



The path to success

Foraging paths and behaviour of
oystercatchers in relation to their food supply

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Summary

In this research the influence of food distribution on the walk patterns of oystercatchers *Haematopus ostralegus* was studied. Oystercatchers feed on bivalves and worms that live below the surface in the sediment of mudflats. Oystercatchers were expected to follow different walk paths on basis of their foraging success. Oystercatchers are expected to follow a more sinuous path in a patch with a lot of food and a straighter path in a patch with a low food availability. When an oystercatcher performs a more sinuous, random walk the chance that it walks out of a patch is smaller, which would be profitable in a high quality patch.

Soil samples were taken to determine the food distribution of one mudflat and films were made to study the foraging success and walk paths of individual oystercatchers.

The hitrate (number of hits per second of foraging) of individual oystercatchers was calculated. For individual walk paths we looked at the turning angle, average interval distance (distances an oystercatcher walked until it stood still or changed direction) and average walk speed.

There was no significant relation between foraging success and food distribution on the mudflat, oystercatchers did not find more food in patches with more food available.

The results show that oystercatchers turned more and walked shorter interval distances during foraging when the hitrate was higher. An analysis on a smaller scale showed that oystercatchers made a larger turning angle after a successful interval. The walk speed was significantly related to the presence of other oystercatchers and wind speed.

Introduction

Ecology is the study of the relation between organisms and their environment. The environment includes both the living components of an organisms surroundings, such as other organisms, and the nonliving components, such as the physical conditions of the environment. The relation consists of interactions between the organisms and the environment (Smith & Smith, 2003). Because ecology is such a broad field of science, it can be divided into many categories ranging from ecology on a small scale, such as the study of micro-organisms, to a large scale, for instance global ecological processes.

This ecological research deals with the relation of a wader species, the oystercatcher *Haematopus ostralegus*, and its prey. Oystercatchers mainly eat bivalves and worms that live in mudflats and are pecked out of the mud. The research will focus on this predator-prey relation and the effect it can have on foraging movements by oystercatchers and the implications for larger scale distribution of these birds.

Wading birds are always nonrandomly distributed on a mudflat. The reason for this nonrandom distribution has led to a lot of research. Evans & Dugan (1984) showed that the spatial variation in food density correlates with shorebird density. Thus, the nonrandom distribution of birds can partly be the result of heterogeneity in the distribution of food such a molluscs and ragworms.

Optimal foraging

An important theory in ecology is the optimal foraging theory, which was proposed by MacArthur and Pianka (1966). The optimal foraging theory can be used to understand the foraging behaviour and distribution of organisms. For instance, why do organisms only eat certain size classes of prey or eat only part of their prey? The optimal foraging theory can help to understand these kind of questions by looking at the effort it takes to get to a prey (travelling time) or eat a prey (handling time) and the energy that would be eventually gained by eating a prey. The Optimal Foraging Theory can help to explain this trade off between different aspects of foraging in terms of profitability. For wading bird species, fooditems that are below a certain size are not profitable because they take too much effort to eat in comparison to the energy they provide. Shells that are above a certain threshold may be very energy rich, but may take a lot of time to handle. This is why waders will usually only eat prey that are within a certain size range that is most profitable, factors such as searching time, handling time and energy content are taken into account. Predators try to optimize their energy intake per time unit spent searching for food and eating it to get the highest intake rate.

The optimal foraging theory can also be applied to study the movement of organisms. If an organism is searching for food in a patchy environment, i.e. the food is spatially clumped, then a density dependent movement strategy may be expected because it can yield a higher intake rate to move

differently with different food densities than using one constant movement in each area.

In this research two types of movements are distinguished: 'random walk' and 'correlated walk'. These two movements differ in the direction that is taken in different intervals.

In a random walk the direction of the movement in each interval is independent of the direction which is followed in other intervals. A random walk is a simple stochastic process, the directions are completely random. A correlated walk consists of intervals in which the directions of the movements are dependent of each other. A correlated walk will result in a straighter walk pattern than a random walk, because directions of intervals are correlated. The end position of a random walk after a certain number of intervals is closer to the start position than the end position of a correlated walk after the same number of intervals. After a random walk the net displacement that is covered will be smaller than that of a correlated walk, but a random walk can still cover a large area.

This idea is used here to describe the movements of oystercatchers on a mudflat.

In a high quality patch there are more food items available, so the chance of finding one when pecking randomly for food is higher. Foraging in a high quality patch is therefore more profitable for an oystercatcher.

Because a high quality patch is more profitable, it would benefit an oystercatcher to stay there to feed instead of going to another patch that is possibly lower in food. The best way to stay in its patch would then be to take a random walk. Because the net displacement is smaller in a random walk, the chance that an oystercatcher walks out of this patch is smaller. The area that is searched stays the same as in a correlated walk.

On the other hand, if an oystercatcher is foraging in a patch with a low amount of food available, it can take a straighter, correlated walk instead of a random walk, because this would take him to another, possibly higher quality patch, faster.

Hypothesis



Figure 1. Schematic representation of the relation between Food Abundance, Hitrate, Walk path and Distribution of oystercatchers on a mudflat.

Oystercatchers are expected to make decisions on how to move on basis of their hitrate (number of fooditems found per unit time). This is visualized in Figure 1: the hitrate is a result of the food abundance (energy) in the foraging site, assuming that the oystercatcher doesn't hunt visually, but rather pecks randomly for food. The feeding rate of oystercatchers increases when more food is available (Goss-Custard et al. 1996), so Oystercatchers foraging in high quality patches (high energy content) are expected to have a higher hitrate than oystercatchers foraging in low quality patches. If the hitrate is high, the oystercatcher will do a random walk and walk slower to stay in the patch, whereas if the hitrate is low it will do a faster, correlated walk.

Both this random movement and the slower foraging speed will then result in foraging in the same patch for a longer period of time. Oystercatchers in low quality patches on the other hand are expected to walk faster, in a more correlated (straighter) line, because this would take them out of their patch sooner, hopefully to another, higher quality, patch.

So if the food density is known for an area, the foraging behaviour of individual oystercatchers on a certain spot in this area can possibly be predicted.

This idea leads to our null model that predicts the distribution of larger groups of birds (in this case oystercatchers) on a mudflat if only food availability is taken into account.

According to the Ideal Free Distribution model (IFD, Fretwell and Lucas 1969) organisms will choose the habitat that gives them the highest fitness. Following this model, individual oystercatchers that start foraging at any point on a mudflat will eventually end up foraging in the highest quality patches by adapting their foraging behaviour to the patch characteristics (food abundance). This will lead to a nonrandom distribution of oystercatchers on the mudflat, oystercatchers will be concentrated in the high quality patches.

Food is not the only factor determining shorebird distribution. In homogenous environments a nonrandom distribution of birds can also occur (Moody et al. 1997). Other factors that can determine bird distribution may be group effects such as the lesser predation risk for individuals foraging in a group and the intraspecific information sharing in a group and competition (Sernland et al. 2003, Beachamp 2002, 2004ab).

This research focuses on the effect of food density on the foraging paths of individual birds in the nonbreeding season and is part of a larger research by Eelke Folmer on the distribution of waders in the Dutch Wadden Sea. The foraging path and foraging success of oystercatchers *Haematopus ostralegus* L. on a mudflat will be studied to test whether the movement of animals reflect their foraging success and food density of the mudflat.

The main goal of this research is to see if there is relation between the successrate of oystercatchers and food abundance and to see if there is a relation between successrate and movement of oystercatchers on a mudflat.

To answer these questions a couple of things were investigated in the field. The food availability on a specific mudflat was investigated through core samples. This was done to quantify the food availability on a mudflat for foraging oystercatchers.

Secondly, individual oystercatchers were observed to reconstruct their foraging paths and to determine their successrate.

Wadden Sea

The research area is situated in the Wadden Sea along the Dutch coast. The Wadden Sea is a shallow coastal sea of about 8.000 km² with large tidal flats and is situated behind a long chain of barrier islands along the coast of the Netherlands, Germany and Denmark. The Dutch Wadden Sea is 2.600 km² in size, with 1.300 km² of tidal flats, that are exposed twice every 24 hours.

The Wadden Sea is of great importance for waders that feed on macro benthos in the upper layer of the mudflats at low tide.

400.000 oystercatchers winter in the Wadden Sea each year, of which ca. 200.00 winter in the Dutch Wadden Sea (Camphuysen et al. 1996, Van de Kam et al. 1999).

Because the Wadden Sea is a rather homogenous environment in which the food distribution is relatively easy to quantify, it is a good place to study organisms and their prey.

In the methods (p 7) the research area will be described in more detail.

Oystercatchers

Oystercatchers are among the largest shorebirds along the Dutch coast. Because they are rather large, distinct birds, they are very suitable for research (Goss-Custard 1996, Johnstone and Norris 2000).

This research was performed during the nonbreeding season in which the diet of oystercatchers mainly consists of intertidal bivalve molluscs. The main prey species are Cockles (*Cerastoderma edule*) and Mussels (*Mytilus edulis*). Other bivalve prey species are Peppery Furrow Shell (*Scrobicularia plana*), Baltic Tellin (*Macoma balthica*) and Sand Gaper (*Mya arenaria*). The rest of the diet consists of gastropods (*Littorina* sp.), polychaetes, especially ragworms (*Nereis diversicolor*) and lugworms (*Arenicola marina*). Crabs (*Carcinus maenas*) and shrimps (*Crangon crangon*) are mainly eaten in summer (Hulscher 1996, Johnstone and Norris 2000).

While some waders eat the whole bivalves, oystercatchers only eat the flesh within the shells. Because of this oystercatchers can feed on larger sized bivalves. There are two main techniques that oystercatchers use to get the flesh out of the shell. Oystercatchers use their heavy bill to open bivalves either by hammering or by stabbing (their bill between the two valves and cutting the adductor muscle) (Hulscher 1996). Oystercatchers specialize on one of these techniques to feed.

Oystercatchers can find their prey visually and by touch. When hunting by sight they look for tracts of bivalves that are visible on the surface or traces of *Nereis* at the soil surface. When hunting by touch they randomly peck and detect prey with Herbst corpuscles located in their bill tip (Hulscher 1996).

