# Scale dependence of the numerical response in Knots (*Calidris canutus*)

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#### Abstract

The numerical response between foraging waders and their prey species depends on the scale on which it is studied. The lack of a fixed numerical response is due to heterogeneity in the distribution of their food supply. In this study, the numerical response of Knots (*Calidris canutus*) is studied on three different scales on a single mud flat in the western Wadden Sea (the Netherlands); the largest scale concerns the entire mud flat, whereas the other two concern the scales of between and within corners of this mud flat.

The distribution of flocks of Knots is observed on a daily basis, by checking 67 quadrants for the presence of a flock of Knots several times a week. Food supply in these quadrants is measured on a regular basis. Diet composition is measured both through direct observations in the field and by collecting Knot-droppings.

On neither of the three different scales a strong numerical response is observed. On the largest scale our rough measurements of Knot abundance only indicate that Knots can distinguish patch quality on this level. On the scale of interest, the between corners of the mud flat scale, neither significant nor strong relations with the biomass-density of a specific prey species is found, probably due to the small sample size. The average relation between Knot abundance and biomass-density of *Carcinus maenas* on the smallest scale of observation is significant though very weak. Despite of problems following from an incomplete design, it can be concluded that Knots forage on *Carcinus maenas* when this prey is abundant. Otherwise they forage on *Cerastoderma edule* even though *Macoma balthica* is present at rather high densities as well. The ignorance of *Macoma balthica* to the diet might be due to the use of a foraging mode specific for *Carcinus maenas* and *Cerastoderma edule*; the consumption of these shallow living prey species does not require the deep probing of the bill needed for capturing *Macoma balthica*.

# Table of contents

Introduction	4
Methods	6
Study area and species	6
General fieldwork procedure	6
Lab measurements	7
Analysis	8
Results	10
Diet composition	10
Food abundance	10
Variation in biomass-density	10
The numerical response	11
Discussion	12
Diet	12
Variation in hiomass	13
Numerical responses found	14
Further research	14
Acknowledgements	16
References	17
Tables	18
Figures	19
Figure 1. The division of the quadrants in five different groups	19
Figure 2: The different scales on which we measured the numerical response	20
Figure 3. Diet composition per patch derived from Knot-droppings	21
Figure 4: Overall diet composition per week, derived from Knot-droppings	22
Figure 5: The available biomass-density per patch	23
Figure 6: The numerical response on the 'hetween-patches scale'	24
Figure 7: The numerical response on the 'within-patches scale'	25
Figure 8: Average relations between Knot abundance and food supply on the 'within-	
patches scale'.	26
Figure 9: The numerical response on the 'above-patches scale'.	27
Figure 10: The relation between available biomass-density and relevance to the diet	28
Annendices	20
Appendices	29
Appendix 2: Calculation method used to express diet composition in terms of AFDM	30
Appendix 3: Weekly diet composition per patch derived from Knot-droppings	32
Appendix 4. The distribution of the different prev species	34
Appendix 5: Food on offer in the first 5 weeks on the different patches	20
Appendix 6: Regression tables for the variation in biomass-density	40
Appendix 7. Variation in biomass-density	42
Appendix 8: Stomach size in relation to patch use	43
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## Introduction

The scale at which one tries to understand the numerical response between waders and their food supply strongly influences the response found (Schneider 1994, Colwell and Landrum 1993, Wiens 1989). It therefore is not surprising that a fixed relation describing the numerical response between shorebirds and their prey does not exist (Colwell and Landrum 1993) and that studies concerning different scales find different relations. Despite this variation, some general patterns can be derived concerning the scale-dependence of the numerical responses: on a large scale the relations found between shorebird and prey are positive and rather strong; with declining scale this strength disappears and on fine scales either weak relations or even inverse numerical relations are found (Colwell and Landrum 1993; Cummings, Schneider and Wilkinson 1997).

The scale-dependency of the numerical response might be due to heterogeneity in the food supply. Prey of shorebirds namely tend to be distributed over a mud flat patchily rather than randomly (Zwarts and Wanink 1993, Piersma *et al.* 1993, this study). Patches however - especially those on a mud flat where no clear boundaries exist - are not likely to be discrete aggregations of food resources, in which food is distributed randomly as assumed in classical foraging literature. More likely they can be seen as areas differing from their surroundings in nature or appearance. They are likely to consist of smaller patches and are themselves aggregations within larger patches (Kotliar and Wiens 1990). As this hierarchy of patches within patches is likely to be a continuous mosaic (Wiens 1989), a specific scale on which the numerical response should be studied does not exist. The relation between shorebirds and the densities of their prey can be determined on various levels, not necessarily resulting in one and the same numerical response.

The scales relevant to a specific shorebird are bounded by the minimal and the maximal scale of heterogeneity the shorebird can respond to. The smallest scale a shorebird can distinguish heterogeneity on is called its grain and the largest scale, determined by the bird's home-range size, is called its extent (Kotliar and Wiens, 1990). Beyond these boundaries an animal is no longer able to respond to any structure in its food supply. The scale the numerical response is studied on should always be seen in context of these extremes (Kotliar and Wiens, 1990). As grain and extent are likely to vary strongly between shorebird species, the scales relevant to study the numerical response on, depend strongly on the shorebird species studied.

This study concentrates on the numerical response of Knots (*Calidris canutus*). Various studies already have considered the distribution of Knots in relation to the density of their prey, both on the large scale of several kilometres (see Colwell and Landrum 1993) and on the finer scale of several hundreds of meters (Piersma *et al.* 1993; Zwarts, Blomert and Wanink 1992). The grain and extent of foraging Knots however are not yet known precisely, although these previous studies on foraging Knots do indicate the borders of their discrimination ability roughly. One characteristic of Knots is the long distance of their seasonal migrations between breeding- and non-breeding grounds. In their non-breeding areas Knots also are wide-ranged; they can use foraging areas tens of square kilometres in size within a single tidal cycle (Piersma *et al.* 1993). Therefore the maximal scale of discrimination is at least the scale of some hundreds of metres, as on this scale a relation between the distribution of Knots and the density of their prey is found, but it might still be much smaller. Thus the range of scales the numerical response of Knots can be studied on is wide.

In this study the numerical response of Knots is described on one specific scale, the scale of corners of a single mud flat in the western Wadden Sea. As the structure of patches on one scale might both be influenced by heterogeneity at a smaller scale and by patchiness at a larger scale, consideration of three levels is necessary for a full understanding of the processes on the level of interest (Kotliar and Wiens 1990). Therefore this study does not only focus on the scale of corners within one mud flat, but also takes into account the scale of the entire mud flat (one scale larger) and that of patches within these corners (one scale smaller). The criteria available on a mud flat to identify different scales are far from obvious, as almost no visual clues are present. Due to this absence of clear borders and due to the lack of knowledge on the perception of patchiness by Knots on small scales, the criteria used to identify both the smallest and the largest scale of the corners of the mud flat are identified by biotic and environmental characteristics.

