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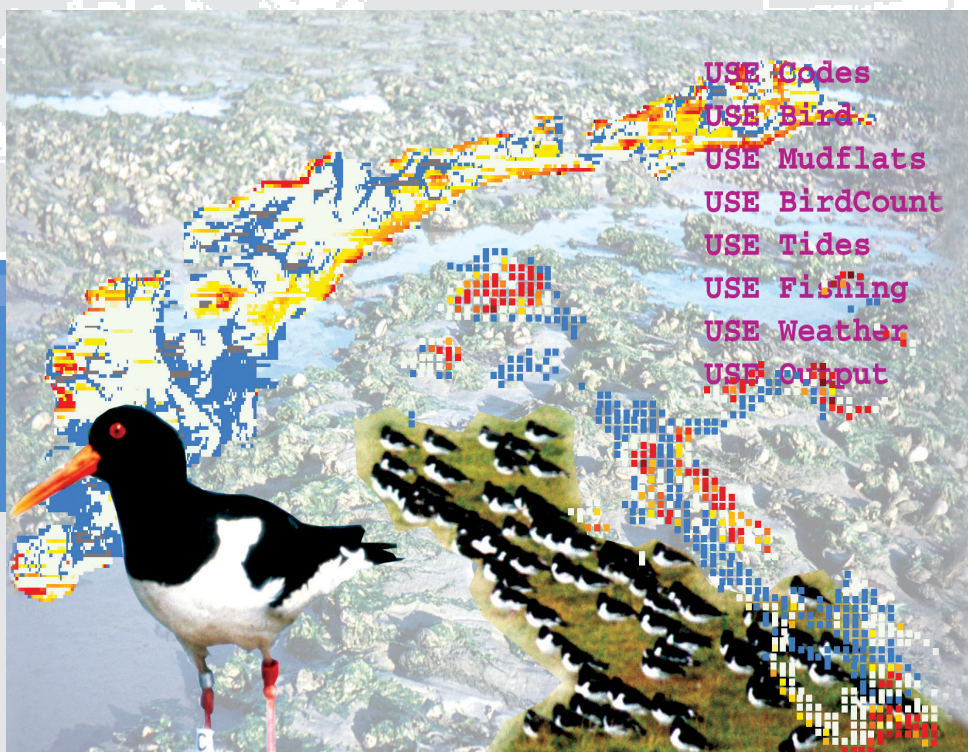
Ministerie van Verkeer en Waterstaat  
Rijksinstituut voor Kust en Zee

# Wader Energy Balance & Tidal Cycle Simulator WEBTICS

Technical Documentation version 1.1

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Alterra-rapport 869, ISSN 1566-7197





Wader Energy Balance & Tidal Cycle Simulator *WEBTICS*

Commissioned by the ministry LNV in the Netherlands



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C. Rappoldt, B. J. Ens, M. A. J. M. Kersten, E. M. Dijkman

Alterra–Report 869

Alterra, Wageningen, 2004

## ABSTRACT

Cornelis Rappoldt, Bruno J. Ens, Marcel A. J. M. Kersten, Elze M. Dijkman, 2004. *Wader Energy Balance & Tidal Cycle Simulator WEBTICS ; Technical Documentation version 1.1*. Wageningen, Alterra–Report 869. 95 pages; 20 figs.; 15 tables.; 35 refs.

This report describes the Wader Energy Balance and Tidal Cycle Simulator WEBTICS. The model simulates food uptake of Oystercatchers (*Haematopus ostralegus*) and a distribution of the birds over exposed parts of tidal areas. The mudflats are described on input as a number of spots which have a position, height and surface area. Spots may contain prey items characterized by type, weight and density. The program simulates tidal cycles and calculates the fraction of time the average and ideal bird has to spend feeding in order to meet its energy requirements. These foraging intensities are combined into a stress index for the winter. Besides historical data on weather, prey distribution, tides and fishing, there are bird and prey parameters on foraging, prey growth and energy conversion. Model output files can be processed in a spreadsheet. Also bitmapped images and movies are produced.

Trefwoorden: wader, model, simulation, mudflat, food, shellfish, cockle, mussel, shellfishery, foraging, interference.

ISSN 1566–7197

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# Preface (in Dutch)

Voor u ligt de technische documentatie van de Wader Energy Balance & Tidal Cycle Simulator *WEBTICS* dat vervaardigd is ten behoeve van de tweede evaluatiefase van het Nederlands schelpdiervisserij-beleid, EVA II. De betrokken instellingen zijn Alterra, het Centrum voor Schelpdier Onderzoek van het Nederlands Instituut voor Visserij Onderzoek (RIVO-CSO) en het Rijksinstituut voor Kust en Zee (RIKZ). Het onderzoek is verricht met financiering vanuit het ministerie van LNV in het kader van het EVA II deelproject B1 "voedselreservering voor scholeksters in de Waddenzee". Daarnaast is een deel van het werk gefinancierd met geld uit het door LNV betaalde bestek 5a "Voedselaanbod voor vogels".

Het model *WEBTICS* is ontwikkeld ten behoeve van de studie over Scholeksters en hun voedsel in de Waddenzee en Oosterschelde waarvan verslag gedaan is in [Rappoldt \*et al.\* \(2003a,b\)](#). De bedoeling van een technische documentatie is om de invoerparameters, de uitvoerfiles, de rekenprocedures en de programmering van het model te documenteren. De ervaring leert dat het documenteren van technische details over een computerprogramma snel leidt tot een zwaarlijvig en onoverzichtelijk rapport. Ik heb daarom gepoogd me tot de hoofdzaken te beperken: de structuur van het programma, de gebruikte parameters en "waar is wat te vinden". Wil men nog meer weten dan moet de Fortran code geraadpleegd worden die overigens ook uitgebreid van commentaar is voorzien.

Een groot aantal mensen heeft bijgedragen aan de totstandkoming van het model *WEBTICS*. Met vragen over de schelpdiergegevens van het RIVO ben ik vele malen te rade gegaan bij Pauline Kamermans en Joke Kesteloo-Hendrikse. Over de voedsleecologie van scholeksters heb ik veel geleerd van Marcel Kersten, Bruno Ens, Richard Stillman, Jaap de Vlas en Leo Zwarts. Het is opmerkelijk dat veel van de hier gebruikte kennis het resultaat is van wat nog geen 10 jaar geleden fundamenteel onderzoek aan wadvogels was, beschreven in proefschriften en tijdschriftartikelen.

Bert Brinkman heeft geholpen met het berekenen van de verdeling van de vogels over droogvallende voedselgebieden. De stress-index voor het karakteriseren van een winter is het resultaat van een avond praten met Marcel Kersten. Rob Dekker heeft geholpen met de omrekening van mosselgewichten en Jaap van der Meer met een statistische analyse. Resultaten van modelberekeningen zijn een aantal keren besproken met collega's van het EVA II onderzoek en met Marnix van Stralen. Veel ideeën en verbeteringen vinden hun oorsprong in die bijeenkomsten op Texel en in Yerseke. De afbeelding op de voorplaat van dit rapport is deels gebaseerd op fotos van Cor Smit en Gert Eggens.

Tenslotte moet ik mij verontschuldigen voor de onvolkomenheden in deze technische documentatie. Dit rapport is in de loop van enkele jaren “gegroeid” hetgeen een consistente stijl niet ten goede komt. Ik ben echter altijd bereid vragen over het model te beantwoorden en te helpen met de inspectie van de Fortran code in geval van onduidelijkheden.

Wageningen, maart 2004  
Kees Rappoldt

# Summary

This report contains the technical documentation of the simulation model *WEBTICS*, the Wader Energy Balance and Tidal Cycle Simulator. The computer program has been written in standard Fortran 95, which allows the model to run on all major platforms, Linux, Windows, Macintosh, and Unix.