Methods

Study site

Fieldwork was done at the Pieterburenwad, a mudflat located in the Dutch Wadden Sea north of the Dutch mainland (Figure 2). An area of 1,622 x 3 km on this mudflat (coordinates 6°26'00" – 6°28'43" East to 53°26'54" – 53°26'02" North) was used for the research. This area was chosen because it was known to be rich in bird and benthos life (pers comm. E. Folmer). The area is muddy along the coast and becomes sandier and lower northwards. Silt content ranged from 1.7% to 9.6% in the study area and was highest in the south (Zwarts et al. 2004).

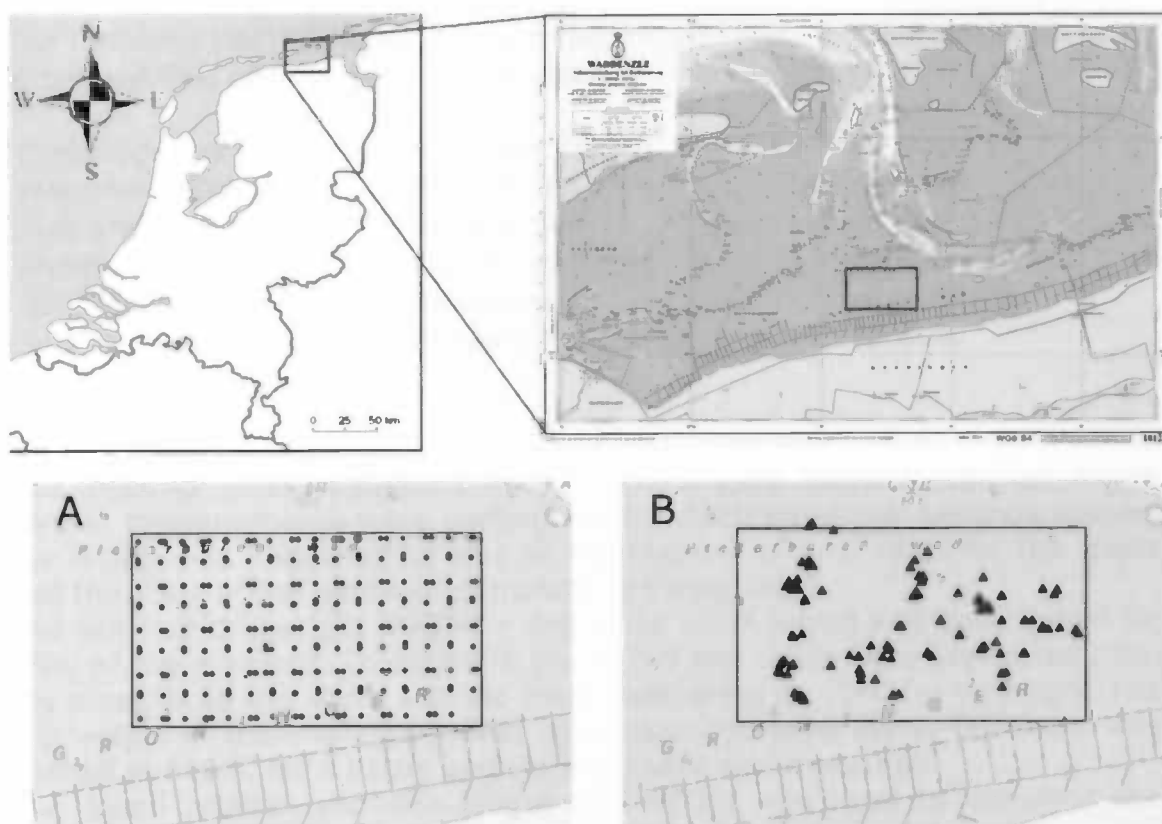


Figure 2. Location of the Pieterburenwad in the Netherlands (upper map), the benthos sampling points (Map A, ●) and the location of observed oystercatchers (Map B, ▲).

Benthos mapping

Field

Soil samples were taken with a 15 cm Ø corer on a 200 m grid in December 2004 and January 2005 and a second time in February and March 2005. Additional points were located 50 m from the 200 m grid points and were sampled only once in December 2004 and January 2005. These points were sampled to look at the benthos distribution on a finer scale. The second samples were taken to investigate the depletion from benthos organisms. There was not no significant difference between the two sampling periods,

so depletion was not significant in the research period. In total 357 soil samples were taken (Figure 2A).

The soil cores were taken to a depth of approximately 20 cm and were divided into a top part (app. 4 cm) and a bottom part (below 4 cm depth). The sample was sieved through a 1 mm Ø-sieve. This was done to determine the food availability for birds with short bills.

In the field, the number of benthos organisms found was recorded. Molluscs, *Nereis diversicolor* and *Nephtys* were identified as either juvenile or adult. Molluscs, shrimps and crabs were taken to the lab for further research.

The percentage surface coverage of *Lanice concilega*, algae, sea weed, shells and mussel bank within a 10 m range of the sampling point was estimated visually.

The following benthos species are in diet of the oystercatcher and were used in the analysis of the oystercatcher data:

<i>Cerastoderma edule</i>	Common Cockle	mollusc
<i>Macoma balthica</i>	Baltic Tellin	mollusc
<i>Mya arenaria</i>	Sand gaper	mollusc
<i>Mytilus edulis</i>	Common Mussel	mollusc
<i>Nereis diversicolor</i>	Ragworm	polychaeta
<i>Scrobicularia plana</i>	Peppery Furrow Shell	mollusc

Lab

The molluscs and crustaceans from the field were taken to the lab where further measurements were performed. For each individual benthos species the length was measured as well as the number of year rings for the shells and the state of the benthos (complete or incomplete).

The ash free dry weight (AFDW = dry mass - ash mass) was determined for 65% of the molluscs. To estimate the AFDW the shells were separated from the meat. Both the shells and the meat were dried at 60°C for 48 hours. The dry weight of the shells and meat was measured separately. The meat was burned at 560°C for 6 hours and the ash mass was measured.

The found relation between length and AFDW was used to calculate the AFDW for the molluscs of which only the length was measured.

Energy content

The energy content of the benthos per position was determined by using the numbers of *Nereis diversicolor* and the numbers and AFDW of molluscs found in the field.

For *Nereis diversicolor* Zwarts (1996) found the following relation between AFDW and length of worms:

$$\ln (\text{mg AFDW}) = -0.898 + 2.208 * \ln (\text{length (cm)})$$

In the field, *Nereis diversicolor* were characterized either as juvenile or adult. For juvenile *Nereis* an average length of 5 cm was used, for the

average length of adults 9 cm was used. The energy content of *Nereis diversicolor* is 22.2 kJ g⁻¹ AFDW (Zwarts et al. 1996)

Oystercatchers don't eat all size classes of prey species. Only the shells above a certain threshold were used in the analysis (Zwarts & Wanink 1993, Goss-Custard, Hulscher 1982, Zwarts et al. (1996):

- *Macoma balthica* > 10 mm
- *Scrobicularia plana* > 13 mm
- *Cerastoderma edule* > 10 mm
- *Mya arenaria* > 15 mm
- *Mytilus edulis* > 20 mm

The relation between shell length and AFDW per species was calculated for these size classes and was used to determine the AFDW of all the molluscs (appendix A):

$$\log \text{AFDW} = -b + a * \log L$$

Species	a	b	Energy (kJ g ⁻¹ AFDW)
<i>Macoma balthica</i>	3.2138	5.4291	22
<i>Scrobicularia plana</i>	2.8557	5.368	21.9
<i>Cerastoderma edule</i>	3.1996	5.4178	22.2
<i>Mya arenaria</i>	3.0794	5.6009	21.7

Energy content per gram AFDW was taken from Zwarts (1996).

Only two mussels (*Mytilus edulis*) were found in the field and for both individuals AFDW was determined. Because of this, no formula for AFDW was made for this species.

These relationships enabled us to calculate the total energy content of the available food for the oystercatchers per sampling station. The data on energy content per sampling point was used to make a map of the sampled area with energy contents using the universal kriging function in ArcMap 9.0 (ESRI).

Birds

Field

Oystercatchers were filmed through a telescope (Swarovski sts 65) using a digital video camera (Sony dcr-pc103E) in February and March 2005. The period of filming was between 2 hours before until 2 hours after low tide to ensure that all of the research area was available to the oystercatchers for foraging. Individual birds were filmed for an average time of 10 minutes on different locations in the research area (Figure 2B) from an average distance of 229 m (105 m – 439 m). Smit and Visser (1993) showed that the fly-off distance for oystercatchers disturbed by man is about 136 m in the Wadden Sea. During filming the birds didn't appear to pay much attention to the researcher. The birds were filmed at different locations on the grid at different times.

Water height, precipitation, cloudiness, number and species of birds in a 50 meter radius around the filmed individual, wind direction and wind speed were determined before and during filming.

The films were analyzed using The Observer 5.0 (Noldus Information Technology).

Behaviour

To estimate the timebudget the following behavioural states were distinguished:

- searching for food: walking or standing still while looking for food. When the bill was directed downward it was assumed that the bird was looking for food.
- walking: walking, running and standing while not searching for food, the oystercatcher's bill was not directed downward and the eyes were not focused on the soil
- pecking: oystercatchers pecks in the soil
- missing: oystercatcher is not in view of the camera, either the camera lost sight of it, or the oystercatcher is hidden from view, for instance because of other birds
- resting: sleeping, preening
- flying away: oystercatcher flies off, end of observation

The success of a peck was also measured: hit, miss or unknown. When an oystercatcher pecked, the success was determined by looking if the oystercatcher swallowed a prey. The handling time of a prey was not measured separately but is part of the total 'peck (hit)' time.

Behaviour was scored while playing the videos at half speed to ensure that small movements, such as swallowing were also observed and that all variables could be entered in The Observer 5.0 software.

Foraging path

To be able to reconstruct the foraging path the following actions were scored:

- step: oystercatcher takes a step
- direction: direction in which an oystercatcher moves in relation to the observer: north, northeast, east, etc. (8 directions)
- standing: oystercatcher stands still
- flying away: oystercatcher flies off, end of observation
- missing: oystercatcher is not in view of the camera

Walk patterns were scored while playing the videos at normal speed.

The direction an oystercatcher walked in and the walking speed were used to calculate the position where it would stand still, forage or turn. The walking speed was calculated using a formula from Speakman and Bryant (1993):

$$\log_{10}(\text{speed}) = -1.18 + 1.46 \log_{10}(\text{pacing rate})$$

For different interval lengths the position of the oystercatcher was determined using a VBA macro in Microsoft excel (appendix B). Intervals

started when an oystercatcher started moving or changed direction and ended when an oystercatcher stopped moving or changed direction again.