# Methods

#### Study area and species

Our study area, the Grienderwaard, is an intertidal mud flat connected to the island of Griend  $(53^{\circ}15' \text{ N}, 05^{\circ}15' \text{ E})$  in the centre of the western Wadden Sea, NW Netherlands. The western Wadden Sea is an important foraging area for wintering waders. It covers an area of approximately 2000 km<sup>2</sup> and contains some high tide roosts and several large mud flats. The Grienderwaard is a sandy mud flat (median grain size 150-200 µm, Piersma *et al.* 1993), that at low tide covers an area of approximately 55 km<sup>2</sup>. Its elevation varies from -30 to +80 cm above mean sea level (Piersma *et al.* 1993). Near neap tide Knots foraging on the Grienderwaard are able to roost on the island of Griend, in the centre of this mud flat. Most Knots, however, roost on the (more open) island of Richel, approximately 7.5 km north-west of Griend, together with birds from other mud flats in the western Wadden Sea.

During the two months of our research, August and September, two subspecies of Knots use the western Wadden Sea. *Canutus*-knots (*Calidris canutus canutus*) use it as a stopover site during their migration from their breeding to their wintering areas. *Islandica*-knots (*Calidris canutus islandica*) use it as their wintering area (Piersma 1994). In our observations of them, we made no distinction between these two subspecies.

## General fieldwork procedure

In order to describe the distribution of Knots over the Grienderwaard we called our smallest unit of observation a quadrant. A quadrant we defined as a circle with a radius of 50 m and we indicated every quadrant with a wooden stick in the middle of it; in field observations we estimated its borders. The size of these quadrants is chosen arbitrarily. On the one hand the quadrants must be small enough to enable us to measure the food supply in it adequately, but on the other hand they should not be too small as the chance on encountering a flock of Knots will diminish with decreasing quadrant size. On every location of the mud flat where we encountered a flock of Knots a new quadrant was started, although no new quadrants were started in the last 2 weeks. Each quadrant we tried to check for the presence or absence of Knots once every day, but if not possible at least a few days per week. As not all quadrants are started on the same day, the period of observation of the quadrants varies from 2 to 7 weeks. In total we used 67 quadrants (Appendix 1), distributed mainly around the island of Griend and eastwards.

During 44 days between July the 27<sup>th</sup> and September the 18<sup>th</sup> 1998 two or three teams of observers checked as many of the quadrants as possible for the presence of flocks of Knots, by walking different routes across the tidal flat. Whenever we encountered a flock of feeding Knots, we counted the total number of Knots in this flock, as well as the number of them in each quadrant. When we saw the arrival and / or the departure of a flock, we recorded the time. When possible, we determined the intake rate of some individuals in the flock for a 5-minute period with the aid of a 20-60x zoom telescope to get an idea of the patch quality.

After a flock had left, we collected a sample of 50 of the most recently produced droppings in order to determine the diet of the flock. Knot-droppings are easily recognisable small bars, consisting of both sand and small fragments of shells and could easily be collected with the aid of a shell valve. However, droppings could not always be collected as they fell apart rapidly, due to the layer of water that most times covered the tidal flat.

For each quadrant we tried at least once to note the moment of emerging, in order to be able to calculate the daily exposure time. Corresponding to this moment of emerging was a certain height of the water in the nearby gully measured by Rijkswaterstaat. Knowing this height we could estimate the moments of exposure and emerging for every day and thus calculated the average daily exposure time.

In order to estimate the distribution of food over the Grienderwaard we collected benthossamples distributed in a 250-meter grid covering the entire mud flat. On each of the 617 sampling points of this grid we took in the entire season one sediment-core. For a more detailed estimate of the amount and the composition of the food available for the Knots in the quadrants, we sampled benthos in the quadrants several times during the season with intervals of five days. As not all quadrants were started on the same day, the number of samples per quadrant varies from 2 to 11. A benthos sample in the quadrants consists of ten sediment cores. Each grid benthos-sample measures  $1/56 \text{ m}^2$  and each quadrant benthos-sample ten times this. Of the sediment cores we treated the top (upper 3.5 cm) and the bottom layer separately, as only the prey in the top layer where within reach of the Knots' bills. We sieved both layers over a 1 mm sieve and collected all potential prey items to store them in a freezer for measurements in the lab.

In both the grid- and the quadrant-sampling method, we also took separated smaller cores width a mesh width of 500  $\mu$ m to measure the highly abundant prey (in practice the mudsnail (*Hydrobia ulvae*), which could reach densities up to several thousands per square meter). Core surface of these smaller cores was 1/259 m<sup>2</sup> and we took one of them with each grid-sample and three with each quadrant-sample.

#### Lab measurements

We measured the length of the bivalves as well as the carapace width of the crabs in the benthos samples to the nearest mm, and the height of the mudsnails to the nearest 0.5 mm with the aid of a vernier callipers. Of each quadrant we determined the ash free dry weight (AFDW) of at least one sample, to get an average relationship representative for the entire Grienderwaard. For all bivalves in these samples longer than 7 mm (smaller shells were too small to handle) we separated the flesh from the shell with the use of a scalping knife. We dried this flesh as well as the intact crabs and mudsnails at 55 to 60 °C for three days, to obtain the dry weight and incinerated them for 5 hours at 550 °C.

The dropping samples are treated as described in detail in Dekinga and Piersma 1993. They are sieved over a 300  $\mu$ m sieve to remove sand and organic material. Then they are dried for three days at 55 to 60 °C and weighted. To obtain the size distribution of the different prey per sample, we measured all bivalve hinges, (concave) movable fingers of the crabs' pincers and broken or intact mudsnails, after collecting them with the use of an 10 to 20x stereo-microscope (for large dropping samples we collected these recognisable pieces only in one half of the sample). To determine the proportion of the diet attributed by each species in terms of shell mass, we sorted all fragments in a sub-sample into species and weighted them. From the combination of the size distribution and this proportion we estimated the contribution to the diet of each species in terms of biomass-density (see Appendix 2 for details).

## Analysis

Our unit of measurements of both benthos, droppings and Knots is a quadrant. These quadrants however are not independent of each other; groups of quadrants have factors like sediment composition, daily emerging time, distance to roosts and predation risk in common, by being situated on the same corner of the mud flat. The quadrants are grouped by a principal component analysis (PCA-analysis) on base of their co-ordinates and their daily exposure time to create groups of quadrants more or less independent of each other (these groups however are not totally independent of each other as a Knot on a quadrant of one of these groups is per definition not on the others). Daily exposure time varies strongly between the quadrants from minimal 8% to at maximum 84% of the tidal cycle (12 h 25 min). This PCA-analysis resulted in five groups of quadrants, differing in size from 5 to 16 quadrants (see figure 1). Within these groups the quadrants are highly dependent of each other on the abiotic factors used in the PCA-analysis. But also other factors characterising the group of quadrants will vary less between quadrants within such a group as variation in such factors decreases with decreasing scale. Food however is patchy on every scale and thus the quadrants within these groups will mainly vary in food abundance (Colwell and Landrum 1993).