*WEBTICS* is a simulation model which means that the food uptake of the birds and their distribution over exposed parts of the mudflats are simulated with time steps of 15 minutes, for instance. The model also calculates the energy requirement of the birds, which depends on their weight and the temperature. If there is plenty of food available the birds may either stop foraging after feeding at maximum intake rate during some time, or they feed at a lower rate during the entire low tide period.

In order to simulate food intake, the model combines the functional response and interference strength of foraging Oystercatchers with basic data on weather, tidal water levels, the height level of a number of foraging spots, the shellfish survey information for these spots, and data on the amount of shellfish removed by fishing.

The core of the model is a few hundred lines of Fortran code in which the rate calculations, integration, output and evaluation of a tidal cycle are organized. From this model structure individual modules are called which perform well described tasks like the calculation of the Ideal Free Distribution of birds, the evaluation of the exposure status of all mudflat spots, the removal of shellfish by fishing etc.

In the introduction the computations during the simulation are briefly explained and important assumptions are discussed. Chapter 2 describes the structure of the model from a programmers point of view. Chapter 3 describes the input files and the most important output files. The stress index which characterizes the workload of the birds during a is introduced in Chapter 4. Chapters 5, 6 and 7 document the meaning of the various model parameters and the values used.

In a few Appendices details on various aspects are given. The most important one is Appendix A in which the results of the interference model in [Stillman \*et al.\* \(2002\)](#) are simplified as simple exponential curves describing the reduction of food intake as function of bird density. The content of Appendix C has little to do with the model *WEBTICS*, but the power analysis has been used in [Rappoldt \*et al.\* \(2003a,b\)](#) without being properly explained.

This technical documentation has probably to be updated and adapted as the *WEBTICS* model is developed further or adapted to special applications. Therefore, this documentation has been written in English and will be made available as a PDF file.



# Chapter 1

## Introduction

This report contains the technical documentation of the simulation model *WEBTICS*, the Wader Energy Balance and Tidal Cycle Simulator. The computer program has been written in standard Fortran 95, which allows the model to run on all major platforms, Linux, Windows, Macintosh, and Unix. *WEBTICS* is a simulation model which means that the food uptake of the birds and their distribution over exposed parts of the mudflats are simulated with time steps of 15 minutes, for instance. The model also calculates the energy requirement of the birds, which depends on their weight and the temperature. If there is plenty of food available the birds may either stop foraging after feeding at maximum intake rate during some time, or they feed at a lower rate during the entire low tide period.

In order to simulate food intake, the model combines the functional response and interference strength of foraging Oystercatchers with basic data on weather, tidal water levels, the height level of a number of foraging spots, the shellfish survey information for these spots, and data on the amount of shellfish removed by fishing.

### 1.1 The tidal cycle

At each time step the exposure status of all mudflat spots is calculated. Then the birds are distributed over the exposed spots in some way. The first distribution method is by maximizing the intake rate. At the richest spots the bird density is high and food intake there is reduced by interference effects. At less rich spots the bird density is lower and the birds can be distributed in such a way that food intake becomes equal at all spots used. This is the so called Ideal Free Distribution. The birds are free to move around without energy costs and have a perfect knowledge of their feeding grounds.

The Ideal Free Distribution has the disadvantage that the birds (in the model) concentrate on just a few good spots to maximize their intake rate and stop foraging when they have eaten enough. If there is plenty of food, the birds also may feed at the average intake rate required, which allows them to exploit spots that would otherwise be marginal.

After calculating the intake rate of the birds, the model calculates cumulative intake and subtracts the eaten prey from the density available at each spot.

At high tide the model evaluates the low tide period which has just passed. The ratio between the eaten amount of food and the amount that could have been found is calculated, which is the foraging intensity. In practice, this foraging intensity is practically equal to the fraction of available foraging time the birds need, but since the length of a low tide foraging period is a somewhat arbitrary quantity, the ratio between eaten amount and the amount that could have been found is a better choice.

If the birds could not eat enough to meet their energy requirements, they loose weight. If the birds eat more than what they need, they gain weight until some prescribed weight is reached which varies somewhat with the season.

From the length of the next low tide period and the temperature a new value for the required amount of food is calculated. If the birds are below their desired body weight, this required amount is increased and a new tidal cycle begins.

## 1.2 Important assumptions

The calculations described above are based on some important simplifying assumptions

**All birds are equal** In reality there are differences between individuals with respect to their foraging abilities and dominance status.

**Perfect knowledge of the area** The birds have a perfect knowledge of the distribution of prey in they area and of the times at which the various spots are exposed. Clearly, this cannot be true, which means that the degree at which the shellfish stocks can be exploited by the birds will be overestimated.

**No costs of displacement** It is assumed that the birds can move from one spot to the other in no time and without energetic costs. This leads, in the model, to displacements over relatively large distances when good spots become exposed, for instance. Also this represents an overestimate of the exploitation efficiency of the birds.

These simplifications imply that the birds considered in the model are a sort of “ideal superbirds”. In the model the birds can survive as long as their foraging intensity stays below 1.0. Real birds will not be able to survive under the same circumstances, at least, a part of the birds will get into difficulties long before the workload of the superbirds reaches a maximum.

The idea of modelling “superbirds” is that they represent a reference. If we compare different years and the superbirds experience more difficulties in one year than in the other, the same is likely to be true for real birds. The level of the foraging intensity which corresponds to “problems for real birds”, however, needs to be found out by comparing model results with field data. In order to do that we need to characterize an entire winter with a number representing workload or risk for the birds.

## 1.3 The winter season

The foraging intensities calculated for the low tide periods for an entire winter are combined into a stress index for the winter. It is assumed that the occurrence of

high values of the foraging intensity represent a serious risk for the birds which is not easily balanced by periods with a low foraging intensity. Therefore a weighted average of the foraging intensities is used as a difficulty measure or stress index for the winter. The simplest choice for the weight of each foraging intensity is simply the value itself which means that the stress index is calculated from the squares of the foraging intensities for the winter period. This stress index indeed appears to be related to the number of birds returning to the area the next year (e.g. [Rappoldt et al., 2003a](#), Fig. 5.29).

Fishing may takes place in the model in the form of removing part of the shellfish. Although fishing takes place over a period of about two months, the shellfish is removed in the model at a particular day, which can be set at October 1, for instance.

## 1.4 On this report

This technical documentation contains a description of the various source files of the model and a description of the input and output files. The last chapters contain a more detailed description of bird prey and fishing parameters.

Parts of this report have been written during the development of the model. Other parts have been written after completion of the model studies for Oosterschelde and Wadden Sea. The report is therefore not as balanced and easy reading as it probably could be, but given the time available for documenting the model this could not be avoided. In case of confusion I am always prepared to answer questions or to help with inspecting the Fortran code.





## Chapter 2

# The structure of the model

The language used is standard Fortran 95. This allows the model to run on all major platforms, Linux, Windows, Macintosh, and Unix.

### 2.1 Program modules

Extensive use has been made of Fortran “modules”. These are program units in which data and subprograms working with these data are combined in a single unit. For instance, the foraging parameters of the birds are stored in module “Bird” together with the subprograms for calculating the functional response and the distribution over the exposed parts of the mudflats. The input data on water levels are stored in module Tides together with a subprogram returning the exposure status of mudflat spots. In the sections below the function of the various modules is briefly described.

All modules make use (by means of the Fortran 95 USE statement) of the definitions in module Codes. This module defines region names, and prey names, prey types and lengths of character strings used throughout the model. Other interdependencies between the modules are indicated below.

