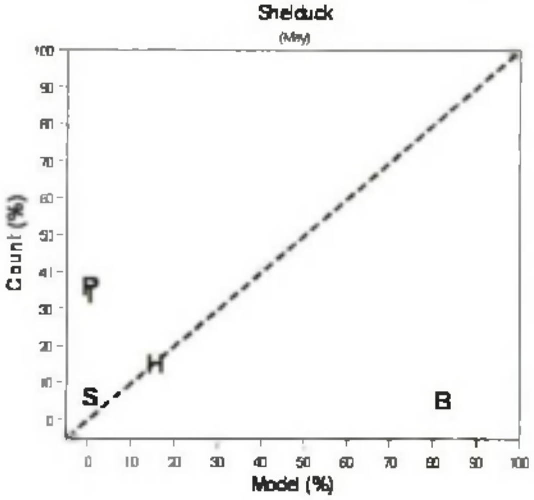
Figure 4-3. Ringed Plover (September): proportion of birds in associated low tide regions (model) and high tide sectors (count). (a) Full annual model. (b) Grouped variables model

4.2.2 Shelduck (May)

The proportion of birds present in the high tide sectors was 37 % (22-58 %) for Paulina, 7 % (4-11 %) for Sloe, 6 % (3-11 %) for Baarland, 16 % (1-35%) for Hoedekenskerke and 35 % (31-40 %) for Terneuzen respectively.

For the full annual model the graph with proportions (Figure 4-4) shows that the occurrence in the low-tide-region related to Baarland is strongly overestimated and is underestimated in the regions related to Paulina and Terneuzen. For the entire area the number of birds estimated by the model is much higher than counted in May 2004 (over 1 million and 2297 birds respectively). For conversions of foraging hours to number of birds a factor of 6 is used. The number of Shelduck observed in the entire area in May 2000-2004 never exceeded 4049 birds, so the model strongly overestimates the occurrence of the species at the scale of the entire study area.

No map could be produced for the grouped variables model because the maximum number of different cell values set by the GIS-software used was exceeded. This error indicates that the grouped variables model, like the full annual model, produces extraordinarily high numbers of foraging hours in parts of the mapped area.



Full annual model

Figure 4-4. Shelduck (May): proportion of birds in associated low tide regions (model) and high tide sectors (count). Source: RIVS RIKZ.

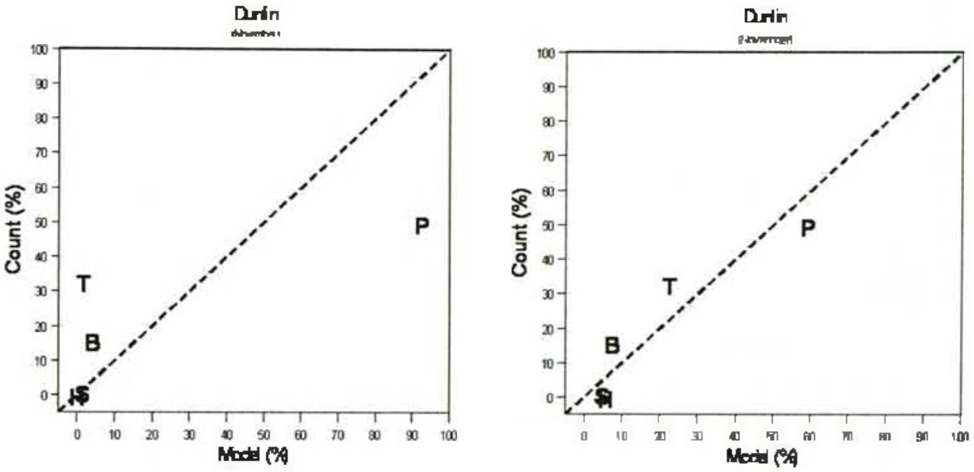
4.2.3 Dunlin (November)

For this species November 2003 had to be omitted from the analysis (counts not complete). In November-counts of the remaining years the proportion of birds present in the five high tide sectors varied considerably. In sector Paulina the average proportion was 50 % (46-60 %), in sector Sloe 1 % (0-1 %), in sector Baarland 16 % (6-28 %), in sector Hoedekenskerke 0 % and in sector Terneuzen 33 % (11-56 %).

The graph with proportions for the full annual model (Figure 4-5a) shows a dominance of sector Paulina. The model however strongly overestimates this dominance and underestimates the proportions in low tide regions related to sectors Baarland and Terneuzen. The number of birds present in the entire area, as estimated by this model, is about 53.500. The number of birds counted in November of the years 1999-2002 varied from 15.927 to 29.402. So most probably the model overestimates the number of birds at the scale of the entire study area. For conversions of foraging hours to number of birds a factor 8.25 was used.

Figure 4-5b shows the proportion of birds in the low tide regions as calculated with the grouped variables model and as observed in related high tide sectors in November 1999-2002. The model reproduces the relative distribution reasonably well. Also the predicted number of birds present in the entire area, estimated at about

24.500 by this model, lies well within the range of numbers observed (average 22.542, range 15.972 - 29.402 birds).



Full annual model

Grouped variables model

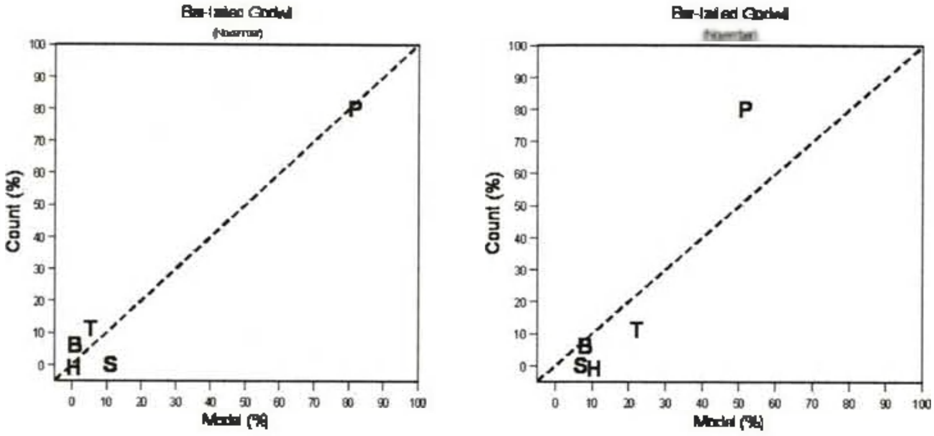
Figure 4-5. Dunlin (November): proportion of birds in associated low tide regions (model) and high tide sectors (count). (a) Full annual model. (b) Grouped variables model. Source: RIVS RIKZ.

4.2.4 Bar-tailed Godwit (November)

The distribution of this species over the high tide sectors was fairly constant from year to year. With the exception of November 2000 82 to 86 % of the birds were seen in sector Paulina. All five seasons included, the proportion in sector Paulina was 81 % (66-86 %), in sector Sloe 1 % (0-3 %), sector Baarland 7 % (0-27 %), sector Hoedekenskerke 0% and in sector Terneuzen 12 % (6-17 %).

The full annual model reproduces the relative distribution over the area very well (Figure 4-6a). The number of birds to occur in the entire area, as estimated by the model, is 3862. This is 5.3 times the number observed in November 2003 and also exceeds the maximum number observed in November of the years 1999 to 2002 (1068 birds). For conversions of foraging hours to number of birds a factor 5 was used.

For the grouped variables model the graph with proportions (Figure 4-6b) shows that the numbers in the low tide region associated with high tide sector Paulina is underestimated, while the numbers related to sectors Hoedekenskerke and Terneuzen are overestimated. The numbers present in the entire study area are estimated at about 7000 birds. Both the relative distribution over the different areas and the total amount of Bar-tailed Godwits present are better reproduced by the full annual model than by this model.