Now we can consider the abundance of Knots in response to the density of their prey on three different scales. The scale particularly of interest is the scale on which patches are defined as groups of quadrants. We call this the 'between-patches scale'. Patches on this scale are identified on objective biological criteria rather than on (arbitrary) methodological criteria. On this scale we are able to take patchiness on both a smaller and a larger scale into account. 'Quadrants within a group of quadrants' is the smallest scale we can consider the numerical response on. We will call this the 'within-patches scale' (see figure 2). The largest scale we can investigate the numerical response on is the scale of the entire mud flat as two different areas can be seen as patches here; one area in which Knots are seldom seen and in which no quadrants are started by lack of flocks of Knots and one in which Knots were abundant, this scale we will call the 'above-patches scale'. Although consideration of patchiness on both the 'above-' and the 'within-patches scale' will help to understand the numerical response on these two scale (above- and within patches) as we have defined patches on these scales only on arbitrary considerations.

Although intake rate might be the most straight measure of patch-quality, as it combines both the numbers of prey on offer as the search- and handling time necessary to gather these prey, we decided to use biomass-density to express patch-quality. Our field observations of intake rate compared with the diet of the Knots do not seem to include the entire diet and are therefore no proper measure of intake rate. Though we still could estimate potential intake rate from the measured densities of the prey, this introduces new and complex problems. To avoid these we decided to use a more primary currency. Both the numbers of prey and the biomassdensity can be used as such a measure. As both measures result in almost identical outcomes, we chose to present only results based on biomass-density (in g AFDM), to link to existing literature. Biomass-density was calculated by regression functions derived from our own data, and thus specific for the Grienderwaard 1998 (see table 1).

All calculations concerning the food of the Knots are executed in terms of the available part of the food on offer as described in Zwarts and Blomert 1992. Zwarts and Blomert distinguish accessible, ingestible, profitable, available and harvestable prey items. Accessible are those prey items that are buried within reach of the Knots-bill. In this research all prey items in the upper 3.5 centimetres of the sediment (the top-layer) are considered to be accessible. As both *Cerastoderma edule* and *Carcinus maenas* live either on the surface or always in the upper 3.5 centimetres, individuals of these species encountered in the bottom layer are concerned as sampling errors. To correct for this sampling error, they are added to those encountered in the top-layer. Ingestible prey items are those that are not too large to be swallowed: in this research all *Carcinus maenas*, all *Hydrobia ulvae*, all *Cerastoderma edule* smaller than 17 mm and all *Macoma balthica*, *Mytilus edulis* and *Mya arenaria* smaller than 19 mm are considered as such. Profitable are those prey items that are not too small. Harvestable prey items are both accessible, ingestible and profitable, whereas available prey are only accessible and ingestible. We chose to consider only available prey items, as the choice to include or reject a certain prey item does not depend on its profitability alone, but on the combination of its profitability and the densities of other prey items. Therefore the lowest profitability accepted depends strongly on prey-density and no clear border for acceptance exists between the profitability of certain size classes.

As a measure of Knot abundance we calculated the intensity of area use of Knots (per hectare). This intensity follows from multiplying the average flocksize with the chance on Knots per location. Average flocksize per quadrant is calculated as the average of the daily maxima. Average flocksize per patch is calculated as the average of the daily averages of the maxima of the different quadrants in the patch. The chance on Knots is calculated as the proportion of days of observation on which we saw a flock. Only those quadrants and patches are used for which more than three observations were done.

With a General Linear Model (GLM) we tested whether variation in food abundance of the four main prey species (in terms of biomass-density) could be explained by a temporal factor ('week') or by spatial factors ('patch' and / or 'quadrant within patch') or by a combination of them. The tests were performed both on the level of prey species (all length-classes together) and of prey-types (1-mm length-classes within a species).

On the 'above-patches scale' we did not measure Knot abundance properly. In order to understand something of patchchoice on this scale, we separated the areas where Knots were abundant (i.e. the quadrants) from the areas where Knots were rarely seen (all other places). We tested nonparametically with a Mann-Whitney test whether the average numbers of the different prey were higher in the areas where Knots were abundant (our study area) than in those where Knots were rare. The average biomass-density in the study area was calculated by counting the four grid-sampling points closest to each quadrant to our study area.

# Results

# **Diet composition**

In all patches the diet is composed of a combination of prey species, though in patch C one single species does attribute more than 90 % to the diet (figure 3). In total six species occur in the diet of the Knots, though only four of them appear to be quantitatively important; both the Blue mussel *Mytilus edulis* and the clam *Mya arenaria* are encountered only sporadically in the droppings. Further analysis therefore concentrates on the other four prey species only. Although these four species - the cockle *Cerastoderma edule*, the mudsnail *Hydrobia ulvae*, the Shore crab *Carcinus maenas* and the Balthic tellin *Macoma balthica* - attribute all to the diet, their relative importance varies strongly both between patches and in time (figure 3). Main prey species per patch varies from *Cerastoderma edule* in patch A and patch B, *Hydrobia ulvae* in patch E to *Carcinus maenas* in patch C and patch D. Although diet composition varies strongly between weeks in some patches (patch D and E) it stays rather constant in others (patch A and C) (see appendix 3). The overall diet composition however seems to be more or less constant in the first five weeks, with both *Carcinus maenas* and *Cerastoderma edule* as the most important prey species (figure 4). It then seems to switch, and *Hydrobia ulvae* becomes the major prey in the last two weeks.

# Food abundance

Figure 5 shows the biomass-density of the four major prey species available on the different patches (see for distribution of the different prey Appendix 4 and for weekly mean biomass per patch Appendix 5) in the first five weeks. Available biomass-density of other potential prey, for instance that of *Mya arenaria* and *Mytilus edulis*, is not included, since biomass-density of these species turned out to be very low. The prey most available in terms of biomass-density turns out to be *Hydrobia ulvae* on the patches A, B and E, *Macoma balthica* on the patches A, D and E and *Carcinus maenas* on patch C. The density of *Carcinus maenas* is high compared to previous studies in the Wadden Sea (Piersma *et al.* 1993, Zwarts, Blomert and Wanink 1992); in one of the patches the highest available biomass-density is even that of *Carcinus maenas*.

# Variation in biomass-density

On the level of prey types no variation at all can be explained for both *Carcinus maenas* and *Cerastoderma edule*, whereas only the two spatial factors explain variation in abundance of *Hydrobia ulvae* and *Macoma balthica* on this level (results not shown). Therefore we restrict our analysis to the level of prey species and no longer concern the level of prey types.