#### 2.1.1 MudFlats

Module MudFlats stores all spot variables. Spots are locations on the mudflats for which prey data are collected during the RIVO prey survey. The survey data are assumed to be representative for the surface area associated with the spot. Almost all prey related calculations in the model are carried out per spot and the calculation of an output parameter like the fresh weight of the eaten Cockles, for instance, requires a summation over all spots.

The spot data are stored as an array of spot records. Each spot record contains all the variables for a certain spot: surface area, height in various years, exposure time in various years, coordinates, etc. A special spot variable points to the prey items belonging to the spot. The prey items are simply a part of the prey array which stores prey size, fresh weight, wet weight, fished amount, eaten amount etc.

Most subroutines in module Mudflats are input routines for reading the prey survey, the height and exposure time data from file.

Module Mudflats also contains the prey parameters describing growth and death of the various prey items. To these parameters belong the subprograms for calculating the rates of change of fresh weight and wet weight as function of time. The prey parameters and the associated subprograms might be moved to a separate module Prey in a future version of the model.

Module Mudflats uses some functions from module Tides to calculate spot heights from exposure times or the reverse.

### **2.1.2 Bird**

Stores the foraging parameters and contains the subprograms for calculating the functional response, the degree of interference and the distribution of the birds over the exposed spots. Module Bird uses module Weather in calculations on the energy requirement of the birds.

### **2.1.3 BirdCount**

Reads the monthly bird counts from file and calculates a number at any moment in time by linear interpolation between the counts.

### **2.1.4 Codes**

Contains codes used by other modules like prey names and prey age class names used in the RIVO prey survey, the corresponding numbers used in the prey record, names of regions (e.g. “Oosterschelde” or “Waddensea”) for which the model can run, etc. Also some special variables like “Mossel” and “Kokkel” are defined here which improves the readability and reliability of the Fortran code.

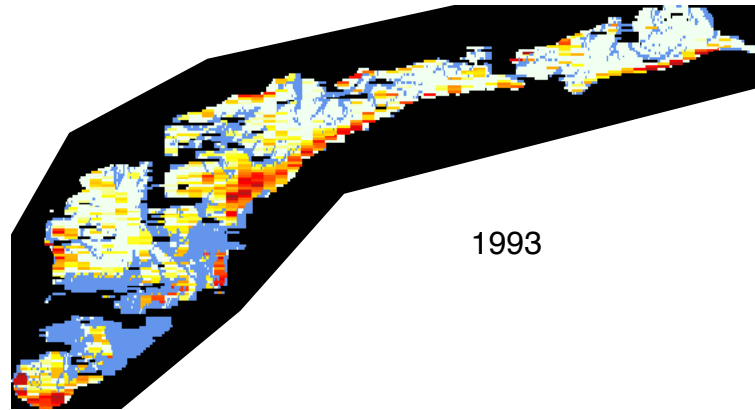
### **2.1.5 Fishing**

This module contains the fishing parameters describing the various options and the subroutines for carrying out the fishing in the model. Details of the fishing procedures in the model can be found in Section [2.3.6](#).

Module Fishing uses module Mudflats for information on the fished fraction and exposure time of the various spots.

### **2.1.6 Output**

An important output file produced by the model is named “HighTideYYYY.out”, where “YYYY” stands for the year in which the simulation began. This file is discussed in more detail in Chapter [3](#).



**Figure 2.1.** *Example of TIFF file output for a Wadden Sea model run. The image shows the distribution of prey wet weight at the begin a the simulation run starting at September 1, 1990. The colour scale goes from white (less than 0.1% of the maximum) via yellow to red (the maximum). In the printed version these colours are just levels of grey. In [Rappoldt et al. \(2003b, Fig. 3.2\)](#) a print in colour can be inspected.*

Module Output contains some dedicated output procedures. Heavily used are the routines for generating simple maps for the visualisation of all sorts of prey, eaten prey and bird distributions on the mudflats. Figure 2.1 shows an example. These simple and coarse grained maps are TIFF images directly produced by the model. This greatly simplifies the inspection of results since no postprocessing is necessary.

The TIFF files produced are so called indexed colour images. Every pixel is represented by an integer value in the range  $[0, \dots 255]$  and the colours coded by these numbers are given in a so called colour lookup table with 256 three byte (24 bit) RGB colours. The TIFF format is a fully portable format which can be displayed, edited and converted by lots of utilities and all major image editors on all computer platforms.

Some of the TIFF files produced by the model are multiple frame TIFF files. This means that a sequence of images is stored in a single file (e.g. the distribution of prey biomass at each day). Multiple frame TIFF files can be converted into a movie which can be embedded into a Powerpoint presentation. On a PC the conversion into an AVI file can be handled by the Animation Shop which is part of Paint Shop Pro ([www.jasc.com](http://www.jasc.com)). On a Macintosh the shareware program GraphicConverter ([www.lemkesoft.com](http://www.lemkesoft.com)) and the freeware program NIH-image ([rsb.info.nih.gov/ni-image/](http://rsb.info.nih.gov/ni-image/)) can do the conversion to a Quicktime movie.

Module Output uses module Mudflats information required in map construction.

### 2.1.7 Tides

Contains the tidal data, subroutines to read them from file and subroutines for the calculation of the exposure status of a given spot at a given time. The tidal data used for the Oosterschelde are a list of times and levels for each high tide and low tide, together with some statistical parameters for the calculation of exposure time as a function of spot height and the low tide level (see Section 2.4).

### 2.1.8 Weather

Stores the minimum and maximum temperatures for each day of the simulated period. A temperature reconstruction subroutine (Goudriaan & van Laar, 1994, Listing 3.3) uses these data for constructing a sinusoidal temperature course during the day and an exponential decrease during the night. The energy requirement of the birds is calculated using this reconstructed temperature curves in order to account for the effect of the short day length during the winter.

## 2.2 The actual simulation model

The simulation model contains the actual foraging model. The model uses the above listed modules for about everything: for abiotic inputs, for the number of birds present, for calculating a bird distribution and food intake rate, for fishing, etc.

The birds in several areas (cf. Oosterschelde Noord, Oosterschelde Midden, etc.) can be simulated simultaneously. A weather station and a tidal station are then specified for each area separately. The birds in each area feed on the prey types available in that area. Hence, the simulations are independent but are carried out simultaneously.

The simultaneous simulation of the various areas allows us to implement forms of interaction between the areas. One of the fishing options, for instance, is to tell the program it should fish a certain amount without specifying where. In that case the fishing routine decides where the fishing takes place (at the richest spots). This is important since the food reservation takes place for the Oosterschelde or Wadden Sea as a whole, whereas the tidal movements of the birds takes place within the various areas.

A simulation run starts with the creation of data structures for the various areas. Modules are initialized which implies that spot data, tidal data, weather data and bird numbers are read from input files (e.g. Chapter 3). The model parameters listed in the Chapters 5, 6 and 7 are read. Finally the state variables of the simulation model are initialized. These are bird weight and stomach content, and the amount and weights of the prey types present at each spot.