Full annual model

Grouped variables model

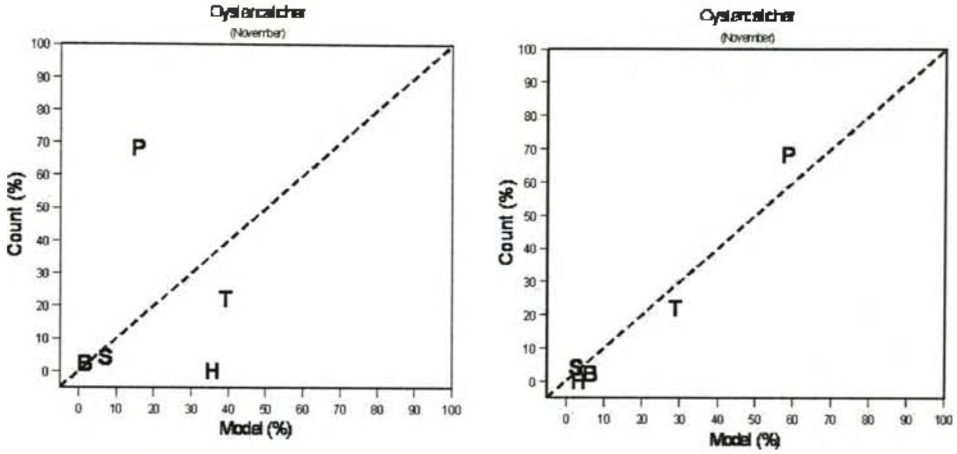
Figure 4-6. Bar-tailed Godwit (November): proportion of birds in associated low tide regions (model) and high tide sectors (count). (a) Full annual model. (b) Grouped variables model. Source: RWS RIKZ.

4.2.5 Oystercatcher (November)

The proportion of Oystercatchers present in the five high tide sectors is fairly constant from year to year. In sector Paulina 69 % occur (64-72 %), in sector Sloe 5 % (3-6 %), Baarland 3 % (2-4 %), Hoedekenskerke 1 % (0-3 %) and in sector Terneuzen 23 % (17-30 %).

The graph of the proportions as calculated with the full annual model (Figure 4-7a) shows that the relative number of birds in the low tide region associated with sector Paulina is strongly underestimated, while those for sectors Hoedekenskerke and Terneuzen are overestimated. The total number of birds present in the area in November is estimated at about 80.000 by this model, which is almost 10 times higher than the number counted in November 2003 (8162 Oystercatchers) and also much higher than the maximum number observed in November of the years 1999-2002 (8850 Oystercatchers). For conversions of foraging hours to number of birds a factor 5 was used.

The grouped variables model shows a good reproduction of the relative distribution of birds over the different areas (Figure 4-7b). With about 10.500 Oystercatchers estimated by this model for the entire study area in November, the observed number in November 2003 is overestimated by a factor 1.3.



Full annual model

Grouped variables model (*)

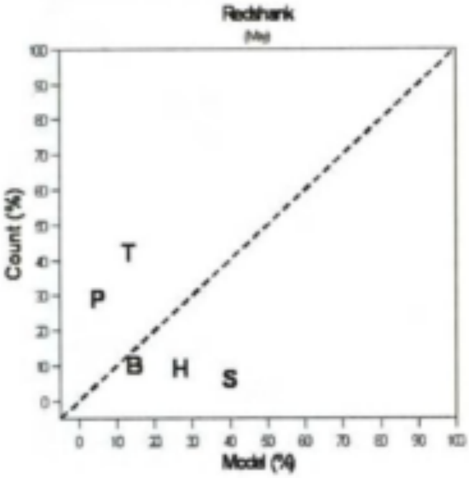
Figure 4-7. Oystercatcher (November): proportion of birds in associated low tide regions (model) and high tide sectors (count). (a) Full annual model. (b) Grouped variables model. Source: RWS RIKZ.

4.2.6 Redshank (May)

The proportion of birds present in the five high tide sectors varied considerably from year to year. In sector Paulina 30 % occurred (16-51 %), in sector Sloe 7 % (2-12 %), sector Baarland 11 % (2-19 %), Hoedekenskerke 10 % (0-35 %) and Terneuzen 43 % (21-68 %). In May 2004 these proportions were: 32 % in Paulina, 8 % Sloe, 8 % Baarland, 3 % Hoedekenskerke and 48 % in sector Terneuzen. So the distribution in that period was not very different from the average situation in the years 2000-2004.

The full annual model for the Redshank in May (figure 4-8) overestimates the proportions in low tide regions associated with sectors Sloe and Hoedekenskerke, while it underestimates those in sectors Paulina and Terneuzen. With about 62.500 Redshanks estimated for the entire study area in May, the model strongly overestimates the number counted in May 2004 (844 birds) and the maximum observed in May of the years 2000-2003 (1178 birds). For conversions of foraging hours to number of birds a factor of 8.25 was used.

No map could be produced for the grouped variables model because the maximum number of different cell values set by the GIS-software used was exceeded. This error indicates that the grouped variables model, like the full annual model, produces extraordinarily high numbers of foraging hours in parts of the mapped area.



Full annual model

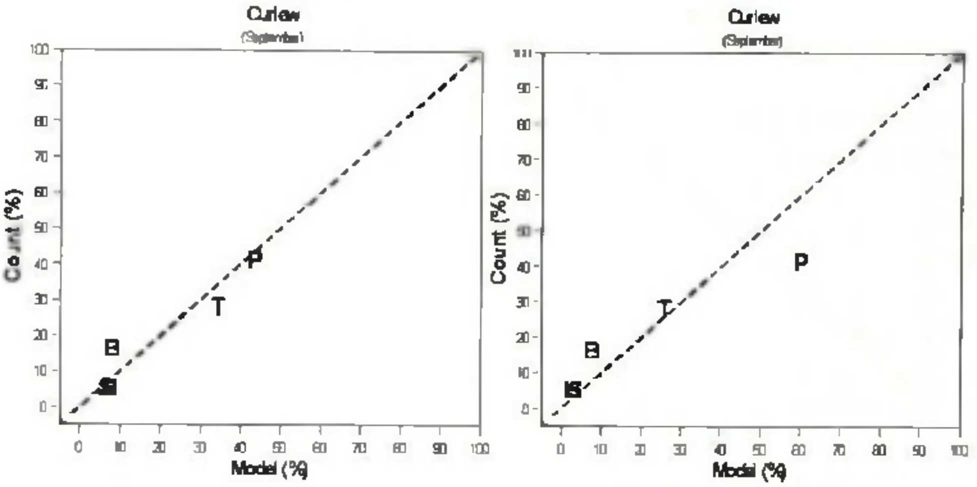
Figure 4-8. Redshank (May): proportion of birds in associated low tide regions (model) and high tide sectors (count). Source: RWS RIKZ.

4.2.7 Curlew (September)

The proportion of birds present in sector Paulina was 42 % (13-57 %), in sector Sloe 6 % (2-12 %), sector Baarland 17 % (12-21 %), Hoedekenskerke 6 % (0-26 %) and in sector Terneuzen 29 % (15 - 40 %). The situation in September 2003 did not differ much from this five year average: Paulina 47 %, Sloe 4 %, Baarland 12 %, Hoedekenskerke 2 % and Terneuzen 34 %.

The full annual model shows a good reproduction of the relative distribution of Curlews over the different areas (Figure 4-9a). With about 44.500 birds estimated by this model for the entire area the number observed is strongly overestimated (September 2003: 3866 Curlews, which is also the maximum observed in de period 1999-2003). For conversions of foraging hours to number of birds a factor of 5 was used.

The grouped variables model overestimates the proportion in the low tide region associated with sector Paulina and an underestimation for the one related to sector Baarland (Figure 4-9b). Like the full annual model, the total number of birds in the area is strongly overestimated (grouped variables model: about 32.500 Curlews, count in September 2003 3866 birds).