Variation in biomass-density in all samples on the level of prey species can only be explained by the two spatial factors 'patch' and 'quadrant within patch'. Only for *Macoma balthica* no variation in terms of biomass-density exists within patches. The temporal factor 'week' does not significantly explain variation, except for *Carcinus maenas* (Appendix 6; table 1a). This is not due to the lack of orthogonality in the design (due to a free rather than a fixed starting date of the quadrants) as the same tests performed on a subsample of the data with a more or less orthogonal design show similar results (Appendix 6: table 1b and figure 1 (design)). In this subsample, the factor week still fails to explain variation in biomass-density for all species but *Carcinus maenas*. As for three of the four prey no seasonal variation exists (Appendix 6, table 1b), we group our benthos-data of different days and calculated an average estimate of biomass-density both per quadrant and per patch, thus excluding variation due to the factor 'week'. For *Carcinus maenas*, however, a separated analysis on a weekly base could be performed.

When only considering samples gathered in the first five weeks (as the diet appears to be more or less constant in this period), variation in biomass-density can be explained by the two spatial factors ('patch' and 'quadrant within patch') for all species (though the spatial factor 'quadrant within patch' does not explain variation in biomass-density of *Carcinus maenas* significantly (p = 0.094); see Appendix 6, table 1c).

# The numerical response

As patch E is the only patch with quadrants situated close to the island, patch E is likely to differ from the other four patches (for instance in occurrence of parasites, in distance to high-tide roosting area and in risk of predation). Numerical responses on both the 'between-patches' and the 'within-patches scale' are therefore tested both with and without (the quadrants in) patch E.

Figure 6 shows the relations between biomass-density and the intensity of area use on the 'between-patches scale'. The intensity of area use by Knots on this scale seems to be positively related with both *Carcinus maenas* and *Macoma balthica* and negatively with *Cerastoderma edule* and *Hydrobia ulvae*. However, none of these relations are either strong or significant (table 2). This is most likely due to the small sample size. When patch E is excluded, the strength of all relations increases, though still none of the relations found is significant (table 2).

On the 'within-patches scale', all relations found between Knot abundance (either expressed as the average flocksize, the chance on a flock of Knots or as the intensity of area use by Knots) are extremely weak and highly insignificant (results not shown). Moreover the relations found in the different patches are not very consistent (figure 7). The relation between the intensity of area use and the biomass density of the different prey species for instance, is only for *Carcinus maenas* rather similar in all but one of the patches (patch E).

Testing for the average relation within the different patches (and thus on the 'withinpatches' level) shows that Knot abundance is significantly related to biomass-density in some cases (figure 8). All relations however are weak. After exclusion of patch E, the relation between the intensity of area use and biomass-density of *Carcinus maenas* is significant, though weak ( $R^2=0.104$ , p=0.029). The chance on Knots turns out to be unrelated with biomass-density, whereas the average flocksize seems to be even better related to biomassdensity than the intensity of area use is; the average relation in the different patches between average flocksize and biomass-density is significant for *Carcinus maenas* ( $R^2=0.159$ , p=0.024) and for *Macoma balthica* ( $R^2=0.143$ , p=0.038).

The average density of the different prey species in- and outside our study area is shown in figure 9. The density of the average available numbers of both *Cerastoderma edule* and *Macoma balthica* inside the study area turns out to be significantly higher scale (p < 0.000 for both species). Therefore Knots seem clearly able to distinguish good and bad patches on the 'above-patches scale'. The density of *Carcinus maenas* however does not vary significantly between the two areas.

# Discussion

#### Diet

Zwarts *et al.* (1992) argue *Macoma balthica* to be the most preferred prey for Knots foraging on the Frisian coast. They consider *Cerastoderma edule* to be an undesirable prey for Knots, as the hard shell of *Cerastoderma edule* would make it less profitable. Piersma *et al.* (1993) predict Knots on the Grienderwaard to prefer *Macoma balthica* when the biomass-density of this prey is above a threshold of 0.8 - 1 g AFDM / m<sup>2</sup>. In years that the biomass-density of *Macoma balthica* is low and the biomass-density of *Cerastoderma edule* is high, they find Knots to forage on *Cerastoderma edule*. As biomass-density of *Carcinus maenas* is low in both studies, neither of them mention *Carcinus maenas* as a potentially important prey for Knots, though Piersma *et al.* 1993 do report some Knots foraging on it.

Compared to Zwarts *et al.* 1992, the biomass-density of both *Macoma balthica* and *Cerastoderma edule* is extremely low; they report the biomass-density of *Macoma balthica* and *Cerastoderma edule* on the Frisian coast to be on average respectively twenty and hundred times as high as found in this study (average biomass-density of *Macoma balthica* 17.22 g AFDW /  $m^2$ , average biomass-density of *Cerastoderma edule* 20.66 g AFDW /  $m^2$ ). The biomass-densities for both *Macoma balthica* (maximum biomass-density is 1.2 g AFDM /  $m^2$ ) and *Cerastoderma edule* (maximum biomass-density is 1.2 g AFDM /  $m^2$ ) on the Grienderwaard reported by Piersma *et al.* 1993, however, are in the same order of size as those found in this study is high enough to be foraged on, at least in the patches A, D and E where biomass-density is above the threshold of 0.8 - 1 g AFDM /  $m^2$ , whereas the biomass-density of *Cerastoderma edule* is low compared to the biomass-density reported by them for the years 1988-1992. Biomass-density of *Carcinus maenas* in this study is high compared to both Zwarts *et al.* 1993.

When comparing the biomass-densities found in this study with results from these previous studies, one would thus expect Knots in this study to feed on *Macoma balthica*, at least in the three patches with biomass-density of *Macoma balthica* above 1 g AFDM /  $m^2$  (patch A, D and E; figure 5). In none of the patches however the contribution of *Macoma balthica* to the diet is more than 20 percent (figure 3). Moreover, as biomass-density of Macoma balthica is high and that of Cerastoderma edule is low (figure 5), one would not expect Cerastoderma to be relevant to the diet. In two patches however (patch A and B), *Cerastoderma edule* is the main prey species fed on (figure 3).

In figure 10 the relation between biomass-density in offer and the contribution to the diet is plotted for each prey species. Knots in this study turn out to feed on *Carcinus maenas* in the patches where biomass-density of *Carcinus maenas* is high (patch C and D). In the other patches they forage on *Cerastoderma edule* (patch A and B). In patch E, however, they feed on *Hydrobia ulvae*, though the biomass-density of *Hydrobia ulvae* in this patch is rather low and the biomass-density of *Cerastoderma edule* rather high. In the four patches far from the island, the diet composition thus can be explained by two prey species. Knots eat *Carcinus maenas* if possible and else they eat *Cerastoderma edule*. The reason why patch E does not fit into this pattern, might be that several factors influencing foraging Knots may be different in this patch, as it is situated close to the island. The risk of encountering a parasitised *Macoma balthica* for instance is higher on the quadrants close to the island. The same probably holds for *Cerastoderma edule*, although we do not know of a parasite for *Cerastoderma edule* yet. Also the risk of predation is likely to be higher on the patches close to the island, as the distance to cover (and thus the probability to be surprised) is much smaller here.