An interval length of 15 seconds was used to calculate the path of an oystercatcher. Every 15 seconds the position of the oystercatcher was calculated. When time was more than the interval length, then the coordinates of the next 'stop' time were taken. For instance, if for the 5 second intervals the oystercatcher didn't stand still at $t=20$ seconds, but it did at $t=21$ seconds, then these coordinates were used.

Using the intervals a discretized representation of the path could be made (Figure 3) (Turchin 1991). The angle between the direction of two intervals is called the turning angle (θ , theta). The standard deviation of the turning angle and the average distance an oystercatcher walked during the intervals were used to characterize the path. The standard deviation of the turning angle was used rather than the average turning angle. The average turning angle of an oystercatcher that would first walk westward and would later walk eastward would result in an average turning angle of 0, just like the average turning angle of an oystercatcher walking in a straight line. The standard deviations however, are different, so this is a better measure for the randomness of the path.

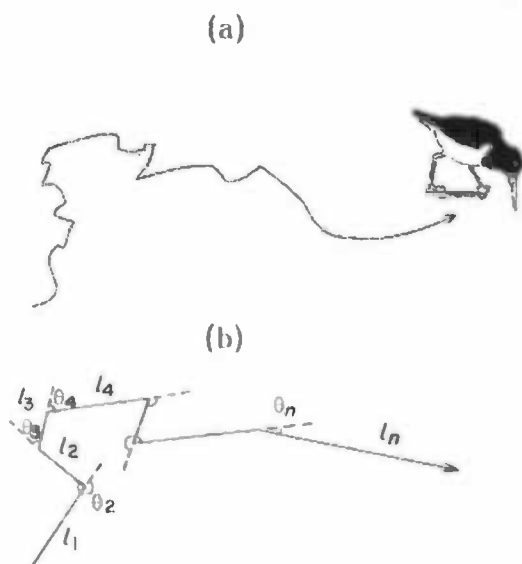


Figure 3. Movement of an oystercatcher represented as a correlated random walk. l_n =interval length, θ_n = the turning angle between interval $i-1$ and interval 1. (a) the actual path as observed in the field. (b) a discretized representation of the path (adapted from Turchin 1991).

Walk paths were made for a total number of 142 oystercatchers. Behaviour was scored for a total number of 138 oystercatchers. Because the scoring of the behaviour required a clear picture to see if the oystercatcher was successful when pecking, not all films could be used for making foraging paths as well as behaviour scoring.

The overall success of an individual oystercatcher was determined by calculating its hitrate. The hitrate is defined as the number of successful pecks (hits) per second searching time minus the total handling time.

Searching time was the time spent searching for food together with the duration of all the pecks (including handling and feeding time during a successful peck).

Time spent on handling prey cannot be used for other things, so the peckrate (number of pecks per time), hitrate and missrate (number of unsuccessful pecks per time) would be under estimated if handling time wasn't left out. In this case a successful oystercatcher would then have a very low hitrate, so a correction for handling time has to be done. Handling time wasn't scored during observation, but was calculated. The average duration of an unsuccessful peck (miss) was taken as a 'standard peck time', i.e. the time it took for an oystercatcher to peck for a prey, minus handling. Now the total handling time can be calculated by subtracting the standard peck time from the duration of successful pecks:

Total Handling time = total duration of successful pecks - (number of successful pecks * standard peck time)

A couple of criteria were used to select paths for the analyses: the relative time that an oystercatcher used for searching had to be higher than 0,8 (80%) to exclude birds that weren't looking for food most of the time and would for instance preen or rest a lot during the observation.

Because fighting was expected to play a great role in the behaviour of individual oystercatchers, oystercatchers that had a fight were excluded from the analysis. Total duration of the observation of an individual had to exceed 250 seconds. Short films could possibly give a wrong representation of the time budget of an oystercatcher.

A complete list of calculated variables from the behaviour and walk paths can be found in appendix C.

Statistical analyses were done with Statistica 7 .0 (StatSoft Inc 2004).

Multivariate analysis of covariance (MANCOVA) models were made for models with 2 or more dependent variables. ANCOVA models were made for models with one dependent variable.

Results

Energy content

Using the benthos species and size classes mentioned in the Methods, the map of energy distribution on the Pieterburenwad was made (Figure 4).



Figure 4. The distribution of energy (kJ/m^2) on the Pieterburenwad. High values represent higher amounts of energy.

The southern part of the research area is highest in energy. Three large patches of high energy content can be distinguished in the area, one is located in the southwest and the two others are located more to the east. Overall, the energy content decreases more northwards on the Pieterburenwad.

There was a significant positive correlation between numbers of *Macoma*, *Nereis* and *Cerastoderma*. This implies that the distribution of separate species is similar to the distribution of total energy content on the mudflat.

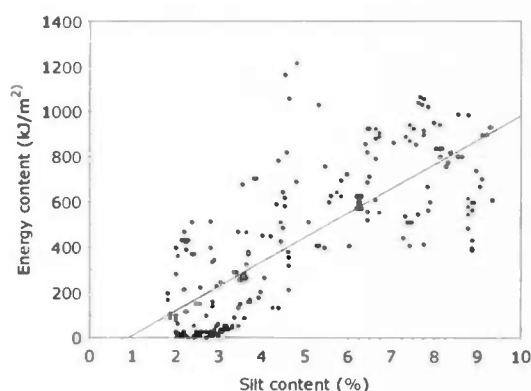


Figure 5. Energy (kJ/m^2) in relation to silt content (%) in the total research area ($p=0.000$, $R^2=0.761$).

The area is muddiest in the south, with a maximum silt content of 9.7% and becomes sandier to the north (Zwarts et al. 2004). The silt content is positively correlated with energy content (kJ/m^2), which is depicted in Figure 5. The energy content increases significantly with a higher silt content ($p=0.000$).

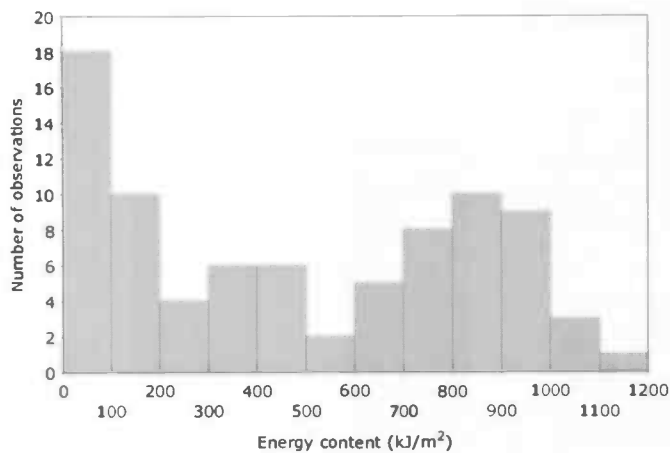


Figure 6. Histogram of Energy values on the oystercatcher observation sites.
 N = 82, Mean = 480.4255, StdDv = 357.2819, Max = 1113.6738, Min = 10.0205;

The distribution of energy content on the sites where oystercatchers were filmed is not a normal distribution (Figure 6). There are two peaks in the energy distribution, the first peak is at an energy content of 0 - 100 kJ/m², with 18 out of 82 observations. The second peak is smaller and lies in the range between 700 - 1000 kJ/ m².

Figure 6 shows that there is a lot of variation in the energy content of the positions that were used in the analyses, which is important when looking at differences in success and walk path as a result of this energy content.

Birds

Time budget

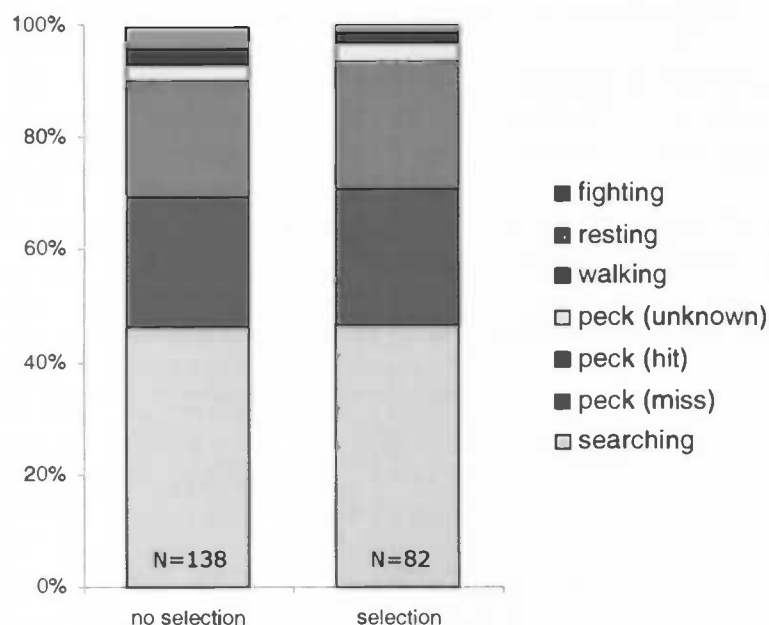


Figure 7. The average time budget of filmed oystercatchers. 'No selection' represents all filmed oystercatchers, 'selection' represents the oystercatchers that did not fight and spent more than 80% of their time on foraging (searching and pecking).

The time budget of oystercatchers was calculated for all observed oystercatchers (Figure 7). The first group represents all observed oystercatchers (N=138), the second group is a selection of these oystercatchers. The second group consists of oystercatchers that foraged for at least 250 seconds, did not fight and spent more than 80% of their time on foraging (searching for food and pecking) ('selection', N=82).

The selected observations were used for the other analyses. The time budget shows that these oystercatchers spent most of their time searching for food and pecking (97%) during the observations.

Walk path

The first three steps of the hitrate diagram (Figure 1) from the introduction were tested. A positive relation between Energy abundance and success was expected and tested by looking at the hitrate.

A univariate regression analysis (general linear model) was performed to test if the hitrate (number of hits/second) of oystercatchers was related to the energy content (kJ/m^2) of the sites where these oystercatchers were filmed.

The result is shown in Figure 8. Despite large variation in Energy as well as in hitrate, the expected relation between Energy content and hitrate was not found ($p = 0.45$).