Full annual model

Grouped variables model

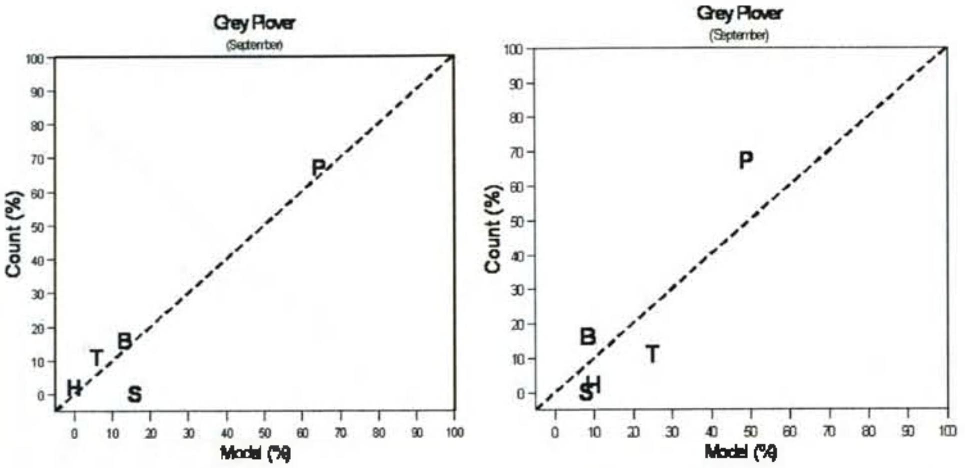
Figure 4-9. Curlew (September): proportion of birds in associated low tide regions (model) and high tide sectors (count). (a) Full annual model. (b) Grouped variables model. Source: RWS RIKZ.

4.2.8 Grey Plover (September)

Observations from September 2000 were not taken into account because the data were not complete. Average proportions for the other four years were: Paulina 68 % (56-78 %), Sloe 1 % (0-1 %), Baarland 17 % (2-26 %), Hoedekenskerke 3 % (0-7 %) and sector Terneuzen 12 % (9-15 %). The distribution in September 2003 differed somewhat from this four-year average, especially in sectors Paulina and Baarland: Paulina 78 %, Sloe 0 %, Baarland 2 %, Hoedekenskerke 7 % and Terneuzen 13 %.

The full annual model shows a dominance of the low tide region associated with sector Paulina, which compares very well with the high tide counts. It overestimates the proportion in the low tide region associated with sector Sloe, but otherwise shows good agreement between estimated and observed proportions of birds (figure 4-10a). This model overestimates the total number of Grey Plovers in the area in September by a factor 1.7 (estimated number = 3655, observed number in September 2003 = 2478, the maximum in the years 1999, 2001 and 2002 being 2508 birds). For conversions of foraging hours to number of birds a factor of 8.25 was used.

The agreement of the grouped variables model estimates with counts is not as good as that of the full annual model (figure 4-10b). With a total of 1546 birds estimated for the entire area in September the actual number, as observed at high tide in September 2003 (2478 Grey Plovers), is underestimated.



Full annual model

Grouped variables model

Figure 4-10. Grey Plover (September): proportion of birds in associated low tide regions (model) and high tide sectors (count). (a) Full annual model. (b) Grouped variables model. Source: RWS RIKZ.

4.3 Conclusions

Generally speaking the models for most species overestimate the total number of birds in the study area. The best prediction is produced by the grouped variables model for Dunlin. Both the total number of birds and the relative distribution over the area are close to what is expected from high tide counts. The models for Redshank and Shelduck show the largest differences between predicted and counted number of birds. Compared to the full annual model, the grouped variables model for the Oystercatcher shows a much improved resemblance between predicted and observed number of birds. From these cases a major factor causing a better or worse agreement between predicted and modelled number of birds, appears to be the form of the individual response curves in the multiple regression model. The Redshank models, Shelduck models and the full annual model for the Oystercatcher show increasing response values at one or both sides of the ranges of the explaining variables. On the other hand the Dunlin model and grouped variables model for the Oystercatcher only show optimum response curves for all variables. In these models the response values strongly decrease on both sides of the optimum values of the explaining variables. Those optimum values lying very well within the ranges occurring in the study plots.

Compared to the grouped variables model the relative distribution of Bar-tailed Godwits is better reproduced by the full annual model. The same can be said about the models for the Grey Plover. In both species the observed distribution shows higher numbers in the most western part of the study area, as compared to the eastern part. This aspect is best reproduced by the full annual model, which includes salinity as a variable with a west to east gradient.

5 Discussion

The aim of the project was to develop a reliable tool to predict the distribution of a selected set of shorebird species as a function of environmental variables. It is clear that this goal was not achieved, except perhaps for Dunlin and Grey Plover. The most important question that we need to tackle in this discussion is therefore why the model validation showed that the models were not reliable at the scale of the entire western part of the Westerschelde. Before we do this, we will first reflect on the factors determining the feeding distribution of the waders during low tide and then reflect on the various aspects of the approach that we adopted in this study. After discussing the disappointing validation results, we briefly consider alternative statistical models.

5.1 What determines the distribution of waders during low tide?

Goss-Custard (1985) reviewed many studies suggesting that the attractiveness of an area for feeding waders largely depends on the rate at which they can collect food. This rate will depend on the harvestable food supply as defined by Zwarts & Blomert (1992) and Zwarts *et al.* (1992). The harvestability of the food depends on many factors, including prey density, prey size, calorific content, digestibility, burying depth and surface activity. More recently, an increasing body of evidence has accumulated, indicating that the feeding decisions of the birds also depend on the risk that they themselves are being eaten by predators (Cresswell 1994; Cresswell & Whitfield 1994; Hilton *et al.* 1999; Lank & Ydenberg 2003; Whitfield 2003; Ydenberg *et al.* 2004). Finally, at a large spatial scale, winter severity is also important, as it determines both the energy costs of the birds and the availability of their food (Goss-Custard *et al.* 1996; Wiersma & Piersma 1994; Piersma *et al.* 2003). According to Austin & Rehfisch (2005) a considerable number of wader species have shifted their wintering distribution in the United Kingdom in response to climate change: during warmer winters, smaller proportions of seven species wintered in southwest Britain. Despite these complications, a large number of studies have reported positive correlations between stocks of the preferred food and particular wader species at spatial scales ranging from tens of square kilometres down to scales of hundreds of square meters (Goss-Custard 1970b; Bryant 1979; Zwarts 1981; Hicklin & Smith 1984; Meire 1993; Yates *et al.* 1993; Kalejta & Hockey 1994; van de Kam *et al.* 2004).

In our study we found strong evidence that Oystercatchers feed primarily on Cockles in the Westerschelde and that the distribution of large Cockles, which are the most profitable prey for the Oystercatchers (Zwarts *et al.* 1996b), is the prime determinant of the distribution of the Oystercatchers over the Westerschelde. In contrast, for the other bird species we failed to find such clear relationships and the actually measured prey densities did not contribute significantly to models already containing abiotic variables, either with or without salinity as a possible proxy for site. Two possible explanations for this failure require further investigation. First, most of the benthic biomass consisted of Cockles, yet most of the birds fed on worms. Perhaps, sample sizes were sufficient to obtain good estimates for Cockle densities, but insufficient to obtain good estimates for worm densities. Second, in the analysis we included all counts, yet the benthic biomass was only measured in September 2003. It is known that biomass of benthic animals varies systematically in the course of the season and can vary considerably between years (Beukema 1974; Beukema 1982). Perhaps, better results are obtained if correlations are restricted to bird densities and benthic food stocks measured in the same winter season. It would certainly be premature to conclude that, except for Oystercatchers, food stocks do not influence the distribution of the waders in the Westerschelde.