The reason for not foraging on *Macoma balthica* might be that foraging on this prey species requires a different foraging mode than foraging on the other potential prey species. Foraging on either *Carcinus maenas*, *Cerastoderma edule* or *Hydrobia ulvae* (as well as on *Mytilus edulis*) does not require deep probing of the bill in the sediment, as these species live either on the surface of the mudflat or buried only shallowly. As *Macoma balthica* (as well as *Mya arenaria*) is buried deeper in the sediment, foraging on this species requires a different foraging mode; the bill has to be putted deeper into the sediment in order to reach the prey. The choice to forage on a (combination of) specific prey species (and thus to use a specific foraging mode), therefore might exclude a (combination of) other prey species from the diet. In our study the choice to forage on *Carcinus maenas* and *Cerastoderma edule* would thus explain the absence of *Macoma balthica* in the diet. Apparently the unusual high biomass-density of *Carcinus maenas* (in combination with the available *Cerastoderma edule*?) has made the Knots to choose for foraging shallowly instead of choosing to forage on the rather high biomass-density of *Macoma balthica*.

# Variation in biomass

Only for *Carcinus maenas* the variation in biomass-density in our data turns out to be partly due to temporal variation (Appendix 6). For all other species variation in biomass-density in our data is only due to the two spatial factors ('patch' and 'quadrant within patch'). Is this absence of an effect of the temporal factor 'week' for the other species in our data likely to be due to the actual absence of this effect in the field, or is it due to our method of measuring?

We examine whether or not the absence of temporal variation is likely to be realistic on the basis of *Macoma balthica*. The average biomass-density of *Macoma balthica* in the quadrants during the seven weeks of our study is 1.29 g AFDM / m<sup>2</sup>. Assuming the average flocksize within a quadrant to be 300 Knots / m<sup>2</sup>, when a flock is present, the average number of Knots in this quadrant is  $300 / (50)^2 * \pi = 0.038$  Knots / m<sup>2</sup>. Further assuming each quadrant to be occupied by a flock of Knots for on average five minutes per tide, the foraging pressure per day is (2 \* 5 \* 60 (s)) \* 0.038 Knots / m<sup>2</sup> = 23 knot-seconds / m<sup>2</sup> per day (this foraging pressure can be practised either by 23 Knots all foraging 1 second or by one Knot foraging 23 seconds). Assuming the minimal required intake rate to be 0.4 mg AFDM / s (Zwarts *et al.* 1992), this results in a minimal decline of 0.0004 (mg AFDM / s) \* 23 knot-seconds / m<sup>2</sup> = 0.009 g AFDM / m<sup>2</sup> per day, corresponding to a decline of 0.064 g AFDM / m<sup>2</sup> per week. This is a decline of the average density of *Macoma balthica* of 0.7 % per day or 5 % per week.

The amount of variation due to our measuring method can be calculated when knowing the coefficient of variation for each species (see Appendix 7). The standard error due to our sampling method namely can be calculated by dividing the coefficient of variation by the square root of the number of samples. Our average number of samples per quadrant per week is 1.15. This corresponds with 11.5 cores a week (though the effective number of cores will be much lower by collecting cores in groups of ten together). For *Macoma balthica* the minimal methodological standard error per week is therefore 29.8 %.

Thus the variation in biomass-density of *Macoma balthica* per week due to depletion by foraging Knots only is already likely to be considerable. Incorporating depletion by other predators as well, results in an even stronger biological variation. The fact that there is no effect of the temporal factor 'week' in our data is therefore unlikely to be due to the actual absence of this effect in the field. Moreover as our methodological standard error is rather high, the lack of temporal variation in our data is more likely to be due to our sampling method.

#### Numerical responses found

On the scale of interest, the 'between-patches scale', we find a positive relation between the distribution of Knots and that of biomass-density of *Carcinus maenas* when considering only the four patches far from the island (excluding patch E; figure 6, table 2). None of the relations on the 'between-patches scale' however is significant; probably due to the small number of samples.

On the 'within-patches scale' we find a weak average numerical response between Knot-abundance and the biomass-density of *Carcinus maenas* in the four patches far from the island (excluding patch E; figure 8). Zwarts *et al.* also find a relation between the intensity of area use and biomass-density on a comparable scale. In their study this relation was mainly due to a relation between the 'chance on Knots' and biomass-density. In our study this relation is absent. As we estimate the 'chance on Knots' by checking once a day for the presence of Knots, whereas Zwarts *et al.* (1992) base their estimate on observation each 30 minutes, the reason why we do not find a relation between 'chance on Knots' in this study is not representative for the actual chance on Knots. This will weaken the relations with the intensity of area use and the actual relations with the intensity of area use are thus likely to be stronger.

On the 'above-patches scale' Knots seem able to distinguish good and bad patches, though mainly for *Macoma balthica* and *Cerastoderma edule*. They do not distinguish good and bad patches for *Carcinus maenas*. As the relations on the 'between-' and the 'within-patches scale' corroborate the idea derived from the diet composition that the most preferred prey in this study was *Carcinus maenas*. The absence of a relation with biomass-density of *Carcinus maenas* on the 'above-patches scale' therefore is unexpected. It seems that selection of patches on this scale is based on biomass-densities of *Cerastoderma edule* and *Macoma balthica* more than on that of *Carcinus maenas*, even though they seem to prefer *Carcinus maenas* most. On the 'between-' and the 'within-patches scale', the distribution of Knots is explained best by the biomass-density of *Carcinus maenas*, although we can neither find significant relations on the 'between-patches scale' nor strong relations on the 'within-patches scale'.

## **Further research**

Two major improvements can be made to increase the quality of the method required for a proper research on numerical responses. The first concerns the design of the field observations and the second the quality of the estimates of abundance of both the predator and the prey.

On regard of the design the importance of orthogonality and the importance of the maintenance of initial variation should be stressed. The lack of orthogonality in our design, due to the fact that there was a free rather than a fixed starting date for the quadrants, made the statistical tests in this research lose much of their power. A fixed design for both observations and benthos sampling would have increased the power of our data considerably. Problem in obtaining such a design in case of the Knots is that the distribution of Knots is quite unpredictable. By selecting one's quadrants in front, one risks the possibility that no Knot will visit these quadrants. One can avoid this risk by studying a shorebird more loyal to his foraging sites or just run the risk.

The maintenance of initial variation is the second important improvement of the design. As we only added those areas to our study on which we had observed Knots to forage, we on forehand selected the richer areas. By doing so we did not measure the areas with lower biomass-density and thus we lost a lot of the variation in biomass-density present in the field. This made the understanding of the numerical responses more difficult. One therefore should also include unexploited areas to one's design.