Average hitrate was 0.036 hits/s, with a standard deviation of 0.018.

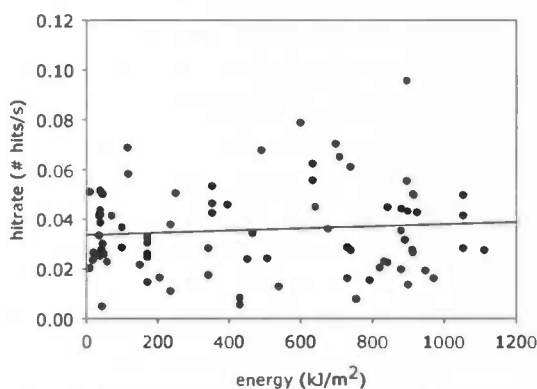


Figure 8. Hitrate (number of hits/s) in relation to energy (kJ/m^2) ($p=0.45$).

The turning angle (sd θ), average length of the path in one interval (average length, L) and average walk speed were chosen as variables that describe the walk path.

Sd θ showed a significant positive correlation with the hitrate ($p=0.03$, $\beta=0.33$). Average length was also significantly correlated with hitrate ($p=0.00$, $\beta=-0.64$) (Figure 8). When oystercatchers had a higher hitrate, they turned more and walked shorter distances until the next stop or change of direction.

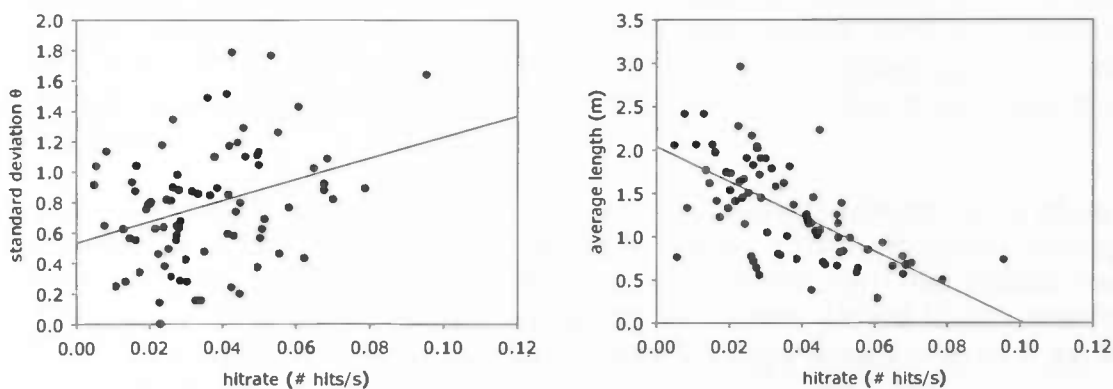


Figure 9. (A) The standard deviation of the turning angle (θ) as a function the hitrate (number of hits per second) ($p=0.03$, $\beta=0.33$), (B) The average length (m) of the walked distance in one interval as a function of the hitrate (number of hits per second) ($p=0.00$, $\beta=-0.64$).

A MANCOVA model was used to test which variables had a significant relation with the walk path variables combined. A MANCOVA model can test whether multiple variables have a combined effect on multiple dependent variables, when these dependent variables are correlated themselves. In this model the combined effect of hitrate, wind speed, water depth, other oystercatchers, gulls and sediment on the walk path variables sd θ , average length (L) and average walk speed is tested. This model can be represented as a function:

$$(Sd \theta, L, speed) = f(\text{hitrate, wind speed, water depth, other oystercatchers, gulls, sediment})$$

Hitrate was hypothesized to be very important for an oystercatcher in determining the walk path, but walk path can be influenced by other factors as well. Wind speed and water depth may have an impact on the walk path, because it can slow an oystercatcher down or make it walk faster. Other birds can also influence the walk path variables. Gulls are known to steal prey from other birds and other oystercatchers can both act as competitors for food and as a source of information on where to find food (Sernland et al. 2003, Beachamp 2002, 2004ab). Sediment, in this case silt content, can also influence the walk path, oystercatchers cannot forage well in very muddy substrate (Johnstone & Norris 2000).

The model was adjusted by stepwise backward multivariate analysis, which led to the deletion of gulls, water depth, sediment, oystercatchers and wind speed respectively. This was done by deleting variables with the highest p value one by one, until only variables with significant p values were left in the model.

This led to the following model:

$$(Sd \theta, L, speed) = f(\text{hitrate})$$

Only hitrate remained after stepwise deletion. A higher hitrate makes the walk of an oystercatcher less correlated and decreases the distances walked between turning or stop positions.

Hitrate was significant with a p value of 0.000 for this model. Sd θ showed a significant p value of $p=0.003$ ($\beta=0.328$) with an adjusted R^2 of 0.096. Average length was significantly correlated with hitrate with a p value of 0.000 ($\beta=-0.637$) and an adjusted R^2 of 0.397. The Average speed did not significantly change with a different hitrate ($p=0.151$, $\beta=-0.160$, adjusted $R^2=0.013$).

This model shows that 40% of the variation in average length, 10% of sd θ and only 1% of the average speed is explained by hitrate. Because average speed was not significantly correlated with hitrate and the model only explained a small part of the variation in speed ($R^2=0.013$), another MANCOVA model was made, now using only average length and sd θ as the dependent factors.

$$(Sd \theta, L) = f(\text{hitrate, wind speed, water depth, other oystercatchers, gulls, sediment})$$

The model was also adjusted by stepwise backward multivariate analysis, which led to the deletion of the insignificant p values. Water depth, oystercatchers, gulls and sediment had the highest p values and were deleted respectively.

This resulted in the following model:

$$(Sd \theta, L) = f(\text{hitrate, wind speed})$$

Hitrate and wind speed together had a significant effect on sd θ and average length ($p=0.000$ and $p=0.042$, respectively). Adjusted R^2 is 0.105 for sd θ and 0.409 for average length).

This model explains 10.5% of variance in sd θ (R^2 adjusted=0.105) and 40.9% of variance in average length (adjusted $R^2=0.409$).

Wind speed showed significant effects without hitrate for the combination of sd θ and average length ($p=0.026$), but did not show significant results for the individual variables, $p=0.342$ for sd θ and $p=0.063$ for average length.

If wind speed is left out, the model becomes:

$$(Sd \theta, L) = f(\text{hitrate})$$

This model explains almost 10% of variation in sd θ (R^2 adjusted=0.096) and 40% of average length (R^2 adjusted=0.397). This model with hitrate alone explains almost as much variation in the variables as the model with both hitrate and wind speed.

So wind speed does not contribute much to the variance of the walk path variables, most of the variation is explained by hitrate alone.

Relation between energy and path?

Contrary to the hypothesis, there was no significant relation between Energy content and hitrate. The hypothesized relation would result in different walk paths in different patches. Because hitrate was not significantly correlated with energy content, the relation between Energy and the walk paths variables is tested directly. Maybe the oystercatchers get information about the patch quality from other factors that were not tested here, such as visual cues or memory. If this is the case, the hitrate would not have to be related to the patch quality.

A MANCOVA test showed no significant result for the combination of sd θ ($p=0.290$) and average length ($p=0.376$) as dependent variables of energy. This means that the walk path variables do not change significantly between patches of different quality.

Walk speed

Average weighted speed ranged from 0.12 to 0.30 m/s (average=0.22, standard deviation=0.04), this was in the same size range as speeds calculated by Ens et al. (1996).

Walk speed was not significantly correlated with hitrate in the previous model:

$$(\text{Sd } \theta, \text{ average length, speed}) = f(\text{hitrate})$$

The combination of walk speed with sd θ and average length did show a significant result, but this model only explained 1.3% of the variation in walk speed.

Maybe other factors are more important in determining the walk speed of an oystercatcher. An ANCOVA model was made to test only walk speed as a dependent factor:

$$(\text{speed}) = f(\text{hitrate, sediment, water depth, wind speed, other oystercatchers, gulls})$$

Backward deletion of the variables with the highest p values resulted in the following model:

$$(\text{speed}) = f(\text{wind speed, other oystercatchers})$$

The presence of other oystercatchers had a negative effect on the walking speed of the foraging oystercatcher ($p=0.012$, $\beta=-0.270$). Wind speed also had a negative effect on the walk speed ($p=0.025$, $\beta=-0.239$).

This model explained 11.8% of the variation in walk speed (R^2 adjusted = 0.118).

Small scale decisions

The analyses on the walk path described until now were all based on data of complete walk paths. The results show that oystercatchers turn more after a number of intervals. It is also interesting to see if the oystercatchers turn more if they hit more after one interval. This would mean oystercatchers make decisions on a small scale, they turn more if the previous interval was successful.

A univariate test showed that the turning angle increased significantly if the oystercatcher was more successful in a previous interval ($p=0.015$). Figure 10 shows that the turning angle (θ) increases with the number of hits in the previous interval.

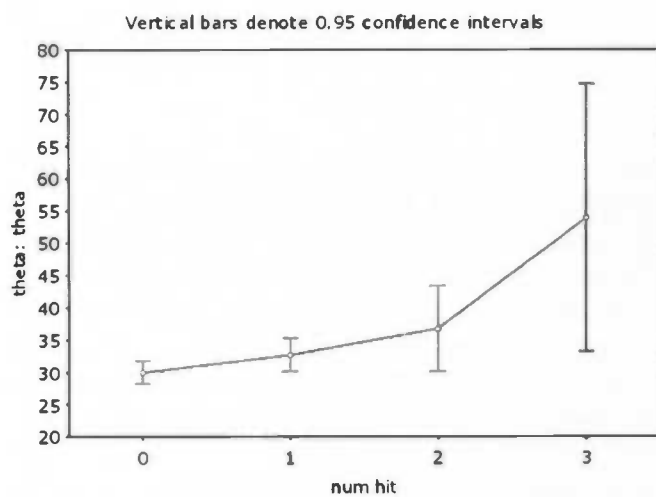


Figure 10. Average number of hits of an interval in relation to the following turning angle ($p=0.015$).

Complete tables of the statistical tests and a correlation diagram can be found in Appendix D.