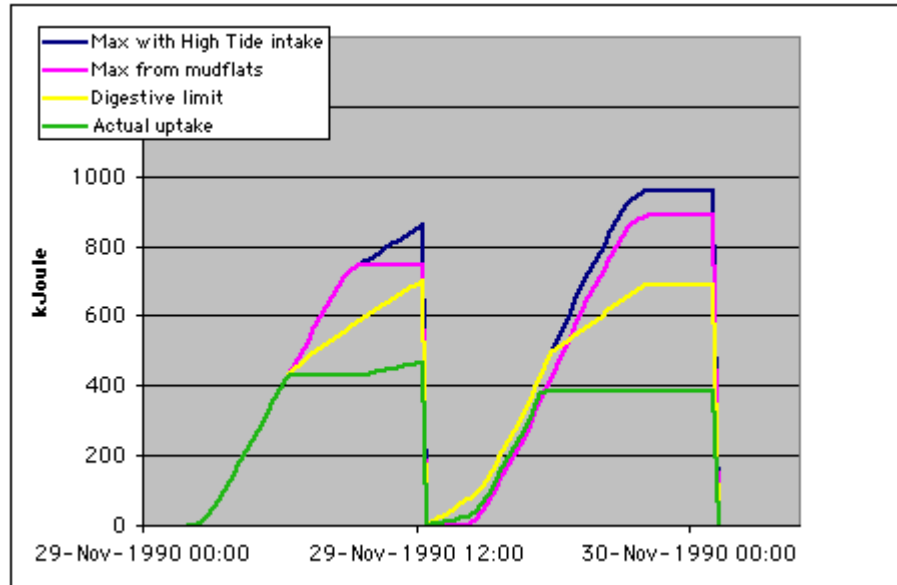
## 2.3 Simulation of a tidal cycle

### 2.3.1 Mudflat foraging

Each time step module Tides is called to get the exposure status of all mudflat spots assigned to an area (cf. Oosterschelde West). If spots are exposed the birds are distributed over the area, initially using an ideal free distribution. This distribution maximizes the intake rate of the birds assuming all birds are equal and have perfect knowledge of the food situation at all spots.

The distribution of the birds is based on the functional response and the degree of interference. Using these functions (cf. Sections 5.5 and 5.11) the ideal free

distribution is calculated for the exposed spots. The intake rate resulting from this calculation is called the *potential intake rate*. Its integral is an increasing amount, the *potential intake*. The curve “Max from mudflats” in Figure 2.2 shows the potential intake for two successive tidal cycles in 1990. At the beginning of the low tide periods the curves go up slowly, since just a few spots are exposed and the intake rate is relatively low. The same happens towards the end of the low tide period and during high tide the curve is horizontal (no uptake).



**Figure 2.2.** *Potential and reduced intakes for a diurnal and nocturnal low tide period. The actual energy uptake in these periods equals the required amount per low tide period. Note that daily amounts are a factor 1.932 larger (cf. Figure 5.1), which is the average number of tidal periods per day (cf. Section sec:TidesPerDay). Note for readers of the printed version: the lines in the legend are in the same order as in the left hand part of the graph.*

The potential intake may be reduced as a result of the following circumstances:

- the birds stomach is full (Section 5.3) and the intake rate is reduced to the maximum digestion rate. In case of high water levels and short exposure times this reduction may limit the food uptake. The curve “Digestive limit” in Figure 2.2 shows the reduced intake.
- the energy goal (Section 5.2) for the current tidal period has been achieved and the intake rate is reduced to zero. Intake is then equal to the energetic requirement, unless there is food shortage. The curve “Actual uptake” in Figure 2.2 shows the actual intake.

The calculations are repeated each time step. Under normal circumstances the two reduction steps listed above take place and the actual intake lies considerably below the potential intake. The distance between potential intake and energetic requirements becomes smaller or even negative due to

- cold weather with a higher energetic requirement (Figure 5.1)
- a low potential intake rate due to a low food density (Section 5.5)
- a short foraging period due to a high low tide water level (Section 2.4)

In these situations the required amount of energy may approach or exceed the potential intake. The ratio between the actual intake and the potential intake is defined in Section 2.3.4 as the foraging intensity. Since the cumulative intake increases linearly with time over a large part of the low tide period, the foraging intensity may be interpreted as the fraction of available foraging time the birds have to use in order to meet their energy requirements.

### 2.3.2 Reduced intake rate distribution

If the foraging time required is less than the available time, the birds may distribute themselves over a larger number of spots and use also spots which are otherwise marginal. In the program this works as follows:

At the beginning of a low tide period the (ideal free) intake rate may exceed the digestion rate for at least a time interval `RIROffsetTime`.

Then the amount of time available for foraging is estimated from the last two completed tidal cycles.

The required (and not yet realized) food intake is equally distributed over the remaining part of the low tide period.

The birds are distributed over all spots where this reduced intake rate can be realized. Bird densities are taken proportional to the distribution of the maximum number of birds that could feed at the required rate on these spots.

The parameter settings controlling this are given on the model parameter input file as

```
! Reduced intake rate during "Above Digestion Rate" time window
RIRandSpread = .true.      ! reduce intake rate and spread birds
RIROffsetTime = 1.0        ! (hour) time offset after reaching ADR time window
```

The first parameter enables or disables the entire mechanism. The second parameter sets the time interval used. If the model switches to a reduced intake rate distribution, the curve for “actual uptake” in Figure 2.2 is gradually rising to precisely the same end level as reached in a much shorter time with an ideal free distribution. The calculation of the foraging intensity is unaffected.

### 2.3.3 High tide foraging

On top of the potential intake in Figure 2.2 (the curve named “Max from mudflats”) there is a contribution from foraging during high tide. The potential rate of high tide foraging is reached if all birds use the grasslands as long as they cannot use the mudflats. This happens only if their regular prey are either not there or not exposed.

Therefore, in the model, the degree at which *the average bird* uses the grassland is a function of the foraging intensity during the previous two tidal cycles. Above a threshold value (parameter `NonMudThreshold` in Section 5.12) an increasing fraction of the birds is supposed to use grasslands for additional foraging and the high tide intake rate of the *average bird* gradually increases to the potential grassland

intake rate `MaxNonMudIntakeRateAFDW` which is reached for the maximum foraging intensity of 1.0.

During the first tidal period in Figure 2.2, the actual intake (the lowest curve) shows a small increase during high tide due to some high tide foraging. Note that this high tide foraging contributes to the energy intake even though the energy requirements were already met. At the beginning of the next cycle (around 12:00 pm) there is also some high tide intake. During the nocturnal high tide, however, no foraging takes place since birds do not use grassland in the night.

Also during periods with temperatures below 0°C there is no grassland foraging since the soil freezes. Therefore the contribution of high tide foraging to the food requirements of the average Oystercatcher in coastal wintering areas is a minor one, also in the model.

### 2.3.4 The Foraging Intensity

The ratio between the actual intake at the end of the tidal period and the potential (non-reduced) mudflat intake is called the **Foraging Intensity**. It is a measure of the workload of the animals for the tidal period that has just passed. The foraging intensity is approximately equal to the fraction of available time actually spent foraging *by the average bird*. A fraction of time, however, is hard to define precisely since begin and the end of the low tide period are somewhat arbitrary.

Even if there is plenty of food available, the birds still need some time to handle their prey. For profitable cockles or mussels in september the foraging intensity amounts to about 0.25. As prey species lose weight during the winter more have to be eaten for the same energetic intake and the foraging intensity slowly increases during the winter. If the prey density is low, searching takes time and the potential intake decreases, thus leading to a higher foraging intensity. Finally, if mudflat exposure time is reduced, the potential intake is reduced as well and again the foraging intensity will be higher.

Hence, the foraging intensity is the ratio of what the birds eat and what they could eat from the mudflats if stomach size would not be limiting. It should be emphasized that this intensity measure refers to the average bird. A value of 1 means that *all* birds are in trouble and a lower value supposedly implies that a certain (small or very small) fraction of the birds (e.g. the subdominant ones) cannot meet its energy requirements or is getting in a bad condition. The interpretation of the foraging intensities is further discussed in Chapter 4, where the intensities for all tidal cycles are summarized into a single number, the stress index.

### 2.3.5 High tide

The tidal cycle ends at high tide. At high tide the model generates a so called time event at which the simulation is halted and a special section of the model is executed. The foraging intensity for the tidal period passed is calculated and the energy balance of the birds is translated into a weight loss or a weight gain.