However, even if food stocks have a clear influence on the distribution of all wader species, that does not detract from the usefulness of constructing models that seek to predict changes in bird numbers directly from changes in abiotic habitat variables. The problem with using benthic variables is twofold. First, the quantification of invertebrate populations in large intertidal areas can only be achieved at very high costs. In the Westerschelde, the only exception to this general rule is probably the Cockle, which has been sampled on an estuary-wide basis since 1992 (Kamermans *et al.* 2004). Second, we need models that predict the population dynamics of the invertebrates in response to abiotic variables. Any uncertainty in these models is multiplied with the uncertainty in the models relating the birds to the food stocks. When Steenbergen *et al.* (2004) constructed a habitat model for the Cockle in the Westerschelde, they could explain 40% of the deviance of Cockle biomass. However, when they tried to predict Cockle biomass for parts of the Westerschelde not used to construct the model, they could only explain 6% of the deviance.

Table 5-1: Sediment composition of the preferred feeding habitat in different studies. Sediment composition was scored as muddy (M), intermediate (I) and sandy (S). The last column gives the extent of agreement between this study and the average picture of the other studies.

Species	(Zwarts 1988)	(Yates *et al.* 1993)	(Ens *et al.* 1993)	(Brinkman & Ens 1998)	(Granadeiro *et al.* 2004)	This study	Agreement
Shelduck		I		M		MIS	medium
Oystercatcher	S	I		MIS		MIS	medium
Avocet			M				
Ringed Plover	M			M		I	medium
Grey Plover	M	S		MI	M	M	good
Knot	I	I		I		I	good
Sanderling	S				S		
Dunlin		M	M	MI	M	M	good
Bar-tailed Godwit	S	S	S	S		I	poor
Curlew	M		M	M		M	good
Redshank	I	M	M	MI		M	good

Comparing different studies on habitat choice, the results of these studies show a fair degree of consistency when it comes to the sediment composition of the preferred feeding habitat and the results of this study tend to agree with the general picture (Table 5-1). For instance, Curlew and Dunlin are found in muddy areas, whereas Bar-tailed Godwit prefer sandy areas. With regard to emersion time, there is much more variation between studies and, partly as a result of this, there is much less agreement between the results of this study and other studies (Table 5-2).

Table 5-2: Emersion time of the preferred feeding habitat in different studies. Emersion time was scored as long (L), intermediate (I) and short (S). The last column gives the extent of agreement between this study and the average picture of the other studies.

Species	(Yates *et al.* 1993)	(Ens *et al.* 1993)	(Brinkman & Ens 1998)	(Le Drean-Quenec'hdu 1999)	(Granadeiro *et al.* 2004)	this study	Agreement
Shelduck	L		L			LIS	medium
Oystercatcher	S		IS	S		LIS	medium
Avocet		L					
Ringed Plover			L			L	good
Grey Plover	S		I	L	S	L	poor
Knot			I	L		I	medium
Sanderling							
Dunlin	S	S	I	LIS		L	poor
Bar-tailed Godwit		S	S		S	I	poor
Curlew	S	S	I	L		L	medium
Redshank	S	S	I		S	L	poor

5.2 Pros and Cons of the approach adopted in this study

5.2.1 Extreme values and unsampled habitats

Many models did not show an optimum curve within the measurement range and thus predicted maximal densities outside the range of measurement. Extreme data points, which occurred in many species, were probably the most important cause. From experience we know that the number of birds feeding in a particular location can sometimes be quite variable from one day to the next. In species that feed in a flock, like Knot and non-territorial individuals of Grey Plover, it may well be that it is partly a matter of chance where the flock will decide to feed on a given day[3]. Thus,

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[3] The suggestion that there may be a random element in where a flock decides to feed on a given day should not be taken as a suggestion that birds that feed in flocks are not limited by their food supply. Some wader species or individuals within a species feed in flocks, whereas other species or individuals defend territories (Goss-Custard 1970a) or pseudo-territories (Ens & Cayford 1996). Flocking species may deplete the harvestable food supply in the course of winter, which means that the number of foraging hours accumulated over the whole winter is not

extreme values are probably unavoidable and the only way to reduce their influence is to increase the number of counts (i.e. not the number of counts on a given day, but the number of days on which a plot is counted).

Another important cause of the problem is that we lacked observations in relatively rare habitats. At the start of the project we did our best to cover all habitats, but as Figure 3-3 shows, our coverage of common habitats was good, but our coverage of rare habitats with extreme values for the predictor variables was insufficient. The low tide validation plots show that many of the more accessible parts of the estuary are in fact the rare habitats that we missed (Figure 5-1). What is needed is an increase in the number of study sites located in rare habitats with extreme values for the predictor variables.

The study of Brinkman & Ens (1998) also suffered from the fact that some habitats were not covered by the counts. In their case it were especially high and sandy areas, which are known to harbour few birds. They therefore included zero counts for these habitats and this increased the number of models with an optimum curve within the measurement range.

5.2.2 Sample sizes

Building a habitat model may require less effort than building models that incorporate prey stocks and the feeding decisions of the birds. Still, the development of such models requires nonetheless a substantial amount of effort. Yates *et al.* (1996) developed habitat models for waders in the Wash and showed that increasing the number of years over which data were collected increased the percentage of the variation in bird numbers that could be explained. Some of the problems that we encountered in developing reliable habitat models are likely related to small sample sizes. In our study we used the data of 7 counts of at maximum 72 study plots. This is a small number when we compare it to the study of Brinkman & Ens (1998), who used the data collected by Zwarts and co-workers along the Frisian coast. These same data were also analysed by Blomert (2002). According to the tables in Blomert (2002), each plot was counted on average 50 times and there were at least 1500 plots. This comparison is not entirely fair, because the number of counts per plot includes several counts per low tide. Probably, the plots were counted during 10 different low tide periods. Thus, the fact that the models that were developed by Brinkman & Ens (1998) performed better than the models developed in this study, may be partly due to the substantial difference in sample size.

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random at all, but strongly linked to the size of the food supply. Sutherland (1996) reviews several examples of birds depleting the food supply in the course of winter. In contrast, Interference may limit the number of territorial or pseudo-territorial birds that can survive in a given area. Goss-Custard *et al.* (2001) provide compelling evidence that this is the case for Oystercatchers feeding on Mussels.

5.2.3 Counting frequency and seasonal changes

Above, we argued that the number of sites and the frequency of counting a site may have been insufficient to derive distribution models with sufficient predictive power. There is another reason why counting frequency should have been higher. All species vary seasonally in their abundance, but they differ in the timing of peak numbers. Some species peak at a time of year when we did not count. This applies to Shelduck and Redshank, which reach peak numbers around July. For several species we had only one count during the time of peak numbers.

Because of the relative scarcity of counts, we could not investigate whether the suggestion of the monthly models that birds changed their distribution pattern in the course of the season was real. At present we are inclined to believe that the differences between months in the monthly distribution models had more to do with outliers and statistical artefacts than with biological reality. However, the data presented by Stuart *et al.* (1990) suggest that it is possible that the distribution does change in the course of the season. Between August and May, Avocets change from west to east. Grey Plover are absent from the east in January, but common there in May and August. Finally, Bar-tailed Godwit are absent from the east in August and January, but common in May.

Another argument for seasonal changes in distribution are known seasonal changes in prey availability and diet of birds. Curlews for instance, eat Shorecrabs in summer and autumn, but not in winter, when the crabs have moved to deeper water and are not available to the birds. The birds also switch more to feeding in fields during winter (Ens & Zwarts 1980).

5.2.4 Size of the counting plots

A larger size of the study plots would have been better so as to have more birds in the plot. However, this would have increased the heterogeneity in the abiotic variables. Although we did not engage in a formal study of the optimal size of the study plots, our impression was that they had just about the right size. Ideally, one would try to obtain a quantitative criterion to decide on the optimal plot size. On the basis of our study we conclude that any effort spent on studying optimal plot size must be considered wasted. The simple fact is that the problems with the modelling were not related to the size of the counting plots, but to extreme values in the bird counts and to the fact that our study plots did not cover all habitats.

5.2.5 Silt content as predictor variable

Since current velocity and silt content were correlated, and since maps for current velocity are regularly produced, whereas maps for silt content are not, we used current velocity instead of silt content in our models. However, we also used emersion time in our models and this variable showed a strong and significant correlation with current velocity. Emersion time was also significantly correlated with silt content, but the correlation was less strong, even more so for median grain size instead of silt content. From a statistical point of view it would have been better to use median grain size, or silt content, instead of current velocity.