Discussion & Conclusions

Hitrate

The expected relation between energy content of the patches and hitrate of the oystercatchers was not found. The expected relation was based on the assumption that oystercatchers pecked randomly for food in the substrate. The chance to catch a prey would be higher if more prey was available in the sediment. The peckrate was not correlated with energy density, so oystercatchers pecked as many times per unit time in low quality patches as they did in high quality patches. In an area with high food density random pecking would result in a higher hitrate, but the results show it did not.

In the introduction some attention was paid to the specialization of oystercatchers. Different techniques can be used to catch and eat prey (Hulscher 1982, 1996). The specialization on food can be either feeding on shells or feeding on worms (*Nereis* sp.). An oystercatcher feeding on *Macoma* can locate its prey by touch as well as sight, but sight cannot always be used, because *Macoma* do not always leave clear visible tracks on the surface. Touch is used predominantly (Hulscher 1982, Zwarts 1996). An oystercatcher hunting for *Nereis* mainly uses its sight, because *Nereis* leave visible tracks on the surface (Hulscher 1982).

This specialization is represented in the oystercatcher's foraging behaviour: the walk speed of *Macoma*-specialists is slower and the number of pecks is higher per walked distance. Because oystercatchers use touch predominantly when hunting for *Macoma*, their success is mainly based on chance. *Nereis*-specialists walk faster, because they can hunt by sight and have to be in time to catch a prey when they see it before the prey recedes in the soil (Ens et al. 1996). Hunting for sight is only partly based on chance, seeing a worm coming out of the sediment is based on chance. However, the oystercatcher can actively hunt for the prey as well, it doesn't have to peck in the sediment randomly, but can really look for prey.

Female oystercatchers are more often specialized on *Nereis*, while male oystercatchers specialize on *Macoma* more (Ens et al. 1996). Differences in behaviour can also occur in oystercatchers feeding on one type of prey. Some oystercatchers open shells by hammering a shell until it breaks open, others stab their bill in between the two valves and open the shell. Stabbers walk slower than hammerers, possibly because stabbers specifically look for slightly gaping bivalves (Cayford & Goss-Custard 1990). In this research no oystercatchers were filmed that opened prey by hammering.

These types of specialization may imply that the behaviour, and thus hitrate, is so different between specialized groups of oystercatchers that it is not possible to determine one average hitrate and try to relate it to the total benthos energy content of a mudflat.

Firstly, the hitrate may differ between the specialized groups. If an oystercatcher would only hunt by touch, then the success of a peck would be a stochastic process only depending on food density, which would mean that the oystercatcher would be more successful in a higher quality patch. The specialization implies that hunting for one kind of prey is based less on chance, because it makes use of visible cues.

Secondly, oystercatchers that specialize on *Nereis* may have no interest in other prey, so an energy density map with the total energy for all benthos may give the wrong results to analyse the behaviour of specialized groups. However, the numbers of *Macoma*, *Cerastoderma* and *Nereis* are positively correlated, so the food distribution on the total map of energy content would not be similar to separate energy maps for each species.

The results show no relation between hitrate and energy when no difference was made between hunting techniques and a map of the total energy was used. It would be interesting to see if there is a difference in distribution of specialists. It is possible that the oystercatchers that specialize on one species don't forage in the same area as other specialists, maybe they choose lesser quality patches. Unfortunately it was almost impossible to distinguish between *Nereis* specialists and shell specialists, because of the video image quality. In most cases it was not possible to see what kind of prey was taken from the mud.

Even if all the oystercatchers were specialized on the same prey type and caught this prey in the same way, hitrate is not necessarily higher in higher quality patches. In a higher quality patch a predator can choose from more prey items, thus it can choose which prey is most profitable to eat. This in contrast to predators in a low quality patch, that may eat every prey available, because prey is harder to find. This way the hitrate would be lower than expected, because the predator distinguishes between prey items more then it does in low quality patches. In this research this problem is solved by using only the size classes of the prey that oystercatchers are known to eat (Hulscher 1982, Zwarts & Wanink 1993, Zwarts et al. 1996).

Walk path

The MANCOVA models did show a relation between the walk path variables $sd \theta$, average length, walk speed and hitrate. This relation was strongest in average length of the intervals and to a lesser extent in the standard deviation of the turning angle θ . Walk speed was only related to hitrate in combination with the two other variables and the relation was not very strong.

The more prey an oystercatcher caught, the shorter the average path length was. If an oystercatcher finds a prey item, it usually stands still to peck for it, handle and eat it. When an oystercatcher stood still or turned, this was defined as the end of an interval in the model. The result of walking shorter distances is that an oystercatcher will not walk far from its start position.

Oystercatchers turned more when they were more successful, the higher the hitrate, the higher the standard deviation of the turning angle. This means that the path of an oystercatcher is more random when it is more successful. This was also hypothesized. The oystercatcher stays closer to its start position when it is more successful.

Walk speed

Walk speed was negatively correlated with wind speed and negatively correlated with other oystercatchers. This first result seems logical: if the wind speed is higher, the oystercatcher walks slower. When an oystercatcher is in an area with more oystercatchers it also walks slower. The oystercatcher may walk slower when other oystercatchers are around because it has to keep an eye out for potential thieves and because it wants to see what the others find (Beauchamp, 2004ab).

Small scale decisions

The results from the analysis of the small scale effect of number of hits on turning angle showed that the more successful the oystercatcher was in an interval, the higher the turning after this interval was. This concurs with the hypothesis that the oystercatcher tries to stay in a patch if it is more successful.

Null Model

The hypothesis in this research was that the foraging movements of oystercatchers could lead to a null model that could explain the distribution of oystercatchers if the food distribution was given. By adapting their foraging behaviour to the energy content they would eventually end up in the highest quality patches. No relation was found between Energy and hitrate, so the significant relation found between $sd\ \theta$, average length and hitrate does not imply a relation between Energy and $sd\ \theta$ and average length. Energy was not used as a variable in the MANCOVA model for the walk path, because if energy would indeed influence the walk path, it was expected to do so indirectly through the hitrate.

Hitrate does not depend on energy alone. Other factors can also negatively or positively influence the hitrate. The number of gulls at close range may make the oystercatchers more cautious to prevent prey being stolen. The same goes for the number of oystercatchers. On the other hand other oystercatchers may positively influence the hitrate, because oystercatchers can get information of the area by looking at other oystercatchers (Sernland et al. 2003, Beauchamp 2002, 2004ab).

The number of other oystercatchers and gulls in a 50 meter radius were also scored, as well as other factors that could influence the foraging of an oystercatcher: water height, precipitation, cloudiness, wind direction and speed.

Despite all these other factors, the MANCOVA results show that hitrate was the main factor determining $sd\ \theta$ and average length.

The walk path may still take an oystercatcher to the highest profitable patch, but the highest profitable patch does not need to contain the highest energy content. The distribution of oystercatchers would then be different than the food distribution.

The other factors were not significant in the MANCOVA model for the walk path variables. Other oystercatchers for instance did not have a large effect on the path variables, except for walk speed.

Another possibility is that oystercatchers always move randomly when foraging, no matter what the energy content of an area is. It may be more profitable to fly to another patch if the food content in the current patch is low than to walk to another patch by adjusting the path. The patch that an oystercatcher forages in can be chosen on basis of energy content, but also on basis of other factors. Memory can play a role, the oystercatcher may know that a patch is profitable because it has foraged there before. Other oystercatchers can also influence patch choice, maybe an oystercatcher sees other oystercatchers foraging and knows that the patch is profitable. So the influence of factors other than hitrate such as other oystercatchers and gulls may not influence the path, but do influence the initial choice of the foraging site. Once an oystercatcher has chosen the patch, it starts foraging in a random way. The hitrate may then influence the path on a small (patch) scale, but the distribution on a larger (mudflat) scale may not be the result of the path.

Methods – discussion

The behaviour and path of oystercatchers were not studied directly in the field, but were studied by looking at films. The oystercatchers could be seen on a small screen during filming, but the quality and size of the screen would make it very difficult to see the filmed individual (light) or distinguish the individual from oystercatchers nearby. Not all films were of the same quality, but all films that were used in the analyses were of such a quality that all variables could be observed, such as number of steps, direction of the path and success of a peck. In some cases the prey item could be seen, but in most cases it was not possible to determine the prey type. The birds were filmed unprotected from the wind from a tripod in the mud. Because of the sometimes high wind speeds (up to 5/6 Bft), it could be very difficult sometimes to get a steady shot. Some oystercatchers were lost from view because of this which resulted into some small gaps in the observation.

Because the equipment was very sensitive to water damage, no observations could be made during snow or rain, which occurred frequently in the research period (February-March 2005).

The distance from which birds were observed was 105 – 439 m, which is a little below the threshold value of 136 meter for disturbance of oystercatchers by man as determined by Smit & Visser (1993). During the observations however, the oystercatchers did not seem to pay much attention to the observer, so this may not have been a problem.

The oystercatchers were filmed between two hours before until two hours after the low water, so the tidal effect was of less influence to foraging. The wind however, caused some water to stay on the mudflat longer sometimes, so the water depth may have had an influence, but no significant results were found for water depth influence. Water depth was measured by eye on the place from where the bird was filmed, but it would have been better to determine water depth for each observed bird separately by looking at the height of the water compared to the legs of the oystercatcher.

The number of oystercatchers and gulls around the oystercatcher were also scored during filming. The number used in the analyses is the average for the duration of the film. Because it is the average, effects of changes in the group of oystercatchers surrounding the filmed individual could not be investigated. As mentioned before, filming was hard sometimes because of the high wind speed, so a lot of attention had to be paid to keep the observed bird in view of the camera. The number of other oystercatchers and gulls could vary a lot during one observation, but not all changes could be seen by the observer when much attention had to be paid to the filming of one oystercatcher.

The energy maps were made with a GIS (ESRI) using a kriging function. This was done with a dataset of all benthos sampling points and their total energy content (kJ). Instead of making one map using the total energy content, it would have been better to make one map for each prey species. Using the average may lead to loss of data, because the energy content of different prey species may be in very different ranges. For instance, if the energy 0-0,2 for species A and 0-2 for species B, then a point with a high content for species A and low for species B may have an overall low energy content. The data of species A is then lost in the complete map total energy content. If one map was made for each prey species, the maps could have been summed later for a total map using relative number instead of the total energy content.