The energy requirement  $E_2$  for the next tidal cycle is calculated by integrating the function in Figure 5.1 to the next high tide time. Further, the current bird weight

is compared to the prescribed weight curve for the region, Oosterschelde or Wadden Sea (Zwarts *et al.*, 1996c), and the difference is converted into an increase or decrease of the energetic requirement for the next tidal period.

Temperature differences between day and night, differences between the two daily tidal periods and the possibility of high tide foraging in grassland during the day may lead to loss of bird weight during the night and a compensating weight gain during the day. Some measures are taken to prevent such oscillations from happening:

The energetic requirement used in setting the intake goal for the next tidal period is the average of  $E_1$  for the previous cycle and the just calculated  $E_2$  for the next cycle. Hence, the “model birds” regulate their food intake on the basis of a daily (or actually a two-tides) average.

A small energy gain is not immediately converted into body weight but first stored “as kiloJoules”. This is probably what also happens in reality. The liver buffers small differences between intake and expenses in the form of easily convertible glycogen. This prevents losses associated with energy conversion to and from structural body weight.

### 2.3.6 Fishing

The fishing which takes place in the model is carried out during the first high tide at a specific date, usually set to 1 October. Hence, if this date has been reached, the fishing routine is called. Fishing results in a change in prey amount and prey distribution over the various spots. No other effects on the birds or on food availability are accounted for.

The fishing in the model depends on two types of input.

- The distribution of fishing over the various spots is derived from the black box data and read from file “FishedAreaFile” (cf. Section 3.1.1).
- The total amount fished per area are read from file “POFishedFile” (cf. Section 3.1.1).

The most straightforward way of implementing fishing in the model is to remove prey according to the fished fractions derived from the black box data. Due to errors in the prey survey and in the actual fished fraction, the total amount fished, however, will not be equal to landed amount. Various solutions for this problem are discussed in Chapter 7 together with the parameter settings required.

### 2.3.7 High tide output

The most important output file produced by the model is named “HighTideYYYY.out”, where “YYYY” stands for the year in which the simulation began. At the end of each tidal cycle a record is written to this file containing number of birds, bird weight, foraging intensity and amount of prey left (See also Chapter 3).

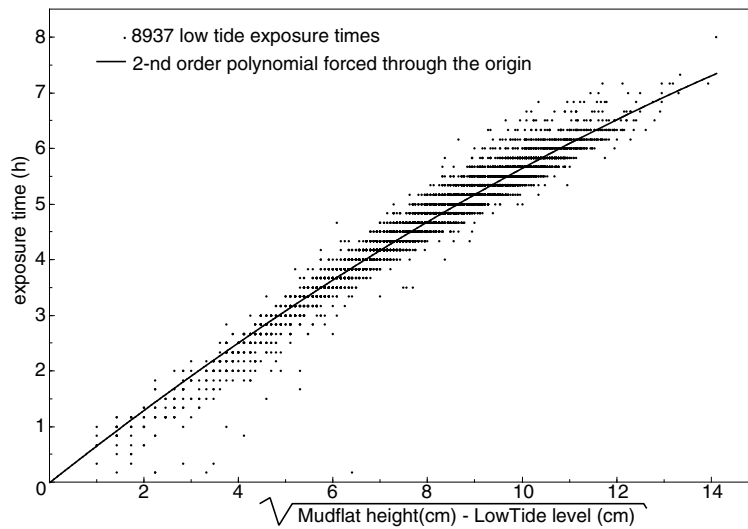
The high tide output concludes the tidal cycle. Tidal intake variables are reset and a new cycle begins.



## 2.4 Mudflat Exposure

Mudflat exposure time is a key element of the model. A tidal station is assigned to each area (e.g. Oosterschelde Noord, Oosterschelde West) in order to account for the variation in exposure time.

The easiest way to use the historical tidal data would be to compare the tidal water level at a particular moment with the height of the spot. The spot is exposed if its height exceeds the water level. This attractively simple procedure does not make use of the maps of average exposure time prepared by the RIKZ. These maps take into account different tidal stations in the region and have been prepared also for 2010 on the basis of expected changes in the region. The maps, however, deliver only the average exposure time. This problem has been solved in the following way.



**Figure 2.3.** *Historical exposure times of a mudflat spot at  $-50$  cm at the location of the tidal station Roompot Binnen. The exposure times have been plotted as function of the difference between the mudflat height ( $-50$  cm) and the low tide level. From the regression line an exposure time can be derived for any given low tide level. Regression line as these were calculated for a wide range of mudflat heights and the regression parameters themselves are somewhat dependent on spot height.*

### 2.4.1 step 1

The historical data of the tidal station associated with the area are analysed. For a certain mudflat height there is a relation between the exposure time and the low tide water level. A lower low tide level leads to a larger exposure time. Figure 2.3 shows such a relation for the station “Roompot Binnen” and a height of  $-50$  cm. Clearly, the use of only the low tide level in explaining the variation in exposure time represents a simplification. Lunar phase and wind would probably explain most of the remaining variability. For the birds, however, the short exposure times of especially somewhat lower parts of the mudflats are an important factor. These are represented very well by this method.

### 2.4.2 step 2

Using the relations shown in Figure 2.3 for a series of heights, the model only requires low tide water levels and the heights of all mudflat spots. The full historical record need not to be entered into the simulation model. Still, however, the information from exposure time maps cannot be used. This requires an additional step.

### 2.4.3 step 3

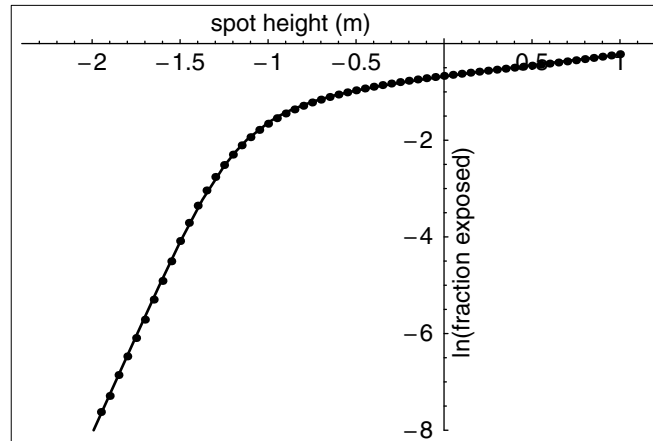
For each tidal station (e.g. Roompot Binnen) a relation exists between the mudflat height  $H$  and the *average* fraction of time it is exposed  $\overline{FE}$ . This relation is described very well by the following regression model.

$$\overline{FE}(H) = \text{Exp} \left[ e + f H + d \left( \frac{\left( \frac{a+H}{c} \right)^b}{1 + \left( \frac{a+H}{c} \right)^b} \right)^{\frac{1}{b}} \right], \quad (2.1)$$

where  $a, b, c, d, e$  and  $f$  are regression coefficients. The model is valid for spot heights  $H > -a$ . For the tidal station Roompot Binnen the fitted function is (with  $H$  in meters)

$$\overline{FE}(H) = \text{Exp} \left[ -7.21 + 0.427 H + 7.63 \left( \frac{(2 + H)^{4.57}}{1 + 1.99 (2 + H)^{4.57}} \right)^{0.219} \right], \quad (2.2)$$

for which Figure 2.4 shows a graph. Using this relation any average exposure time for a certain spot (e.g. read from a RIKZ map) can be converted into an *effective* spot height. This spot height, in combination with the historical low tide levels for the station will result in the desired variation of exposure times while at the same time the *average exposure time* remains equal to the one that was read from the map.