Another argument in favour of silt content is that this variable seems to vary over a smaller geographical scale than current velocity. This is clear when one compares the sediment map (Figure 2-13) to the map of current velocity (Figure 2-16). Whether this is actually true depends on the extent to which the geographical map produced by Stelzer (2003) truly reflects the silt content of the sediment. Our study casts doubt on this idea, since the silt content that we measured in the plots showed a very poor correlation with the value for silt content derived from the sediment map (Figure 3-2).

A possible argument against silt content as a predictor variable is that it might also vary over short time scales (unless it also influences the birds over these short time scales). We did not attempt to measure sedimentation and erosion in our study plots, but the impression of the observers was that the sediments in some of the study plots were extremely mobile and dynamic (Marcel Kersten, pers. obs.).

5.2.6 Salinity as predictor variable

It is well known that salinity has a strong influence on the distribution and abundance of invertebrate benthic animals that are preyed upon by the waders feeding on the intertidal flats (McClusky 1981; Wolff 1973; Ysebaert 2000). By restricting the study to the polyhaline central and western part of the Westerschelde it was hoped that salinity would not be a prominent habitat factor. However, our study indicates that even within the central and western part, salinity correlated with the distribution of the birds. The study of Ysebaert *et al.* (2000) showed a clear zonation of the waterbird communities along the entire salinity gradient of the Schelde estuary. Even with the polyhaline part, differences between bird species remained apparent. Thus, salinity is a factor that cannot be ignored. The study of the effect of salinity would be helped by increasing the measuring range. Hence, future studies should include the brackish eastern part of the Westerschelde.

Brinkman & Ens (1998) used the data collected by Zwarts and co-workers along the Frisian coast between Paesens-Moddergat and Wierum to construct their distribution models. They did not investigate the possibility that salinity could be a predictor variable, because the variation in the salinity in the study area of Zwarts was minimal. Since low salinities do occur in the Wadden Sea around the Afsluitdijk in the west this could have been a problem when Brinkman & Ens (1998) validated their model. However, most of the area near the Afsluitdijk is sublittoral, so that the total area of tidal flats experiencing low salinities is small. Hence, ignoring salinity was not a problem.

When Smit *et al.* (2003) investigated the potential impact on birds of a third sluice in the Afsluitdijk, they clearly needed models that included salinity as a predictor variable. They therefore did not use the low-tide counts of Zwarts and co-workers, but low-tide counts from the western Wadden Sea to construct distribution models. They found significant correlations with salinity, but in several cases, the curves were U-shaped leading the authors to conclude that these correlations were probably spurious.

5.3 Validation

A good agreement between predicted and observed number of foraging hours for low tide situations is the best proof of a valid model. The most important problem with the low tide validation plots is that almost all of these plots had combined values for emersion time and current velocity that were outside the range over which we collected data to construct the models (Figure 5-1). Also, the scale of the low tide plots used (average size 2.8 ha, range 0.3 – 6 ha) and the scale of the observations made in those plots (one tidal cycle or less in most plots) were probably too small to avoid that spatial and temporal variation in bird activity hampered this comparison. Finally, the approach to calculate the foraging hours for an entire low water period from observations made during ebb tide only (multiplication by two) is not very realistic. However, the error introduced by this approach is small compared to the error in the predictions.

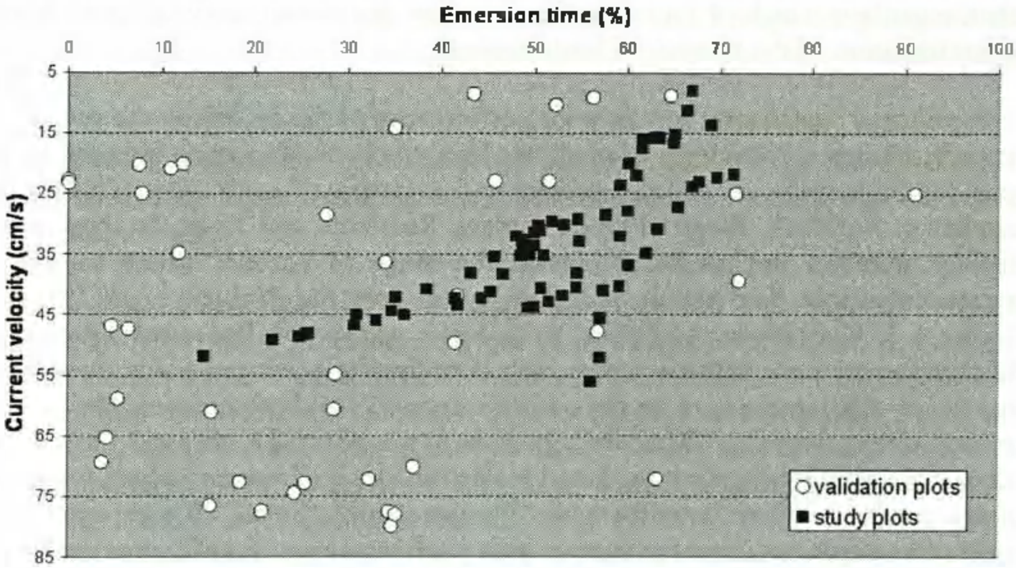

Figure 5-1. Current velocity (cm/s) plotted against emersion time (%) for plots that were used for the low-tide validation. The black squares indicate the study plots used to build the bird distribution models.

For the validation with high tide counts several steps had to be taken, to be able to compare predictions with observations. First, predicted numbers of foraging hours had to be converted to numbers of birds present. Second, low tide regions and the associated high tide sectors had to be identified. Finally, incomplete counts at high tide roosts had to be taken into account.

Regarding the first step: the conversion of number of foraging hours to number of birds was performed without taking into account seasonal variation in activity. As the proportion of available time spent feeding differs by a factor two at most between late summer and winter, and than only for some species (Goss-Custard *et al.* 1977), this conversion appears to be of minor importance for the results of the validation which showed much larger differences between predicted and observed numbers.

Regarding the second step: a correct choice of associated low tide regions and high tide sectors plays no role in the comparison of number of birds predicted and observed in the entire study area. So the comparison of the total number of birds predicted and observed is not affected by mistakes in the assignment. In most species the total number of birds predicted to be present is overestimated by the models. It was not possible to exclude from the validation those parts of the intertidal area where conditions (emersion time, current velocity) were outside the range used for modelling. Only those parts above 85 % emersion time were excluded, because no birds were expected to forage there.

Regarding incomplete counts at high tide roosts: for the months considered these occurred in one species only (Dunlin). To avoid misjudging the predictions from the regression models, not only the counted numbers of birds in 2003/2004 were presented but predictions were also compared with maximum numbers observed during high tide counts in the seasons 1999/2000 to 2002/2003. It was concluded that, regardless which of these numbers is taken, the model shows a relatively small overestimation of the number of birds present.

The principal explanation for the poor performance of the models in the validation is that the models sometimes predicted very high numbers of foraging hours in habitats that were relatively rare and not present in our sample of study plots. This problem applies to Shelduck, Ringed Plover, Curlew, Redshank and Knot. In these species highest numbers are predicted outside the range of habitats where we did our measurements on bird numbers and we gave them the Problem score "High" in Table 5-3. The problem applies to a lesser extent to Bar-tailed Godwit and Oystercatcher, since habitats where high densities are predicted partly overlap with the range of habitats where we did our measurements on bird numbers. We therefore scored these species as "Medium". It does not apply to Dunlin and Grey Plover, since highest numbers were predicted inside the range of habitats where we did our measurements and we gave them the Problem score "Small". We expect that the validation results are best for species with Problem score "Small", intermediate for species with Problem score "Medium" and worst for species with Problem score "High". As is clear from Table 5-3, this is indeed the case. For statistical reasons we also expect that models for common species will generally perform better than models for relatively rare species and for this reason we have ordered Table 5-3 according to abundance. There is no indication from the table that within a problem category, abundant species generally perform better.