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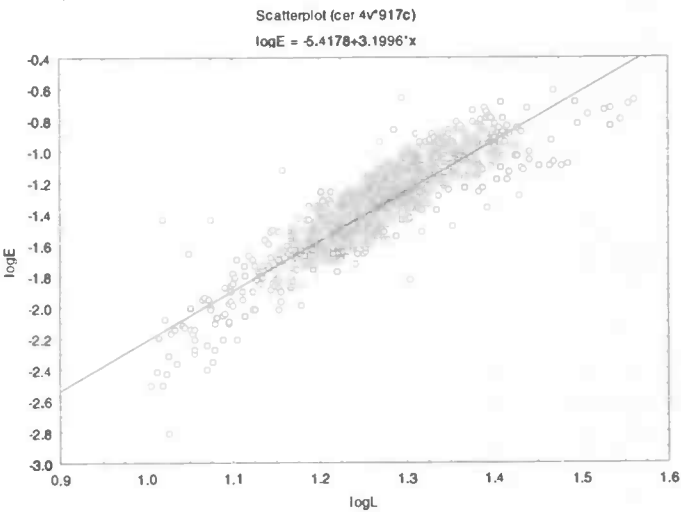
Appendix A

Fits for the relation between mollusc length (l) and energy content (E)(statistica)

Cerastoderma edule

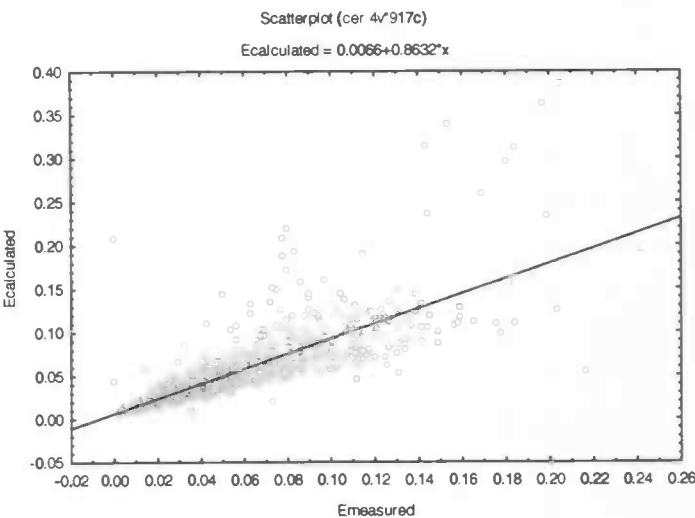
$\log E = -5.4178 + 3.1996 \cdot \log L$

$E(\text{cer}) = L(\text{cer})^{3.1996} / 10^{5.4178}$



fit

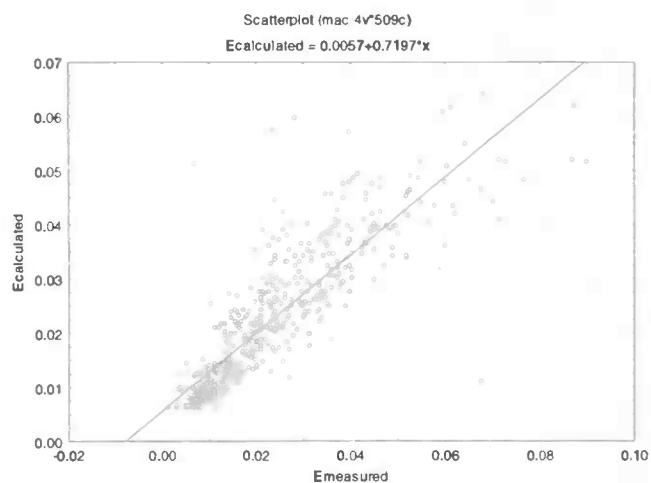
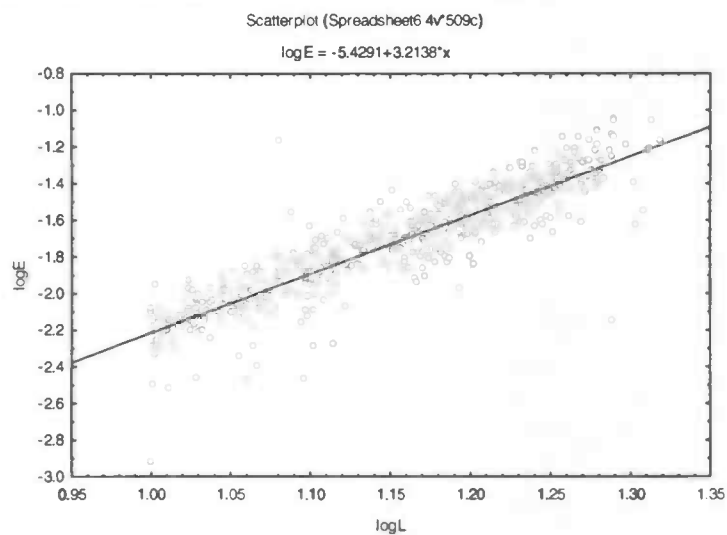
$E_{\text{calculated}} = 0.0066 + 0.8632 \cdot E_{\text{measured}}$



Macoma balthica:

$$\log E = -5.4291 + 3.2138 * x$$

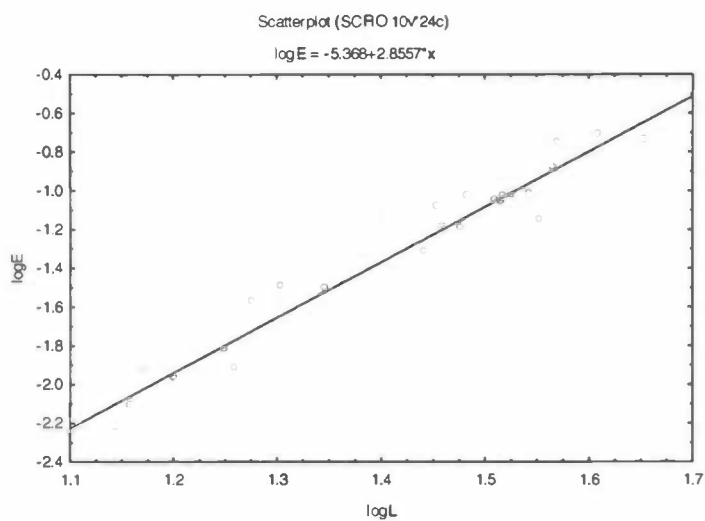
$$E(\text{mac}) = L(\text{mac})^{3.2138} / (10^{5.4291})$$



Fit: $E_{\text{calculated}} = 0.0057 + 0.7197 * E_{\text{measured}}$

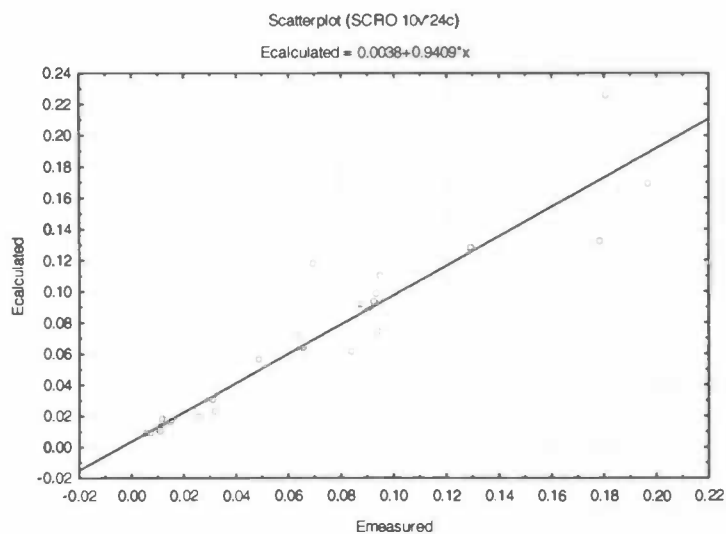
Scrobicularia plana

$$\text{Log}(\text{Energy}) = -5.368 + 2.8557 \cdot \log(\text{Lengte})$$

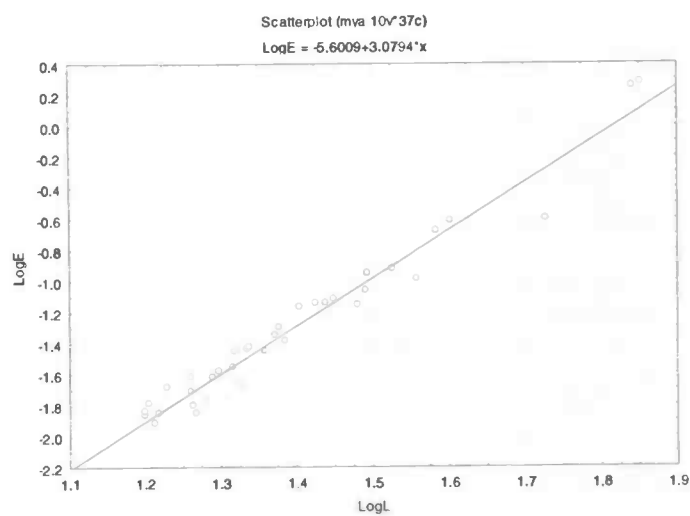


$$E(\text{scro}) = L^{2.8557} / 10^{5.368}$$

$$\text{Fit: } E_{\text{calculated}} = 0.0038 + 0.9409 \cdot E_{\text{measured}}$$