**Figure 2.4.** Graph of the mean exposed time fraction as function of spot height (m) derived for the Roompot Binnen tidal data with height intervals of 5 cm. The regression line is given in Equation (2.2).

As a bonus, the spatial interpolation between tidal stations which is used in constructing exposure time maps is implicitly present in the model, although only a

single tidal station per area is used. The tidal station is used only for generating the variability in exposure time. The average value is read from one of the available maps. For the historical runs this average exposure time is calculated as a time-interpolated value between the various maps available.

#### 2.4.4 step 4

All the above calculations can be done outside the model or before the simulation actually starts. During the simulation the effective spot height is compared with the low tide level for a given tidal period. The resulting exposure time is assumed to lie around the time of low tide. This means that for a given time (reached by the simulation) the exposure status can be determined.

#### 2.4.5 Exposure time and Average Exposed fraction

Fractions of time exposed have been converted to hours exposed by means of the average length of a tidal cycle of 12.42 h.

This number can be calculated from the lunar orbit time  $O_m$  of 2360550 s and the earth sidereal period  $T_e$  of 86164.06 s ([Anonymous, 1990](#)). The number of tides in a solar day (86400 s) is

$$86400 \times \left( \frac{2}{T_e} - \frac{2}{O_m} \right) = 1.9322, \quad (2.3)$$

which is indeed close to the well known ratio of 27 tidal cycles in 14 days ( $27/14 = 1.929$ ).

## 2.5 Mussels

Mussel beds exposed during low tide have largely disappeared from the Oosterschelde region. Furthermore, in the early nineties the beds were not part of the yearly prey survey. This forms a difficulty in attempting to estimate the importance of Mussels as food for Oystercatchers. The only information available is a list of tons and a map of the location of the Mussel beds. Also for the Wadden Sea there is little information on exposed mussel banks in the early nineties.

Fortunately, Mussel beds and Mussel banks are usually not significantly depleted by the birds ([Goss-Custard \*et al.\*, 2001](#)). The food density is high and interference tends to limit the density of the birds feeding on Mussels. Therefore, a surface area, an amount of Mussels and an exposure time is sufficient information to include Mussels in the *WEBTICS* model.

### 2.5.1 Virtual Mussel spots

The Mussel beds are treated in the model as “virtual foraging spots”. They do not have a location like the prey survey spots with Cockles and *Macoma*, but they only

have a surface area, an amount of Mussels, and an exposure time. In the model, part of the birds will feed on these virtual Mussel beds. These birds do not appear then on the BirdDensity output maps (Section 3.5.4). By means of the control variable `AddMusselSpots` the Mussel spots can be included in the calculations or not (cf. Section 3.1.3).

However, the type of data available differs between the Oosterschelde and Wadden Sea regions. The model has been adapted accordingly. The adaptations have been implemented by means of the variable `RegionName` (see Section 3.3 by which the program chooses between the various possibilities. This prevents maintaining different versions of the program code.

### Oosterschelde Mussel beds

The Mussel input files used for the Oosterschelde region contain for each Oosterschelde area the Mussel bed surface area and an indication of the exposure time through spot ID numbers from the spot information file (cf. Table 3.5 in Section 3.4.3). These spot ID are used only for the calculation of an exposure time. The spots have been chosen by mapping some prey survey spots on the locations of the old Mussel beds. An examples of a Mussel input file can be found in Section 3.4.8.

### Wadden Sea Mussel beds

The Mussel input file used for the Wadden Sea region contains for each Wadden Sea area the quantity and the surface area for three ages classes of Mussels and a distribution over a number of exposure time classes. Using these input data the model creates virtual spots with the appropriate prey weight, prey numbers, surface area and exposure time. An example can be found in Section 3.4.9.

## 2.6 Modelling environment

*WEBTICS* has been written as a simulation model for the Fortran Simulation Environment FSE (van Kraalingen, 1995; Rappoldt & van Kraalingen, 2001). This environment organizes the simulation by calling the model for rates of change, integration, output, high tide events etc. Both the FSE environment and the model itself make extensive use of TTUTIL input and output procedures documented in van Kraalingen & Rappoldt (2000) and some numerical procedures described in Press *et al.* (1992), which is available as a (downloadable) commercial product.

## 2.7 Program Size of *WEBTICS*

The core of the program, the tidal foraging model and the high tide calculations on foraging intensity and body weight require about 300 lines of code. The complete *WEBTICS* program, including the various modules belonging to it, consists of about 8000 lines of heavily commented Fortran 95 code. The FSE environment and

linked utilities consist of another 30000 lines of Fortran code, both Fortran 77 and Fortran 95.



## Chapter 3

# Input and Output files

### 3.1 The Control File

There is one input file which has to be present on the directory of the running program, file “control.dat” (Table 3.1). This file contains settings for the run, names of the datafiles, options for using maps, etc. Note that most settings are also documented in the file itself.

The control file is a “TTUTIL” input file (van Kraalingen & Rappoldt, 2000), which means that all items consist of an identifier (a “name”) and a value which may be a character string, an integer variable, floating point value, date-time string or a logical. Both single values and arrays occur. Below, the important settings are briefly discussed.

#### 3.1.1 Filenames

The input and output directory are specified. The output directory should exist ; it is not created by the program. Then the names of the input files are specified.

```
DataDir      = 'OSdata'
ResultsDir   = 'TestResults'
ModelDataFile = 'KOKKEL.DAT'      ! model parameters
AreaList     = 'AreaInformation'  ! list of areas and stations
SpotInfoFile = 'SpotinfoOSBevMgr4' ! spots
PreySurvey   = 'PreySurveyOS2'
BirdCountFile = 'ScholekstersOS'
FishedAreaFile = 'SpotBevistInformationOS' ! black box data
POFishedFile  = 'TotalFished'
```

#### 3.1.2 Movie settings

Movie output is time consuming and may be suppressed. Each spot is represented by a square with size `SpotSizePixels` from of which a part (with size `SpotFillPixels`) is actually painted.

```
Movies = .false.
```

**Table 3.1.** First part of control file. Some variables have a trivial function (e.g. Machine or Movies). The important *W&BTICS* variables are explained in Section 3.1. Some variables belonging to the simulation environment have been documented in [Rappoldt & van Kraalingen \(2001\)](#).

```

Controller = 'StandardControl'
Machine    = 'PC' ! (or 'Macintosh')
DataDir    = 'WaddenzeeData'
ResultsDir = 'TestResults'
ResultsFile = 'Outdat.out'
Movies     = .true.
NRespDays  = 1*0

AddMusselSpots = .false.

AreaList      = 'AreaInformation'
SpotInfoFile  = 'AbiotiekTotaal2'
PreySurvey    = 'PreySurveyWad'
BirdCountFile = 'ScholekstersImpute2'
FishedAreaFile = 'BevistIndexMgr'
POFishedFile  = 'VangstperWaddeelgebied'
MusselAmounts = 'MosselAmounts'
MusselSpotInfo = 'MosselSpots'

RemainderFile = 'RemainingPrey'
AutumnStart = 1 ; WinterStart = 178
AutumnEnd   = 177 ; WinterEnd   = 350

! variable      C O U P L E D   M O D E L S
! =====
ModelName       = 'Kokkels'
Integrator      = 'FSE'
ModelDataFile   = 'KOKKEL.DAT'
IntegSettFile   = 'Control.dat'
NrOfInstances   = 1 ! overwritten by AreaCount
WithModelEvent  = .true.
WithInstEvent   = .true.
. . .