Besides this the estimation of both the abundance of Knots and the abundance of prey can be improved. The estimation of Knot-abundance is based on the estimation of both the average flocksize and of the chance on Knots. Although the first occurred rather roughly by the lack of clear borders to our quadrants, the major improvement can be made on the latter as our daily observation of the presence or absence of Knots is unlikely to be representative for the entire tide. In the ideal case one would be able to measure the average foraging pressure on the location of interest. There are two possible ways to approach the actual average foraging pressure. The first option is to increase the number of observations during one tide. This can either be done by staying the entire tide on the same location, or by using fixed receivers on each patch that only span the surface of one patch. Staying on one patch during the entire tide has the advantage that it enables one to measure with great preciseness the average foraging pressure. The advantage of using stationed receivers to track radio-tacked Knots is that it will result in a good estimate of the average time spent on a patch, though it will not give precise information on the flocksize or the exact location of a flock. The combination of staying on the same patch the entire tide and using receivers on this patch however will result in an accurate estimate of foraging pressure.

A different approach could be to measure on a regular base the density of Knotdroppings on a certain patch. The number of droppings on a patch will give a good indication on the average foraging pressure. This method can only be used during outgoing tide, as incoming tide will spoil the droppings before the density can be measured. Still it will result in a rather good estimate of the foraging pressure. Additive to the previous method of staying on a fixed patch, it may even give more information. Before this method can be used adequately experiments should be performed to verify the number of droppings found with the corresponding foraging pressure.

Increasing the estimation of the abundance of prey can be achieved by increasing the average number of samples. To do so one first should collect all sediment-cores separately in order to maintain information on variance. Moreover one should increase one's number of samples either by taking more samples often or by taking more samples at a time. This can be achieved by increasing the crew or by restriction of the area in study.

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# Tables

**Table 1**: The regression statistics used to derive biomass-density from the densities of the different species. The model used is  $AFDM = 10^a * (length)^b$ . All relations are highly significant (p < 0.000). The small number of crabs on which the biomass-density of *Carcinus meanas* is calculate, is due to the fact that only complete crabs are used. Transport and storage of the crabs in the benthos samples however has resulted in a high number of damaged crabs.

Species	length range used	N	constant (a)	regression coefficient (b)	R <sup>2</sup>
Carcinus maenas	8-19 mm	10	-3.950	2.485	0.972
Cerastoderma edule	<17 mm	91	-6.104	3.922	0.892
Hydrobia ulvae	1-7.5 mm	143	-4.368	2.327	0.862
Macoma balthica	< 19 mm	320	-5.361	3.559	0.906

**Table 2**: The strength and significance of relations between the intensity of area use and the biomass-density of the different prey on between-patches scale. Model used to test the relations is: intensity of area use = constant + biomass-density  $prey_x$ .

No relation is significant, probably due to the small sample sizes used. The relation with *Carcinus maenas* becomes stronger when only the four patches far from the island are considered.

		All patches		patch A, B, C & D				
	R <sup>2</sup>	N	р	R <sup>2</sup>	N	р		
Carcinus maenas	0.485	5	0.192	0.650	4	0.194		
Cerastoderma edule	0.015	5	0.844	0.002	4	0.952		
Hydrobia ulvae	0.662	5	0.094	0.669	4	0.164		
Macoma balthica	0.126	5	0.558	0.221	4	0.541		

#### Figures





Figure 1: The division of the quadrants in five different groups. Figure 1a: The PCA-analysis based on the factors 'daily exposure time' and co-ordinates' results in five groups of quadrants varying in size from 5 to 16. These groups of quadrants are more or less independent of each other, whereas the quadrants within one group are highly dependent. Figure 1b: The distribution of quadrants in the different groups over the Grienderwaard (scale is approximately 1: 100000). Four of the five groups of quadrants are situated relatively far on the mudflat, whereas the fifth, group E, contains all quadrants near the island.





Figure 3: Diet composition per patch, derived from Knot-droppings.

Figure 3: Diet composition, derived from Knot-droppings, differs strongly per patch. Only four species turn out to be relevant to the diet. In patch A and B Cerastoderma edule forms the major part of the diet, in patch C and D Carcinus maenas and in patch E Hydrobia ulvae. The diet is in general composed of a combination of different prey species; only in patch C clearly one prey, Carcinus maenas, is selected solemnly. Macoma balthica does not contribute more than 20 % to the diet in all patches. Vertical bars indicate one standard error.





Figure 4: Overall diet composition, derived from Knot-droppings, during the season varies strongly over weeks. The first five weeks both *Cerastoderma edule* and *Carcinus maenas* are the major components of the diet, whereas in the latter two weeks *Hydrobia ulvae* has become the most important prey. Vertical bars indicate one standard error.



Figure 5: The available biomass-density per patch varies strongly. Biomass-density of *Cerastoderma* edule in all patches is very low, though *Cerastoderma edule* is the major prey in patch A and B. Biomass-density of *Macoma balthica* in patch A, B, D and E is above the threshold value of 0.8 - 1.0 mentioned by Piersma et al. 1993. Biomass-density of *Carcinus maenas* is high in comparison to previous years (in which *Carcinus maenas* hardly occurred). Although relatively important in other years, neither *Mytilus edulis* nor *Mya arenaria* is found available in relevant densities in any of the patches. Vertical bars indicate one standard error.

23





Figure 6: The relations between available biomass-density of the four main prey species and the intensity of area use by Knots on the 'between-patches scale'. Intensity of area use on this scale seems to be positively related only with *Carcinus maenas* and *Macoma balthica*, though none of the relations found is significant. Strength and significance of the numerical response on this scale are summarised in table 2.



Figure 7: The numerical response on the 'within-patches scale'.

Figure 7: The relation between the intensity of area use by Knots and the available biomass-density of the four main prey species on the 'within-patches scale'. The single straight lines indicate the relations found within each patch. Note that the x-axis is not constant for the different prey species. All relations found are insignificant and weak.



# Figure 8: Average relations between Knot abundance and food supply on the 'withinpatches scale'.

Figure 8: Strength ( $\mathbb{R}^2$ ) and significance (p-value) of the average relations within all patches (and thus on the 'within-patches scale') between biomass-density of the different prey species and average flocksize, the chance on Knots and the intensity of area use by Knots. The model used to test for the different relations is: Knot abundance = constant + biomass-density prey<sub>x</sub> + patch, in which Knot abundance is either the average flocksize, the chance on Knots or the intensity of area use. In this models 'patch' is treated as a categorical variable. Tests are performed both including and excluding patch E, though only those excluding patch E are shown. All relations between the intensity of area use and the biomass-density turn out to be weak and insignificant when considering all patches (including patch E). When excluding patch E, only the relation between intensity of area use and biomass-density of *Carcinus maenas* turns out to be significant.





Figure 9: The average available density (in numbers) of three of the four important prey species, both in- and outside our study area. Available numbers are derived from the grid-sampling method. As only the presence or the absence of *Hydrobia ulvae* has been noted in this method, densities of this species are not included. No significant difference exists in the density of *Carcinus maenas* in the two areas (p = 0.346). The density of both *Cerastoderma edule* and of *Macoma balthica* inside the study area is significantly higher than that outside it (p < 0.000 for both species). Vertical bars indicate one standard error.