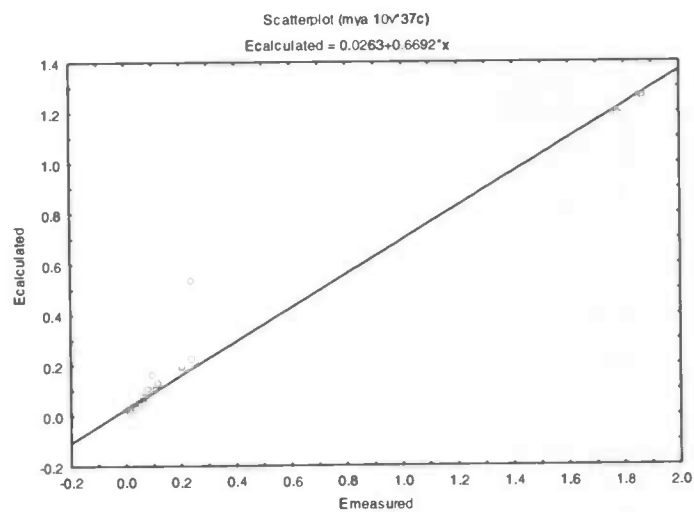


Mya arenaria



$$\text{Log E} = -5.6009 + 3.0794 * \text{L}$$

$$\text{E}(\text{mya}) = \text{L}(\text{mya}) ^ 3.0794 / 10 ^ 5.6009$$



Fit: $\text{Ecalculated} = 0.0263 + 0.6692 * \text{Emeasured}$

Appendix B Macro vba code

```
Sub Calculate_parameters()  
'  
' Macro1 Macro  
' Macro recorded 6/6/2005 by FOLMERO  
'  
' VARIABLES  
    j = 12          'counter of number of lines  
    Pi = 3.14159265358979  
    Tstartstep = 0   'Time of trial duration  
    Angle = 0        'angle based on direction  
    k = 1            'interval number  
    Sumx = 0  
    Sumy = 0  
  
    Rows("1:1").Select      ' verwijder eerste kolom na query  
    Selection.Delete Shift:=xlUp  
  
    'schrijf de namen van de variabelen op  
    Blad1.Cells(1, 1) = "time"  
    Blad1.Cells(1, 2) = "Interval"  
    Blad1.Cells(1, 3) = "Steps"  
    Blad1.Cells(1, 4) = "Duration"  
    Blad1.Cells(1, 5) = "Direction"  
    Blad1.Cells(1, 6) = "Pace Rate"  
    Blad1.Cells(1, 7) = "Log Speed"  
    Blad1.Cells(1, 8) = "Speed"  
    Blad1.Cells(1, 9) = "Int Dist"  
    Blad1.Cells(1, 10) = "X"  
    Blad1.Cells(1, 11) = "Y"  
    Blad1.Cells(1, 12) = "Sum X"  
    Blad1.Cells(1, 13) = "Sum Y"  
  
    Do Until Cells(j, 2) = "{end}"  
  
        numsteps = 0  
        Tint = 0  
  
        Select Case Cells(j, 2)  
  
            Case "north"          ' Directions  
                Angle = 0  
                Direction = "n"  
            Case "northeast"  
                Angle = 1 / 4 * Pi  
                Direction = "ne"  
            Case "east"  
                Angle = 2 / 4 * Pi  
                Direction = "e"  
            Case "southeast"  
                Angle = 3 / 4 * Pi  
                Direction = "se"  
            Case "south"  
                Angle = Pi  
                Direction = "s"
```

```

Case "southwest"
    Angle = 5 / 4 * Pi
    Direction = "sw"
Case "west"
    Angle = 6 / 4 * Pi
    Direction = "w"
Case "northwest"
    Angle = 7 / 4 * Pi
    Direction = "nw"

Case "step"                                'stappen tellen
    If Cells(j, 2) = "step" Then
        Do
            numsteps = numsteps + 1
        Loop Until Cells(j + numsteps, 2) <> "step"
        Tint = Cells(j + numsteps, 1) - Cells(j, 1)
    End If

Case "standing"
    Tint = Cells(j + 1, 1) - Cells(j, 1)

Case "missing"
    Tint = Cells(j + 1, 1) - Cells(j, 1)

End Select

If (k = 1 And Cells(j, 2) <> "standing") Then Tcorr = Cells(13, 1)

    ' configuratie: step
    '     richting
    '     step
    If (Cells(j, 2) = "north" Or Cells(j, 2) = "northeast" Or Cells(j, 2) = "east" Or
        Cells(j, 2) = "southeast" Or Cells(j, 2) = "south" Or Cells(j, 2) = "southwest" Or
        Cells(j, 2) = "west" Or Cells(j, 2) = "northwest") And Cells(j + 1, 2) = "step" And
        Cells(j - 1, 2) = "step" Then
        Tcorr = Cells(j + 1, 1) - Cells(j, 1)
        GoTo Write_to_screen
    End If

    ' configuratie: standing
    '     richting
    '     step
    If (Cells(j - 1, 2) = "north" Or Cells(j - 1, 2) = "northeast" Or Cells(j - 1, 2) =
        "east" Or Cells(j - 1, 2) = "southeast" Or Cells(j - 1, 2) = "south" Or Cells(j - 1, 2) =
        "southwest" Or Cells(j - 1, 2) = "west" Or Cells(j - 1, 2) = "northwest") And (Cells(j
        - 2, 2) = "standing" Or Cells(j - 2, 2) = "missing") And (Cells(j, 2) = "step") Then
        Tcorr = Cells(j, 1) - Cells(j - 1, 1)
        GoTo Write_to_screen
    End If

Write_to_screen:
    If Tint > 0 Then
        Tint = Tint + Tcorr
        'Time
        Blad1.Cells(k + 1, 1) = Cells(j + numsteps, 1)

```

```

'interval number
Blad1.Cells(k + 1, 2) = k
'number of steps per direction
Blad1.Cells(k + 1, 3) = numsteps
'interval duration
Blad1.Cells(k + 1, 4) = Tint
'Direction
If Cells(j, 2) = "standing" Then
  Blad1.Cells(k + 1, 5) = "Staat"
Else
  If Cells(j, 2) = "missing" Then
    Blad1.Cells(k + 1, 5) = "Missing"
  Else
    Blad1.Cells(k + 1, 5) = Direction
  End If
End If

If numsteps > 0 Then
  'pace rate
  Blad1.Cells(k + 1, 6) = (numsteps / Tint)
  'log speed according to Speakman and Bryant 1993
  Blad1.Cells(k + 1, 7) = -1.18 + (1.46 * (Log(numsteps / Tint)) / Log(10))
  'speed
  Blad1.Cells(k + 1, 8) = 10 ^ (-1.18 + (1.46 * (Log(numsteps / Tint)) /
Log(10)))
  'interval distance (interval duration * speed)
  Blad1.Cells(k + 1, 9) = (10 ^ (-1.18 + 1.46 * (Log(numsteps / Tint)) /
Log(10))) * Tint
  'x component
  Blad1.Cells(k + 1, 10) = ((10 ^ (-1.18 + (1.46 * (Log(numsteps / Tint)) /
Log(10)))) * Tint) * Sin(Angle)
  Sumx = Sumx + ((10 ^ (-1.18 + (1.46 * (Log(numsteps / Tint)) /
Log(10)))) * Tint) * Sin(Angle)
  'y component
  Blad1.Cells(k + 1, 11) = ((10 ^ (-1.18 + (1.46 * (Log(numsteps / Tint)) /
Log(10)))) * Tint) * Cos(Angle)
  Sumy = Sumy + ((10 ^ (-1.18 + (1.46 * (Log(numsteps / Tint)) /
Log(10)))) * Tint) * Cos(Angle)
End If
'Sum X
Blad1.Cells(k + 1, 12) = Sumx
'Sum Y
Blad1.Cells(k + 1, 13) = Sumy
Tcorr = 0
k = k + 1
End If

If Int(Cells(j, 1) / 1) >= i_1 Then
  Sheets("sec_pad1").Cells(1, 1) = "tjd"
  Sheets("sec_pad1").Cells(1, 2) = "Sumx"
  Sheets("sec_pad1").Cells(1, 3) = "Sumy"
  Sheets("sec_pad1").Cells(i_1 + 2, 1) = Cells(j, 1)
  Sheets("sec_pad1").Cells(i_1 + 2, 2) = Sumx
  Sheets("sec_pad1").Cells(i_1 + 2, 3) = Sumy
  If ((Cells(j, 1) / 1) > i_1 + 1) Then i_1 = Int(Cells(j, 1) / 1)
  i_1 = i_1 + 1
End If

```

```

If Int(Cells(j, 1) / 5) >= i_5 Then
    Sheets("sec_pad5").Cells(1, 1) = "tjtd"
    Sheets("sec_pad5").Cells(1, 2) = "Sumx"
    Sheets("sec_pad5").Cells(1, 3) = "Sumy"
    Sheets("sec_pad5").Cells(i_5 + 2, 1) = Cells(j, 1)
    Sheets("sec_pad5").Cells(i_5 + 2, 2) = Sumx
    Sheets("sec_pad5").Cells(i_5 + 2, 3) = Sumy
    If ((Cells(j, 1) / 5) > i_5 + 1) Then i_5 = Int(Cells(j, 1) / 5)
    i_5 = i_5 + 1
End If

If Int(Cells(j, 1) / 10) >= i_10 Then
    Sheets("sec_pad10").Cells(1, 1) = "tjtd"
    Sheets("sec_pad10").Cells(1, 2) = "Sumx"
    Sheets("sec_pad10").Cells(1, 3) = "Sumy"
    Sheets("sec_pad10").Cells(i_10 + 2, 1) = Cells(j, 1)
    Sheets("sec_pad10").Cells(i_10 + 2, 2) = Sumx
    Sheets("sec_pad10").Cells(i_10 + 2, 3) = Sumy
    If ((Cells(j, 1) / 10) > i_10 + 1) Then i_10 = Int(Cells(j, 1) / 10)
    i_10 = i_10 + 1
End If

If Int(Cells(j, 1) / 15) >= i_15 Then
    Sheets("sec_pad15").Cells(1, 1) = "tjtd"
    Sheets("sec_pad15").Cells(1, 2) = "Sumx"
    Sheets("sec_pad15").Cells(1, 3) = "Sumy"
    Sheets("sec_pad15").Cells(i_15 + 2, 1) = Cells(j, 1)
    Sheets("sec_pad15").Cells(i_15 + 2, 2) = Sumx
    Sheets("sec_pad15").Cells(i_15 + 2, 3) = Sumy
    If ((Cells(j, 1) / 15) > i_15 + 1) Then i_15 = Int(Cells(j, 1) / 15)
    i_15 = i_15 + 1
End If

If Int(Cells(j, 1) / 20) >= i_20 Then
    Sheets("sec_pad20").Cells(1, 1) = "tjtd"
    Sheets("sec_pad20").Cells(1, 2) = "Sumx"
    Sheets("sec_pad20").Cells(1, 3) = "Sumy"
    Sheets("sec_pad20").Cells(i_20 + 2, 1) = Cells(j, 1)
    Sheets("sec_pad20").Cells(i_20 + 2, 2) = Sumx
    Sheets("sec_pad20").Cells(i_20 + 2, 3) = Sumy
    If ((Cells(j, 1) / 20) > i_20 + 2) Then i_20 = Int(Cells(j, 1) / 20)
    i_20 = i_20 + 1
End If

If numsteps <> 0 Then
    j = j + numsteps
Else
    j = j + 1
End If

Loop

Sheets("sec_pad1").Select
Columns("A:A").Select
Selection.AutoFilter