```

```

SpotSizePixels = 5      ! pixels
SpotFillPixels = 4      ! pixels

```

### 3.1.3 Mussel settings

These variables specify the Mussel input files for the model. Depending on the region for which the model is used the content of these files is different (see Sections 2.5, 3.4.8, 3.4.9).

```

AddMusselSpots = .true.      ! add virtual mussel spots ?
MusselAmounts  = 'MosselAmounts' ! input file
MusselSpotInfo = 'MosselSpots'  ! input file

```



### 3.1.4 Timing

The timing of the model is organized by means of the following variables. The start time and finish time are in arbitrary units, but the variable “OneDay” tells the program that the unit of time is “day”. The variables “WinterStart” and “WinterEnd”, etc. are used in the stress index calculation.

```
ShellStartTime      = 0.0
ShellFinishTime     = 212.0

! integration step
DeltFSE = 0.0104166667 ! this value is 15 minutes

OneDay   = 1.0          ! one day in user time units, e.g. 1.0 or 86400.0
StartYear = 1990        ! the start year of the simulation
StartDOY  = 244.0       ! Day Of Year beginning from 1.00000
                        ! note that the time specified by StartYear and
                        ! StartDOY is associated with ShellStartTime.

AutumnStart = 1 ; WinterStart = 178 ! tides after model start
AutumnEnd   = 177 ; WinterEnd   = 325 ! tides after model start
```

### 3.1.5 Maximum number of lines on HighTide output

This maximizes the number of output lines per area on the HighTide output file, which is convenient in case the file is loaded in a spreadsheet.

```
MaxOutputLines = 407 ! this standardizes spreadsheet output blocks
```

### 3.1.6 Maps of Height and Exposure time

The information on spots height and exposure time on the Spot Information file (variable “SpotInforFile” in Section 3.1.1) contains readings from several maps. The variables “HeightMapDates” and “DVTMapDates” specify the years to which these maps refer. With the switch “FixedHeight” the usual time-interpolation between the maps can be switched off and replaced by a fixed date (independent of the start year). The option “UseFETmapForTides” should be set true if the exposure times of the map(s) should be converted in effective heights (cf. Section 2.4).

```
HeightMapDates = 1-jul-1989, 1-jul-1994, 1-jul-2001, 1-jul-2010
DVTMapDates    = 1-jul-1983, 1-jul-1989, 1-jul-2001, 1-jul-2010
FixedHeight    = .false.
FixedHeightDate = 1-Sep-1983
UseFETmapForTides = .true. ! use ‘effective heights’
```

### 3.1.7 Bird number options

The switch “NumberFromCounts” is usually true. If false a fixed number of birds is read for each area from the AreaInfoFile (Section 3.1.1). Just as for the exposure times, also here the bird number season can be fixed at “BirdNumberSeason” in order to use bird numbers of a certain year in combination with the prey and abiotic data from a different year. Finally, the number of birds can be multiplied by a factor. This is used in calculations for the evaluation of fishing.

```

NumberFromCounts = .true.      ! number of birds option
                                ! .true. => number from counts on file
                                ! .false. => fixed number from
                                ! AreaInformation file
BirdNumberSeasonFixed = .false. ! .true. => use BirdNumberYear for counts
                                ! .false. => historical data over the years
BirdNumberSeason = 2001       ! the year used
                                ! (no effect if NumberFromCounts = .false.)
BirdNumberMultiplier = 1.000  ! multiplies the number of birds (1.352)

```

### 3.1.8 Fishing EVA-luation options

The flag “EVAFishing” is used to switch between normal (historical) fishing (see Section 2.3.6 and Chapter 7) and special fishing for evaluation of the fished amount.

The first thing to do if fishing is evaluated is choose the year of the prey survey with flag “EVAsurveyYearFixed” and year “EVAsurveyYear”. Then there are two ways to proceed:

**EVAasOneArea = .false.** The PO fished amounts per area for “StartYear” (see Section 3.1.4) are used after multiplying them with “EVAmultiplier”.

**EVAasOneArea = .true.** A total amount “EVAfishedTons” is fished for all areas lumped. The distribution of this amount over the various areas is done by the model.

For both options the variable “EVAfishedFraction” replaces the black box fished area fractions and all prey survey data are multiplied by “EVApreyMultiplier”, which may be used to account for uncertainties in the prey survey.

```

EVAFishing      = .true.      ! .true. => force AutoDistribute ;
                                ! use EVAmultiplier if EVAasOneArea OFF
                                ! use EVAfishedTons if EVAasOneArea ON
                                ! .false. => normal fishing
EVAsurveyYearFixed = .true. ! .true. => use EVAsurveyYear for preys
                                ! .false. => historical data over the years
EVAsurveyYear = 2001       ! the year used
EVAasOneArea  = .true.      ! .true. => all area's are fished as a
                                ! single one tons are set to
                                ! EVAfishedTons
                                ! .false. => EVAmultiplier is used on
                                ! PO-data from file
EVAmultiplier = 0.0         ! multiply PO-fished amounts
                                ! in case EVAFishing is ON
                                ! == only used if EVAasOneArea is OFF ==
EVAfishedTons = 5000.0      ! tons used if EVAasOneArea ON
                                ! Note that open areas are all areas with
                                ! SOME PO amount specified (even if the
                                ! amounts is overwritten by EVAfishedTons)
EVAfishedFraction = 0.5     ! smaller means that fewer spots will be
                                ! affected by LEVELOFF fishing
EVApreyMultiplier = 0.8     ! multiplies the RIVO prey survey
                                ! (only in case of EVA fishing)

```

## 3.2 The model parameter file

The model parameter file, with name specified by variable `ModelDataFile` on the control file (see Section 3.1.1), is discussed in the Chapters 5, 6 and 7. The model parameter file used in the historical runs can be found in Appendix B.

## 3.3 Area information file

The name of the area information file is specified by variable `AreaList` on the control file (see Section 3.1.1). Table 3.2 shows the file used for Oosterschelde calculations.

The file shows that the “Oosterschelde” region is subdivided into four areas. For each area a tidal station, a weather station and a number of birds is specified (which is used only if the control variable `NumberFromCounts` is set `.false.` (cf. Section 3.1.7).

**Table 3.2.** *Area information file (cf. Section 3.3)*

```
RegionName = 'Oosterschelde'

AreaName TidalStation WeatherStation NumberOfBirds
'OSW'    'Roompot'    'Vlissingen'    20000.0
'OSN'    'Yerseke'    'Vlissingen'    20000.0
'OSC'    'Yerseke'    'Vlissingen'    20000.0
'OSO'    'Yerseke'    'Vlissingen'    20000.0

AddLumpedArea      = .true.
LumpedTidalStation = 'Yerseke'
LumpedWeatherStation = 'Vlissingen'

! NOTE: number of birds is used if the "fixed number option"
!       is switched on by setting NumberFromCounts = .false.
!       in the control file.
```

As an option, the model may combine all spots into an additional area which spans the entire region. The birds in this “lumped area” make use of the entire region and do not stay in “their” area. The simulation of the lumped area is independent of the (simultaneous) calculations for the separate areas. The addition of a lumped area doubles the computing time, however.

## 3.4 Data base input

The other files required are based on databases of the prey survey, weather, tides, etc. Also readings from height maps and exposure time maps is included in this section. The information is read by the program as ASCII files, however, that have been prepared from the original data bases and maps.

### 3.4.1 Tidal Stations

The tidal stations used are listed in the area information file (cf. Section 3.3). For each tidal station the program looks for a file “TidesName.txt” at the input directory. Table 3.3 is the first part of a tidal station input file.

Note that after a line <Begin> the file just contains a list of times and levels of all high and low tides. The list must cover the simulated time interval. For days or weeks lacking in the historical record for the station, data from a nearby station are inserted.