In chapter 7 we provide suggestions how these modelling problems might be solved, including an estimate of the amount of extra effort needed. Below, we explore the possibility that alternative correlation methods would have yielded a better result.

Table 5-3. Comparison of the number of birds counted during high tide in a particular month with the number predicted from the full annual model. The penultimate column gives the number predicted as a percentage of the number counted. The final column indicates the extent of the extrapolation problem described in the text.

Species	month	Counted	Predicted	Predicted/Counted	Problem
Dunlin	Nov	23000	53500	233%	Small
Oystercatcher	Nov	8162	80000	980%	Medium
Curlew	Sept	3866	44500	1151%	High
Grey Plover	Sept	2478	3655	147%	Small
Shelduck	May	2297	1000000	43535%	High
Ringed Plover	Sept	1340	45000	3358%	High
Redshank	May	844	62500	7405%	High
Bar-tailed Godwit	Nov	729	3862	530%	Medium

5.4 Alternative correlation methods

Granadeiro *et al.* (2004) compared GAM (Generalized Additive Modelling) to GLM in a study on the distribution of shorebirds with respect to abiotic variables in a Portuguese estuary. They concluded that the results of GAM were much better than the results of GLM. However, they allowed only monotonic relationships in their GLM models, so the comparison is not fair. Furthermore, even though a GAM model may have a better fit than a GLM model, this does not mean that it has a higher predictive power. The problems with our modelling would not have been helped by GAM. Extreme values also affect GAMs and extrapolating beyond the range of measurements is even more difficult, if not impossible with a model based on GAM.

Neural networks or quantile regression would not have solved these problems either. What is needed are larger sample sizes and measurements in habitats that we missed in the current study.

This does not mean that GLMs are beyond doubt the best statistical models available. In Appendix 2 we explore the use of regression trees (De'ath & Fabricius 2000) to identify habitats which differ consisntely in the densities of feeding waders. The algorithm underlying the technique requires massive computational power and for this reason has become only recently available. Several advantages of regression trees compared to GLM are apparent. Regression trees deal better with non-linearity and interaction between explanatory variables than GLM (or GAM for that matter). They also indicate which explanatory variables are more important and are not influenced by correlated variables. Finally, in validations the predicted bird hours will not reach unrealistic high values if the explanatory variables reach values that are higher or lower than those used to construct the models.

6 Conclusions

In nearly all bird species studied, emersion time, current velocity and salinity significantly correlated with the distribution of the birds over the tidal flats. Thus, when human activity has an impact on one of these variables, it is likely to affect the birds. A recent assessment of the Strategic Environmental Impact Study of the proposed deepening of the Westerschelde concluded that this impact study did address changes in habitat areas but did not provide sufficient information on the actual quality of these habitats for benthic organisms and therefore, indirectly, on the quality of the habitats as feeding grounds for (internationally important) birds (Commissie MER 2004). This study shows that to assess the impact of deepening of the Westerschelde on the birds, one should, at the very least, be able to predict how deepening will affect the emersion time, the current velocity and the salinity of the tidal flats. It does not suffice to simply predict the effect of deepening on the area of tidal flats.

We succeeded in deriving models that can "explain" quite well the data that we collected to construct these models. However, the validation indicated that for many species, the predictive power of these models was rather poor. Reasonably reliable predictions can only be obtained for Dunlin and Grey Plover. These two species are both common and do not suffer from the problem that high bird usage is predicted for relatively rare habitats that we did not encounter in our study locations. For the other species we obtained, in most cases, an impression for their preferences for particular common habitats, which may be of use in expert judgements on impacts, but we failed to construct models that can be used for quantitative predictions on impact.

Since we think that the partial failure of our programme can be remedied (see below for recommendations), we see no need to abandon the idea that bird usage can be predicted directly from abiotic variables to a considerable degree. Our argument for this optimism is that when the distribution patterns of the birds are compared, there are obvious differences. Redshank, for instance, are restricted to areas with long emersion times and low current velocities, whereas Shelduck occur over a broad range of habitats and also occur in high densities in areas with short emersion times and high current velocities where no Redshank are found. On the basis of our study we can make provisional estimates how much extra effort is needed to substantially improve the models for the species other than Dunlin and Grey Plover, as well as the best way to allocate this effort.

7 Recommendations

The obvious solution to remedy the poor performance of models that predict high bird usage in habitats that are relatively uncommon is to selectively study bird usage in these rare habitats. This means increasing the number of study sites, since our study indicates that, not surprisingly, study sites differ systematically with regard to abiotic variables (Figure 3-3). Increasing the number of study plots per site above 20 will not increase the number of habitats and will make it difficult to count all the plots within 30 minutes at times when bird numbers are high. Furthermore, to increase the number of habitats, it is more efficient to increase the number of study sites (see e.g. Appendix 1). For a given study site, the number of habitats is limited. Thus, if the aim is to cover more habitats, the only solution is to increase the number of study sites.

The analyses suggested that the birds changed their distribution pattern with regard to abiotic variables in the course of the season. However, since we had only one count for most months, doubt remains whether this was actually true. To test if the birds systematically change their distribution pattern in the course of the season, many more counts are needed.

The analyses suggested that salinity had a significant impact on the distribution of the birds, despite the fact that the brackish eastern part was not part of the study. Including study sites in the brackish eastern part would increase the range of values for salinity and would improve the possibilities to obtain proper estimates of the effect of salinity on bird distribution.

The present study was based on study plots in four sites being counted seven times, i.e. a total of 28 counts. This effort proved insufficient to produce reliable models for the majority of bird species. Some quick and cheap improvement of the models might be possible by including the low-tide counts used for validation in the data set used to build the models that we describe in this report. As demonstrates, all the rare habitats would be covered. These (hopefully) improved models could be validated with the high tide counts, but new data are needed for a validation with low tide counts.

A more radical and more costly solution would be to initiate a completely new study. For such a new study we suggest exploring the possibility to use the number of bird hours in a study plot averaged over the year as the dependent variable. A problem in our study were extreme values during single counts and these are likely to average out when the results of several counts are added.

To obtain a proper estimate of the annual number of foraging hours in a plot, at least one count per month is needed, given the clear changes in numbers between months. This amounts to a minimal number of 12 counts per site (since numbers vary between years, a counting program covering several years would be better of course). suggests that it might be possible to cover both the rare and the common habitats with approximately 15 counting sites. In all, a minimum number of 180 counts would be needed to construct the models (in this context one count is taken to mean a visit to one study site to count all the plots at that site during an entire low water period). If one wanted to validate the models with low-tide counts, a similar number would be needed for the validation data. Clearly, the new study sites should be chosen carefully at the start of the study, to make sure that all habitats are covered, especially habitats with (combinations of) extreme values for the abiotic variables.

A few more words on the use of average annual number of bird hours are in place. Just as the total number of bird hours in a tide does not distinguish between a large number of birds feeding for a short period in the plot and a small number of birds feeding there for a long period, the average annual number of bird hours in a plot does not distinguish different seasonal patterns of usage. In a way the problem whether the birds distribute themselves differently over the estuary in the course of the season is thus solved by choosing a dependent variable that does not require one to study the problem. A potential disadvantage of taking the annual usage as the dependent variable, is that it is not possible to take account of the fact that for most bird species, the Westerschelde is of international importance during a selected number of months. Furthermore, different populations of the same species may use the Westerschelde at different times of the year. Finally, managers may have the option to choose in which months potentially disturbing activities are allowed to take place. Thus, users of these models may want to be able to make predictions for particular months.