```

```

Selection.AutoFilter Field:=1, Criteria1:="<>"
Sheets("sec_pad5").Select
Columns("A:A").Select
Selection.AutoFilter
Selection.AutoFilter Field:=1, Criteria1:="<>"
Sheets("sec_pad10").Select
Columns("A:A").Select
Selection.AutoFilter
Selection.AutoFilter Field:=1, Criteria1:="<>"
Sheets("sec_pad15").Select
Columns("A:A").Select
Selection.AutoFilter
Selection.AutoFilter Field:=1, Criteria1:="<>"
Sheets("sec_pad20").Select
Columns("A:A").Select
Selection.AutoFilter
Selection.AutoFilter Field:=1, Criteria1:="<>"

```

```

Sheets("sec_pad1").Select
Columns("A:C").Select
Selection.Copy
Sheets("sec1").Select
Range("A1").Select
Selection.PasteSpecial Paste:=xlPasteValues, Operation:=xlNone, SkipBlanks _
:=True, Transpose:=False
Columns("A:A").Select
Selection.AutoFilter
Selection.AutoFilter Field:=1, Criteria1:="<>"

```

```

Sheets("sec_pad5").Select
Columns("A:C").Select
Selection.Copy
Sheets("sec5").Select
Range("A1").Select
Selection.PasteSpecial Paste:=xlPasteValues, Operation:=xlNone, SkipBlanks _
:=True, Transpose:=False
Columns("A:A").Select
Selection.AutoFilter
Selection.AutoFilter Field:=1, Criteria1:="<>"

```

```

Sheets("sec_pad10").Select
Columns("A:C").Select
Selection.Copy
Sheets("sec10").Select
Range("A1").Select
Selection.PasteSpecial Paste:=xlPasteValues, Operation:=xlNone, SkipBlanks _
:=True, Transpose:=False
Columns("A:A").Select
Selection.AutoFilter
Selection.AutoFilter Field:=1, Criteria1:="<>"

```

```

Sheets("sec_pad15").Select
Columns("A:C").Select
Selection.Copy
Sheets("sec15").Select
Range("A1").Select
Selection.PasteSpecial Paste:=xlPasteValues, Operation:=xlNone, SkipBlanks _

```

```

:=True, Transpose:=False
Columns("A:A").Select
Selection.AutoFilter
Selection.AutoFilter Field:=1, Criteria1:="<>"

Sheets("sec_pad20").Select
Columns("A:C").Select
Selection.Copy
Sheets("sec20").Select
Range("A1").Select
Selection.PasteSpecial Paste:=xlPasteValues, Operation:=xlNone, SkipBlanks _
:=True, Transpose:=False
Columns("A:A").Select
Selection.AutoFilter
Selection.AutoFilter Field:=1, Criteria1:="<>"

Sheets("samvat").Select

End Sub

```


Appendix C Variables

Variables calculated from field data (benthos, walk patterns and scored behaviour)

Variable name	Variable meaning	
x	x coordinate of the position of the oystercatcher on the grid	
y	y coordinate of the position of the oystercatcher on the grid	
cloudiness during filming	percentage of clouds	
other birds during filming	number and species of other birds in a 50 m radius	
wind speed during filming	Bft	
wind direction during filming		
water height during filming	cm	
Behaviour Variables		
Tsearching	Time spent searching for food (s)	
Twalking	Time spent walking (walking, running and standing still when not searching for food) (s)	
Trest	Time spent resting / preening (s)	
Tmissing	Time that oystercatcher was missing from view (s)	
Tfight	Time spent fighting (s)	
Ttot	Total duration of the observation (s)	> 250 seconds
Tpeck_miss	Total time spent pecking; miss (s)	
Tpeck_hit	Total time spent pecking; hit (s)	
Tpeck_unk	Total time spent pecking; unknown (s)	
Num_miss	Number of unsuccessful pecks; miss	
Num_hit	Number of successful pecks; hit	
Num_unk	Number of unknown pecks; unknown	
hit_miss_ratio	Number of hits / Number of misses	
perc_miss	Number of misses / (Number of hits + Number of misses + Number of unknown) *100	
perc_hit	Number of hits / (Number of hits + Number of misses + Number of unknown) *100	
perc_unknown	Number of unknown pecks / (Number of hits + Number of misses + Number of unknown) *100	
Tdecision_per_peck	Tpeck_miss / Num_miss	Duration of 'decision time' per peck; see 'methods' for explanation
Thandling_tot	Tpeck_hit - (Num_hit * Tdecision_per_peck)	Total duration of 'handling time'; see 'methods' for explanation
Thandling_per_peck	Thandling_tot / Num_hit	Total duration of 'handling time' per peck; see 'methods' for explanation

Tpeck_zonder_handling	$Tpeck_hit - Thandling_tot$	
Trl_peck_miss:	$Tpeck_miss / (Ttot - Tmissing)$	Relative time (per Total time - Time missing)
Trl_peck_hit:	$Tpeck_hit / (Ttot - Tmissing)$	Relative time (per Total time - Time missing)
Trl_peck_unk:	$Tpeck_unk / (Ttot - Tmissing)$	Relative time (per Total time - Time missing)
Trl_searching:	$(Tpeck_miss + Tpeck_hit + Tpeck_unk + Tsearching) / (Ttot - Tmissing)$	Relative time (per Total time - Time missing) > 0,8
Trl_walking:	$Twalking / (Ttot - Tmissing)$	Relative time (per Total time - Time missing)
Trl_rest:	$Trest / (Ttot - Tmissing)$	Relative time (per Total time - Time missing)
Trl_missing:	$Tmissing / Ttot$	Relative time (per Total time - Time missing)
Trl_fight:	$Tfight / (Ttot - Tmissing)$	Relative time (per Total time - Time missing) 0 seconds
Peck_rate:	$(Num_miss + Num_hit + Num_unk) / (Tsearching + Tpeck_unk + Tpeck_hit + Tpeck_miss - Thandling_tot)$	Number of pecks per time spent searching
Trl_peck_tot:	$Trl_peck_miss + Trl_peck_hit + Trl_peck_unk$	
Hirate:	$Num_hit / (Tpeck_miss + Tpeck_hit + Tpeck_unk + Tsearching - Thandling_tot)$	
Missrate:	$Num_miss / (Tpeck_miss + Tpeck_hit + Tpeck_unk + Tsearching - Thandling_tot)$	

Walk path variables

sd_length	standard deviation of the length of the path moved during one interval (5, 10, 15 and 20 sec)
avg_length	average length of the path moved during one interval (5, 10, 15 and 20 sec)
avg_turning angle	average of turning angles (5, 10, 15 and 20 sec)
sd_turning angle	standard deviation of turning angles (5, 10, 15 and 20 sec)

Benthos variables

sed_slb50	sediment composition	
AFDW cer	$length \wedge 3,1996 / (10 \wedge 5,4178)$	AFDW of Cerastoderma edule

Energy_cer	AFDW cer * 22,2	(g) Energy content of Cerastoderma edule (kJ)
Energy_cer_m2	Energy_cer / 0,0176714589	Energy content of Cerastoderma edule (kJ / m2)
AFDW mac	length ^ 3,2138 / (10 ^ 5,4291)	AFDW of <i>Macoma balthica</i> (g)
Energy_mac	AFDW mac * 22	Energy content of <i>Macoma balthica</i> (kJ)
Energy_mac_m2	Energy_mac / 0,0176714589	Energy content of <i>Macoma balthica</i> (kJ / m2)
AFDW mya	length ^ 3,0794 / (10 ^ 5,6009)	AFDW of <i>Mya arenaria</i> (g)
Energy_mya	AFDW mya * 21,7	Energy content of <i>Mya arenaria</i> (kJ)
Energy_mya_m2	Energy_mya / 0,0176714589	Energy content of <i>Mya arenaria</i> (kJ / m2)
AFDW scro	length ^ 2,8557 / (10 ^ 5,368)	AFDW of <i>Scrobicularia plana</i> (g)
Energy_scro	AFDW scro * 21,9	Energy content of <i>Scrobicularia plana</i> (kJ)
Energy_scro_m2	Energy_scro / 0,0176714589	Energy content of <i>Scrobicularia plana</i> (kJ / m2)
AFDW mytilus	AFDW <i>Mytilus edulis</i>	AFDW of <i>Mytilus edulis</i> (g)
Energy_mytilus	AFDW mytilus * 23,2	Energy content of <i>Mytilus edulis</i> (kJ)
Energy_mytilus_m2	Energy_mytilus / 0,0176714589	Energy content of <i>Mytilus edulis</i> (kJ / m2)
Energy_Bivalves_m2	Energy_mac_m2 + Energy_mya_m2 + Energy_scro_m2 + Energy_mossel_m2 + Energy_cer_m2	Energy content of all bivalves (kJ / m2)
Ner_juv	number of juvenile Nereis	
Ner_ad	number of adult Nereis	
Energy_Ner_gem	Ner_ad * 1,2 + Ner_juv * 0,3	average energy content of <i>Nereis diversicolor</i> (kJ)
Energy_Ner_min	Ner_ad * 0,7 + Ner_juv * 0,1	minimum energy content of <i>Nereis diversicolor</i> (kJ)
Energy_Ner_max	Ner_ad * 1,8 + Ner_juv * 0,7	maximum energy content of <i>Nereis diversicolor</i> (kJ)
Energy_Ner_avg_m2	Energy_Ner_gem / 0,0176714589	average energy content of <i>Nereis diversicolor</i> (kJ / m2)
Energy_Ner_min_m2	Energy_Ner_min / 0,0176714589	minimum energy content of <i>Nereis diversicolor</i> (kJ / m2)

Energy_Ner_max_m2	$\text{Energy_Ner_max} / 0,0176714589$	maximum energy content of Nereis diversicolor (kJ m2)
E_avg	total amount of energy on a certain position (energy bivalves/m2 + Ner_avg)	
E_min	total amount of energy on a certain position (energy bivalves/m2 + Ner_min)	
E_max	total amount of energy on a certain position (energy bivalves/m2 + Ner_max)	