27



# Figure 10: The relation between available biomass-density and relevance to the diet.

<u>Figure 10</u>: The relation between available biomass-density and relevance to the diet for the four main prey species. Relevance to the diet is calculated as explained in Appendix 2; values are identical to those in figure 3. Knots turn out to feed on *Carcinus maenas* when the biomass-density of this species is high (patch C & D). Otherwise they feed on *Cerastoderma edule* (patch A & B). Patch E turns out not to fit in this pattern; reason for this might be deviating circumstances in this patch.

benthos	observation	quadrant	fieldname	bent
samples	davs			sam
5	12	<u>C7</u>	bp5	6
5	14	<u>C8</u>	bp8	5
8	17	<u>C9</u>	bpe	5
0	0	C10	h	6
3	3	<u>C11</u>	I	6
0	0	D1	1008	2
0	0	D2	bp13	3:
2	8	D3	bp17	2
2	8	D4	bp26	4
2	7	D5	bp44	0
0	0	D6	bp9	4
2	6	D7	f	1
0	0	D8	g	1
0	0	E1	2001	5
0	0	E2	997	4
0	0	E3	999	0
1	2	<b>E</b> 4	a	8
1	3	E5	b	4
1	2	<b>E6</b>	bp14	1
1	3	E7	bp16	1
5	10	E8	bp20	0
0	5	E9	bp3	3
0	4	E10	bp31	1
6	14	E11	bp32	1
4	9	E12	bp6	4
5	13	E13	bp7	4
0	1	E14	bpSim	0
5	8	E15	bpc	2
2	3	E16	bpd	4
5	7	E17	c	2
4	8	E18	d	1
4	10	E19	m	1
3	5	E20	q	1

#### Appendix 2: Calculation method used to express diet composition in terms of AFDM.

By sorting all hard fragments in the dropping samples to species and weighing them, a measure of the dry mass of each species in the droppings can be derived  $(DM_{drop})$ . Knowing both this  $DM_{drop}$  and the size distribution of a specific prey-species, the contribution to the diet of this species in terms of biomass can be estimated. This contribution to the diet is either expressed as ash-free dry weight of the meat (AFDM<sub>meat</sub>) or as ash-free dry weight of the entire prey (AFDM<sub>total</sub>; meat and hard parts together) depending on the ease with which meat and shell can be separated.

The size distribution of the different species in the dropping samples can be derived by measuring species-specific recognisable parts related with the length of the prey; height of hinge and top for *Macoma balthica*, height of hinge alone for *Cerastoderma edule*, width of the last whorl for *Hydrobia ulvae* and length of the movable finger of *Carcinus maenas*. Table 1 shows the relations between the size of the recognisable parts and the length of the prey ingested. As small *Hydrobia ulvae* remain intact more often than large ones, the average length of *Hydrobia ulvae* reconstructed from the width of the last whorl (x) will be an overestimation of the average length of the *Hydrobia ulvae* actually ingested (y) (Dekinga and Piersma 1993). The relation between the reconstructed length (x) and the actual length of *Hydrobia ulvae* ingested (y) is: ln (y) = 0.438 \* (x) - 0.200.

For Cerastoderma edule and Macoma balthica the meat can easily be separated from the shell and  $AFDM_{meat}$  is used to express the contribution to the diet.  $AFDM_{meat}$  can be calculated by multiplying the dry mass of shell fragments ingested ( $DM_{shell}$ ) with the ratio  $AFDM_{meat} / DM_{shell}$ .  $DM_{shell}$  can be estimated from  $DM_{drop}$  ( $DM_{shell} = DM_{drop} * 0.994$ for both Cerastoderma edule and Macoma balthica). The ratio  $AFDM_{meat} / DM_{shell}$  can be derived by incinerating prey-items of all length-classes. In this research this ratio turns out to be length-depended only for Macoma balthica and not for Cerastoderma edule (see figure). Therefore the ratio used for Macoma balthica has to be weighed by its size distribution in the droppings.

Meat of *Hydrobia ulvae* and that of *Carcinus maenas* can hardly be separated from the shell and the exoskeleton respectively. For these two species meatmass is expressed as AFDM<sub>total</sub>, whereas 'shellmass' is expressed as the total dry weight of the ash (DM<sub>ash</sub>). To calculate DM<sub>ash</sub> for *Hydrobia ulvae*, DM<sub>drop</sub> should be multiplied with 1.267 (Dekinga & Piersma 1993), whereas for Carcinus such a correcting factor is not yet determined; it is assumed to be 1. Incineration of *Hydrobia ulvae* and *Carcinus maenas* of all size classes results in the ratio AFDM<sub>total</sub> / DM<sub>ash</sub>. For *Hydrobia ulvae* and *Carcinus maenas*, this ratio turned out to be length-independent (see figure). Multiplying the ratio with DM<sub>ash</sub> results in the AFDM<sub>total</sub>.



<u>Figure 1</u>: The relation between size of consumed prey and a) the ratio  $AFDM_{meat} / DM_{shell}$  for *Cerastoderma edule* and *Macoma balthica* and b) the ratio  $AFDM_{total} / DM_{ash}$  for *Carcinus maenas* and *Hydrobia ulvae*. Only for *Macoma balthica* a significant relation existed (ratio = 0.255 - 0.007 \* (length) (R<sup>2</sup>=0.950, p<0.000)). For *Cerastoderma edule* the ratio  $AFDM_{meat} / DM_{shell} = 0.073$ , for *Carcinus maenas* the ratio  $AFDM_{total} / DM_{ash} = 0.464$  and for *Hydrobia ulvae* the ratio  $AFDM_{total} / DM_{ash} = 0.171$ .

<u>Table 1.</u> Shell length can best be predicted by the model log shell length = constant + rc \* log (length of part measured), in which rc is the regression coefficient. This relation turned out to be observer specific only for Cerastoderma.

species	observer	part measured (mm)	R-square	N	constant	rc	p-value
Carcinus maenas	1&2	length of movable	0.828	54	0.698	0.836	0.000
		finger					
Cerastoderma edule	1	height hinge	0.934	31	1.245	0.940	0.000
	2		0.865	31	1.286	0.768	0.000
Hydrobia ulvae	1&2	width last whorl	0.903	51	0.277	1.230	0.000
Macoma balthica	1&2	height hinge & top	0.922	83	1.149	0.840	0.000







Appendix 3: Diet composition, derived from Knot-droppings, for the different patches on a weekly base, expressed as percentage of the estimated amount of AFDM (see appendix 2). Although diet composition varies strongly between weeks in some patches it appears to be most constant during the first five weeks. Diet composition is more constant in some patches (A and C) than in others (B,D,E). Vertical bars are one standard error.

Scale dependence of the numerical response in Knots (Calidris canutus)

Appendix 4: The distribution of the different prey species.

Appendix 4: The distribution of the available numbers of *Carcinus maenas* (a), *Cerastoderma edule* (b), *Hydrobia ulvae* (c) and *Macoma balthica* (d) over the Grienderwaard. Densities are derived from the grid-sampling. For *Hydrobia ulvae* only the presence or absence was noted. All prey species turn out to be distributed in patches rather than randomly.