An alternative option is available for those species where we have sufficient information on the so-called generalized functional response, which describes the intake rate of the food as a function of the density of competitors and prey (van der Meer & Ens 1997). For the Oystercatcher, models exist that can calculate how the birds will distribute their foraging effort with respect to a particular food supply (Stillman *et al.* 2000; Rappoldt *et al.* 2004). The first model keeps track of individuals that differ with respect to competitive ability and foraging efficiency. The second model does not distinguish between different types of individuals, but is able to deal efficiently with a large number of birds in a large number of sites differing in prey density and habitat characteristics. This second model is called WEBTICS (Rappoldt *et al.* 2004) and was successfully applied to the Wadden Sea (Rappoldt *et al.* 2003a) and the Oosterschelde (Rappoldt *et al.* 2003b). The data required to perform calculations with this model are available for the Westerschelde. Furthermore, our observations indicated that Cockles are the main prey of the Oystercatchers in the Westerschelde and that the abundance of this prey predicted the distribution of the birds over the estuary. Last, but not least, WEBTICS is not a model built on correlations, but it is built on knowledge of the processes known to govern the distribution of the birds. WEBTICS can be used to predict the effect of changes in emersion time due to dredging activities, assuming Cockle stocks are unaffected. Alternatively, one may first predict how both morphology and Cockle stocks are affected by for instance dredging, and then calculate the impact on the birds.

Much of the information needed to build a model like WEBTICS is also available for Knots, see e.g. Van Gils *et al.* (2003), Zwarts & Blomert (1992) and Van Gils & Piersma (2004). However, the model has not been built yet, so instead of putting a model to use, as is possible for Oystercatchers, the first step would be to reformulate some equations and parameterize the simulation model on the basis of the information in the literature. At the very least, this would take several months, perhaps even years.

A third species for which a WEBTICS-like model is within reach is the Curlew. Extremely detailed studies on the feeding ecology of this species were conducted along the Frisian coast by Zwarts and co-workers. Although this work has resulted in several publications (see e.g. Ens & Zwarts (1980), Zwarts & Wanink (1984) and Zwarts & Esselink (1989)), a massive body of data remains to be analyzed (or re-analyzed). It would take at least a year, and more likely two years, to extract all the information and subject it to the kind of analyses needed to parameterize a WEBTICS-like model.

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Appendix 1 Multivariate analysis of birds and predictor variables

We used multivariate analysis to explore if and how the bird community was linked to environmental variables. The idea being that this exploratory analysis might help to guide our subsequent more detailed investigations for each individual bird species. The theoretical background and the details of the analysis are provided by Brinkman *et al.* (2005). Here, we provide a short summary of some important results. Due to the exploratory and preliminary nature of the analysis, the abiotic variables used here are different from the abiotic variables used for the GLM analyses (see section 3.1).

First, we used Principal Component Analysis (PCA) to study the abiotic variables. The first axis (PC1) explained 47.8% in the variation of the abiotic data, the second axis (PC2) another 22.5% and the third axis (PC3) 16.5%. Thus, with three axes 86.8% of the variation could be explained. The coefficients of the various abiotic variables of each PCA axis are given in Table 7-1.

Table 7-1. Summary of the coefficients of the various abiotic variables of each Principal Component Axis. Data are normalized values.

Variable	**PC1**	**PC2**	**PC3**
Hmean (mean height)	0.456	-0.481	-0.130
Salt (Salinity	0.184	0.407	-0.777
Dyn (classification as highly dynamic or not)	-0.348	-0.176	-0.546
M0 (median grain size measured in plot)	-0.535	-0.020	-0.139
Vmean (mean current velocity)	-0.573	0.069	0.158
Sfloat (mean silt content according to map)	0.148	0.753	0.191

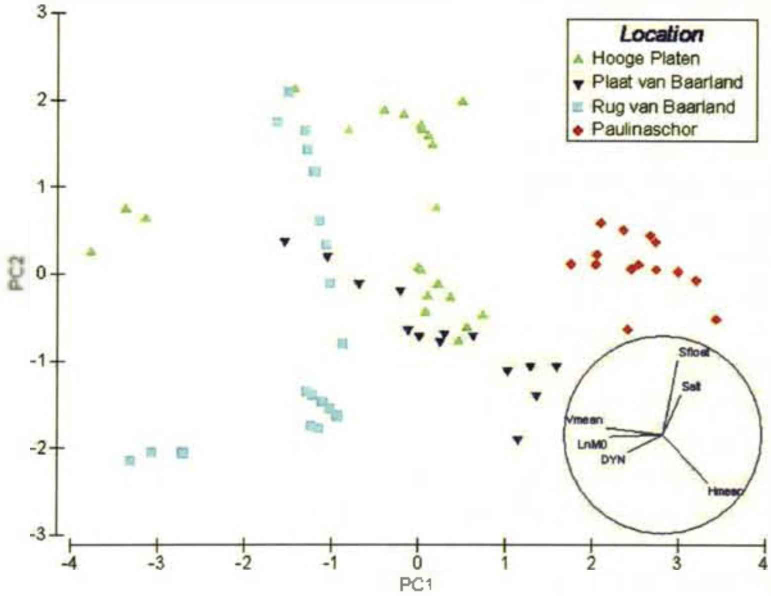

Figure 7-1. PCA plot of the sampled plots on the basis of 6 abiotic variables. Data are normalized values. Each dot represents a study plot. The circle gives a vector plot of the variables.

The most important components of PC1 are all variables that are related to current velocity: mean height, median grain size and current velocity. The mean silt content according to the sediment map (Sfloat) is the most important component of PC2 and PC3 is primarily determined by salinity. This gives an indication of the environmental regimes that are of particular importance at the study sites. Plotting the results of the PCA-analysis in two dimensions (i.e. ignoring PC3) shows a strong tendency of the study plots of a particular study location to cluster together (Figure 7-1). This means that the most efficient way to increase the variation in habitats is not to increase the number of study plots at a given site (since this will amount to more of the same), but to increase the number of study sites. At Hooge Platen and Rug van Baarland, several study plots appear to differ considerably from the other plots (Figure 7-1). In both cases these study plots are characterized as highly dynamic. When we used Multi Dimensional Scaling (MDS) to study these relationships, a very similar picture emerged, supporting our conclusions. (PCA is generally used to depict relationships in two dimensions. MDS works much better than PCA when the ordination is best performed in more than two dimensions. If the MDS plot results in a similar pattern than a PCA plot, the MDS can be seen as a strong indication that two dimensions is enough to show the most important (groups of) variables.)

Next, we studied the predicted benthos densities. It turned out that the MDS plot of the predicted benthos densities strongly resembled the MDS plot of the abiotic variables. The greatest similarity between the pattern in abiotic variables and the pattern in predicted benthos densities was obtained when the abiotic variables height and salinity were used. The strong resemblance between patterns in abiotic variables and predicted benthos densities does not come as a surprise, since benthos densities were predicted from abiotic variables. However, it provides an argument against the inclusion of predicted benthos densities as predictor variable in models predicting the bird foraging hours that already contain abiotic variables.

Finally, we applied MDS to study the variation in the bird community between different study plots (Figure 7-2). As with the abiotic variables it is very clear that the study plots at a given study site tend to cluster together, i.e. plots from the same site are more similar to each other than to plots from other sites. To investigate if the pattern in abiotic variables was similar to the pattern in the bird community, we correlated the abiotic similarity matrix with the bird similarity matrix (a similarity matrix contains for each combination of plots a value indicating how similar they are with respect to the value for certain variables). Basically this means that, if we think in two dimensions, we are looking with what abiotic variables we would get a plot that would look as much as possible as the plot that we would result with the biotic data. However, the analysis we used does not compare the plots, but uses the underlying similarity matrices, thereby, becoming independent of the 2 dimensional ordinations. For the abiotic similarity matrix, we varied the abiotic variables that were included, until we found the abiotic matrix that had the highest correlation with the bird matrix. We selected the abiotic variables from the list in Table 7-1 and performed the analysis for individual counts and for the average of all counts. The results of this analysis are given in Table 7-2. The abiotic variables that are included in the best correlating abiotic matrix vary between counts.