Scale dependence of the numerical response in Knots (Calidris canutus)

35





Scale dependence of the numerical response in Knots (Calidris canutus)

37





# Appendix 5: Food on offer in the first 5 weeks on the different patches.

Appendix 5: Food on offer in the first 5 weeks on the different patches. Note that not all y-axes are equal. Biomass-density of the different prey species turns out to be rather constant during the five weeks of our study. No declining effect due to depletion is shown in our data (see also Appendix 6). Vertical bars are one standard error.

# Appendix 6: Regression tables for the variation in biomass-density

<u>Table 1</u>: Regression tables for the variation in biomass-density of the different prey in all samples (1a), in a subsample with a more or less orthogonal design (1b) and in samples from the first 5 weeks only (1c). Bold numbers indicate significant effects. Model used is:  $Log (AFDM_{species}) = constant + week + patch + quadrant within patch for table 1a and 1b and Log (AFDM_{species}) = constant + patch + quadrant within patch for table 1c. All factors are treated as categorical variables (cofactors). Design used for the different tests as in figure 1.$ 

all samples	Carcinus maenas			Cerastoderma edule		Hydrobia ulvae			Macoma balthica			
Biomass	N=1	73, $R^2 = 0$	.543	N=1	73, R <sup>2</sup> =0	.677	N=169, R <sup>2</sup> =0.831			N=173, R <sup>2</sup> =0.512		
(g AFDM/m <sup>2</sup> )	SS	df	р	SS	df	р	SS	df	р	SS	df	р
Regression	152.6	47	0.000	168.3	47	0.000	459.6	46	0.000	66.2	47	0.000
week	26.3	7	0.002	2.3	7	0.826	7.6	7	0.204	4.5	7	0.269
patch	27.6	4	0.000	43.4	4	0.000	196.7	4	0.000	15.9	4	0.000
quadrant within patch	57.9	36	0.051	47.6	36	0.002	162.2	35	0.000	22.2	36	0.207
error	133.4	125		80.2	125		92.4	122		63.2	125	

'orthogonal' design only	Carcinus maenas		Cerastoderma edule		Hydrobia ulvae			Macoma balthica						
Biomass	N=96, R <sup>2</sup> =0.493		omass N=96, R <sup>2</sup> =0.493 N=96, R <sup>2</sup>		N=96, R <sup>2</sup> =0.493		$96, R^2 = 0.$	594	N=9	$94, R^2=0.$	833	N=9	$96, R^2 = 0.$	459
(g AFDM/m <sup>2</sup> )	SS	df	р	SS	df	р	SS	df	р	SS	df	р		
Regression	80.7	23	0.000	76.6	23	0.000	242.8	23	0.000	35.8	23	0.001		
week	25.4	6	0.003	0.6	6	0.991	5.2	6	0.292	5.2	6	0.196		
patch	36.5	4	0.000	54.3	4	0.000	120.5	4	0.000	20.6	4	0.000		
quadrant within patch	12.5	13	0.622	14.1	13	0.141	101.6	13	0.000	6.9	13	1.556		
error	83.0	72	0	52.2	72		48.7	40		42.2	72			

first 5 weeks only	Carcinus maenas		Cerastoderma edule		Hydrobia ulvae			Macoma balthica				
Biomass	N=91, $R^2$ =0.551		N=91, R <sup>2</sup> =0.748		N=87, R <sup>2</sup> =0.676			N=91, R <sup>2</sup> =0.808				
(g AFDM/m <sup>2</sup> )	SS	df	р	SS	df	р	SS	df	р	SS	df	р
Regression	49.8	29	0.001	34.4	29	0.000	4199.3	27	0.000	118.6	29	0.000
patch	2.2	4	0.000	3.4	4	0.003	1579.5	4	0.000	45.8	4	0.000
quadrant within patch	3.0	25	0.094	16.1	25	0.000	2433.7	23	0.000	52.6	25	0.000
error	40.6	61		11.6	61		2013.4	59		28.1	61	



Figure 1: Design of the benthos samples in the quadrant-sampling method. All dots represent a single quadrant-sample consisting of ten sediment cores. Tests for variation are performed on all samples (table 1a), but also on a subsample with a more or less orthogonal design (white dots; table 1b) and on all samples in the first five weeks (separated from the other weeks by the dotted line; table 1c).

# Appendix 7: Variation in biomass-density.

<u>Table 1</u>: Some statistics concerning the variation in biomass-density. The coefficient of variation is derived from a previous study on the Grienderwaard (Koolhaas, A. unpublished). Methodological standard error is high compared to the biological variation per week.

species	coefficient of	average density	Biological variation per	Methodological
	variation (%)	$(g AFDM / m^2)$	week (% of average)	SE per week (%)
Carcinus maenas	300	0.19	34	88.5
Cerastoderma edule	151	0.22	29	44.5
Hvdrobia ulvae	52	4.51	1	15
Macoma balthica	101	1.29	5	29.8



Figure 1: The effect of sample size on the methodological sampling error. Example shown is for *Macoma balthica*. The methodological sampling error is the standard deviation divided by the square root of the number of samples: SE = SD / sqrt (N). It declines steeply with increasing sample size when sample size is low. With low sample sizes, the methodological standard error is large. Coefficients of variation are derived as in table 1.

#### Appendix 8: Stomach size in relation to patch use.

In the first week of our study, a radio-transmitter was attached on 42 Knots (caught on the island of Richel), in order to follow their daily distribution over the varies mud flats with the aid of receivers. According to differences in their use of the different patches on the Grienderwaard, these 42 radio-tagged Knots are divided in three groups. Group 1 consists of Knots only observed in patch A and B; group 2 consists of Knots only recorded in patch C and D, while group 3 consists of Knots observed in both groups of patches (patch A and / or B ánd patch C and / or D) (figure 1). After testing with the Tukey test for multiple comparison, the average stomach sizes of the Knots in the three different groups (expressed as the horizontal length of the stomach) turned out to be unequal (p < 0.000). This difference turned out not to be an effect of different delays (figure 2) in observations of the birds (assuming stomach size to be in increasing function of delay). In the patches A and B the main prey species is *Cerastoderma edule*, whereas the main prey species in patch C and D is *Carcinus maenas*. The large difference in average stomach size between group 1 and 2 indicates that the two groups of patches are used by different Knots; those Knots that have large stomachs and that can eat hard prey, forage more in the patches A and B, whereas those Knots that have small stomachs forage on the softer prey in patch C and D.



Figure 1: Average stomach size of radio-tagged Knots on different groups of patches. Stomach size is expressed in terms of the horizontal length of the stomach. Knots only observed in patch A and / or B have larger stomachs than Knots only observed in patch C And / or D, whereas Knots observed in both groups of patches have intermediate stomach sizes.

Figure 2: Average delay in observations of the radio-tagged Knots on different groups of patches. Stomach size of the radio-tagged Knots is assumed to be an increasing function of the delay of observation. Thus differences in stomach size as seen in figure 1 are not the result of differences in delay of observation.