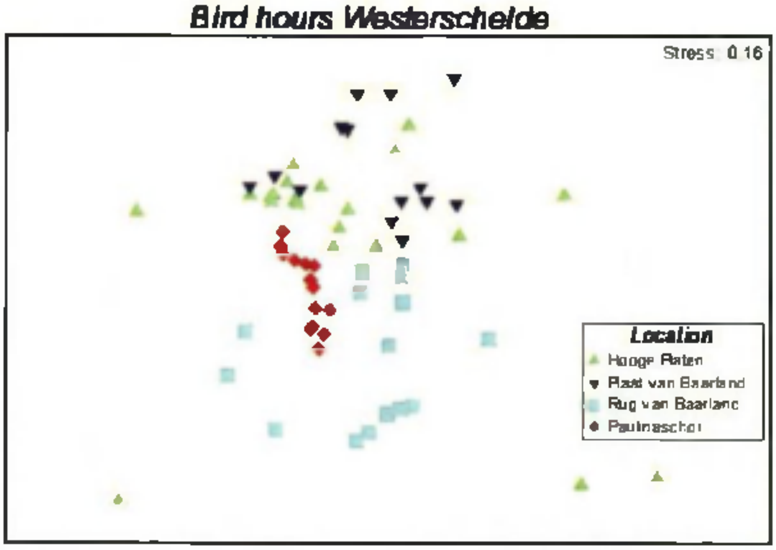

Figure 7-2. MDS plot of the sampled plots on the basis of the bird counts. Each bird species represents a variable and the value of the variable is the number of foraging hours averaged over the counts. Each dot represents a study plot. Data are normalized values.

This could be due to the birds using different habitats in different seasons. Alternatively, it could be due to the differences in phenology between the different bird species. These differences in phenology will cause the bird community of a plot to change in the course of the season and this may change the similarity between plots. Despite this variation between counts, there is also a clear general pattern. Mean height and salinity are nearly always included in the best fitting abiotic matrix. Not surprisingly, they are also included when the bird matrix was calculated from the number of foraging hours averaged over all counts. In that abiotic matrix, a variable indicating whether a plot is highly dynamic or not, is also included. Interestingly, the bird matrix based on the average of the counts has the highest correlation with an abiotic matrix. This suggests that there are general habitat characteristics that influence the distribution of the birds, independent of season.

Table 7-2. Summary of the correlation between the bird matrix and the abiotic matrix. For each count and for the average of all counts, the highest correlation is given, the associated significance level and the abiotic variables included in the abiotic matrix with the highest correlation to the bird matrix.

Count	Best abiotic variables	Correlation (Spearman r)	Significance (P)
September 2003	Hmean, Salt	0.29	0.002
November 2003	Hmean	0.31	0.004
January 2004	Hmean, Salt, Dyn, Vmean, Sfloat	0.47	0.004
March 2004	Hmean, Salt, Vmean	0.47	0.004
April 2004	Salt	0.37	0.004
May 2004	Hmean, Salt	0.36	0.004
Average	Hmean, Salt, Dyn	0.60	0.004

Appendix 2 Classification and Regression Trees (CART)

A relatively new tool in ecological sciences to explore the relationship between one response variable and multiple explanatory variables is a regression or classification tree (De'ath & Fabricius 2000). Tree models deal better with non-linearity and interaction between explanatory variables than regression, GLM and GAM models. Hence, they can be used to find interactions that were not discovered by other methods. CART complement or represent an alternative to multiple regression, analysis of variance, logistic regression, log-linear models, linear discriminant analysis, and survival models. They also indicate which explanatory variables are more important and are not influenced by correlated variables.
Classification trees are used for the analysis of a nominal response variable, and regression trees for a non-nominal/numeric response variable. With classification trees no transformation of the data is necessary (this in contrast with Discriminant Analysis). Regression trees may require transformation of the response variable.

Trees explain variation of a single response variable (Y) by repeatedly splitting the data into more homogeneous groups, using combinations of explanatory variables (Xi) that may be categorical and/or numeric. The algorithms used require massive computational power and have only become recently available for desktop computers. Details can be found in De'ath & Fabricius (2000) and references therein.

As an example the Oystercatcher data of the Westerschelde have been analysed by a regression tree analysis.

We used the following variables:

- Exploratory Variables (untransformed):
    - Hmean: mean height
    - Emean: exposure time
    - Salt: salinity
    - M0AVG: avg. silt content
    - S63: avg. fract. $< 63\mu m$
    - Vmean: avg. current speed

- Response Variable
    - Bird hours Oystercatcher
    - Transformed: (Bird hours Oystercatcher)$^{1/4}$

The results are depicted in Figure 7-3. Concentrating on the right tree which explains most of the variation one should read the tree as follows. Mean height is the first variable that splits most of the data into two groups. The length of each branch is a measure of the amount of variation that is explained by the variable. If Mean height (Hmean) is less than -28.63 one follows the left branch, otherwise the right branch. On the left branch Salt is then used to split the data into 2 groups: if salinity (Salt) is larger or equal to 24.3 the expected number of bird hours is 0; otherwise, if salinity is smaller than 24.3 the expected number of bird hours is 1.4 (SE = 0.006; the standard error is given in the extended text output).

The right side of the tree indicates (Hmean is larger or equal to -28.63) that salinity is the second important variable with salinities larger or equal to 26.9 ending in a predicted number of bird hours of 2.9 (SE = 0.15), otherwise current velocities (Vmean) are important: at high current velocities (larger than 40.6) the model predicts 2.7 (SE = 0.27) Oystercatcher hours while at lower velocities there is a non-linear effect of mean height with expected bird hours of 0.16 (SE = 0.15) at mean heights less than 37.5 and 1.8 bird hours (SE = 0.2) at larger heights.

The regression tree thus indicates that Hmean and Salt are the main variables with some additional variation explained by Vmean. However, the extended output also indicates which variables would give similar results: Mean height could be replaced by exposure time (Emean), Salinity by average silt content (M0AVG), and Vmean could be replaced by Salt or M0AVG or S63.

One apparent advantage of regression trees compared to GLM is that predicted bird hours will not reach unrealistic high values if the explanatory variables reach values higher than those used to construct the models.

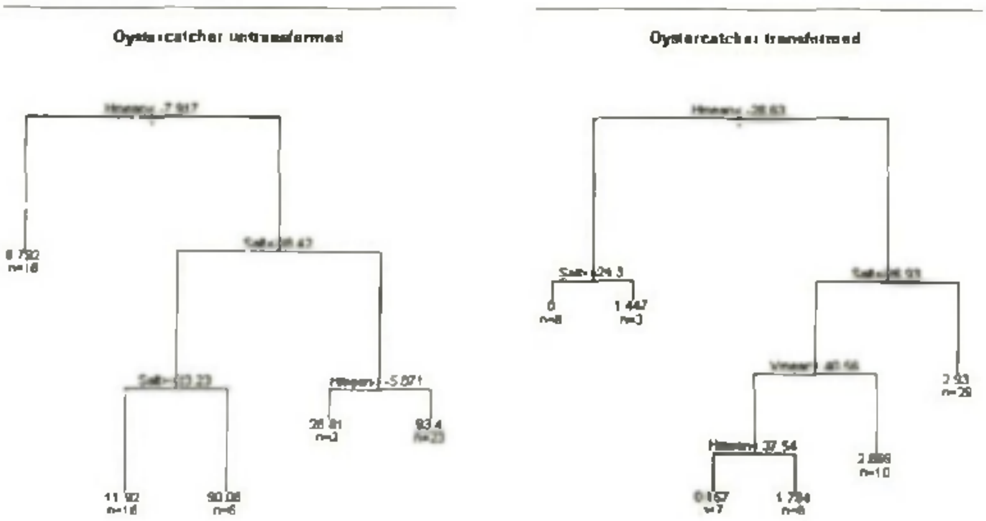

Figure 7-3: Results of regression tree analysis for untransformed observed bird hours (left: r^2=0.75) and transformed observed bird hours (Right: r^2=0.90).