**Table 3.3.** *First part of a tidal station data file (cf. Section 3.4.1).*

```
! polynomial coefficients for calculating C1 and C2
! the formulae are
! C1 = SUM[PAR1(i+1)*x^i, i=0,Order1],
! C2 = SUM[PAR2(i+1)*x^i, i=0,Order2],
! where:

! Order1 - n1-1
! n1      - number of coefficients in PAR1 array
! Order2 - n2-1
! n2      - number of coefficients in PAR2 array
! x       - Mudflatlevel in === meter ===

! With C1 and C2 the Exposure time is calculated as
! ExpTime = C1 * h + C2 * h^2

! where:
! ExpTime - Exposure time in === hours ===
! h       - SQRT (Mudflatlevel - Lowtide) ; levels in ==== cm ====

PAR1 = 0.74052839, 0.069573394, -0.15252838, -0.046204134,
      0.043653669, 0.018099107

PAR2 = -0.013230165, -0.0016012231, 0.010249429, 0.0053860167,
      0.001127074

! See Mathematica file
ABCDEF = -2., 4.571952, 0.85984871, 6.5631016, -7.2139701, 0.42710487

! date      time    level  LH
<begin>
20-Dec-1989 02:30   -85.0  'L'
20-Dec-1989 08:40   120.0  'H'
20-Dec-1989 14:20  -122.0  'L'
20-Dec-1989 21:10   132.0  'H'
21-Dec-1989 02:40   -42.0  'L'
21-Dec-1989 08:50   148.0  'H'
21-Dec-1989 14:50   -65.0  'L'
21-Dec-1989 21:50   155.0  'H'
22-Dec-1989 04:20   -67.0  'L'
. . .
. . .
```

The header before <Begin> contains pre-calculated characteristics of the station which are used in exposure time calculations. As explained in Section 2.4 mudflat

exposure time is calculated with help of two regression coefficients  $C_1$  and  $C_2$ . These coefficients can be calculated for any mudflat height by using the terms of two pre-calculated polynomials which are given in the tidal input file as PAR1 and PAR2. The fitted coefficients of Equation (2.1) are supplied to the model as the six numbers of array ABCDEF.

### 3.4.2 Weather Stations

The weather stations used are listed in the area information file (cf. Section 3.3). For each weather station the program looks for a file “WeatherName.txt” at the input directory. Table 3.4 shows the first part of a weather input file.

**Table 3.4.** *First part of a weather station data file (cf. Section 3.4.2).*

```
! weather station info:
! =====
Latitude   = 50.0   ;   Longitude = 5.0

! Vlissingen data 1980-2002
! =====
! datum TMIN TMAX Wind
<begin>
1-jan-1980  11  44  51
2-jan-1980  11  45  31
3-jan-1980   5  26  67
4-jan-1980  13  56  93
5-jan-1980  34  64  67
6-jan-1980  47  63  62
7-jan-1980  32  60  31
. . .
```

The header of the file (the part before <Begin>) contains the latitude and longitude which are used in constructing sinusoidal temperature course during the day and an exponential decrease during the night according to Goudriaan & van Laar (1994, Listing 3.3).

The remainder of the file is just a list of minimum and maximum daily temperatures (in tens of degrees) and average wind speed which is currently not used. Clearly, the list must cover the simulated time interval. For days or weeks lacking in the historical record for the station, data from a nearby station have been inserted.

### 3.4.3 Spot information

The name of the spot information file is specified by variable **SpotInfoFile** on the control file (see Section 3.1.1). Table 3.5 shows an example.

The coordinates should be in metre in *some* rectangular coordinate system. The surface area (in m<sup>2</sup>) is used to calculate total quantities of prey in combination with the prey densities from the prey survey (Section 3.4.4). The coordinates are only used for the construction of simple maps (Sections 2.1.6 and 3.5.3).

The heights and exposure times are readings from the available maps. The heights

**Table 3.5.** *The spot information file contains for each spot a unique identification number, the name of the area where it belong to, surface area, coordinates and map readings for height and exposure time (cf. Section 3.4.3). The spot numbers and area names need not to be sorted.*

```

! spotID - spot identification
! Area   - name of area spot belongs to
! Surface - surface area in m2
! X, Y   - coodinates (m) in rectangular system
!
! spotID Area Surface X Y Heights and Exposure times
15019,OSW,267503.58,39238.13,405253.48, -468.37,652,-383.08,675, ... 11.65, 176
15020,OSW,267503.15,39815.09,405240.28, -88.70,594,-124.71,647, ... 12.95, 484
15021,OSW,267527.21,40380.95,404759.79, -280.91,673,-263.42,667, ... 12.02, 290
15022,OSW,267478.23,40402.00,405686.61, -141.36,661,-144.14,657, ... 16.68, 655
15024,OSW,267429.25,40423.65,406617.59, -179.04,675,-165.73,672, ... 15.08, 402
15025,OSW,267502.29,40968.42,405210.13, -151.10,674,-150.94,667, ... 3.58, 556
15026,OSW,267477.80,40978.90,405673.54, -170.14,669,-163.02,675, ... 6.37, 675
15027,OSW,267453.31,40989.37,406136.95, -57.35,672,-54.12,664, ... 38.75, 664
. . .
. . .

```

in the example of Table 3.5 are in cm, followed by a count (the number of map “pixels” falling in the spot area) and the exposure times are fractional, i.e. fractions of total time, also followed by a count. The reference dates belonging to the various maps are given in the control file (Section 3.1.6). Details of the map readings and the subsequent handling of heights and exposure times differ between regions for which the model is used. Small adaptations in the program may be required in case of application to a new region.

### 3.4.4 Prey survey

The name of the prey survey file is specified by variable **PreySurvey** on the control file (see Section 3.1.1). Table 3.6 shows an example. The spots are identified using their ID numbers from the spot information file (Table 3.5 in Section 3.4.3). Note that the file need not be sorted and may contain observations for spots outside the areas for which the model is running.

### 3.4.5 Monthly Bird numbers

The name of the file with bird counts is specified by variable **BirdCountFile** on the control file (see Section 3.1.1). The file (e.g. Table 3.7) contains a sorted list of monthly oystercatcher counts. The records for which the area names match a name in the Area information file (Section 3.3) are used.

### 3.4.6 Black Box fished area

The name of the file with fished area fractions is specified by variable **FishedAreaFile** on the control file (see Section 3.1.1). Table 3.8 gives an example. The file contains

**Table 3.6.** The prey survey file (Section 3.4.4) contains prey information for spots identified using their ID number (cf. Section 3.4.3). Each record contains a year, a species name, a species age class and prey density ( $\text{m}^{-2}$ ) and biomass ( $\text{g m}^{-2}$ ) for May,1 and September,1. ‘Kokkel’ is Cockle *Cerastoderma edule* and ‘Non’ is *Macoma balthica*. The prey types or spot ID’s need not to be sorted. Note that for *Macoma* the september numbers are lacking.

! StationID	Jaar	Species	Age	NMayM2	BMayM2	NSeptM2	BSeptM2
15018	2001	'Kokkel'	'nb'	0.00	0.00	0.00	0.00
15019	1992	'Kokkel'	'1j'	70.00	248.07	51.91	398.73
15019	1997	'Kokkel'	'0j'	20.00	19.59	5.73	23.43
15019	2001	'Kokkel'	'nb'	0.00	0.00	0.00	0.00
15020	1996	'Kokkel'	'0j'	10.00	8.64	3.93	13.18
15020	2001	'Kokkel'	'nb'	0.00	0.00	0.00	0.00
15021	1990	'Kokkel'	'mj'	10.00	150.89	7.23	118.04
15021	1994	'Kokkel'	'mj'	10.00	231.54	7.55	166.26
15021	1994	'Kokkel'	'1j'	10.00	47.52	7.55	65.67
15021	1996	'Kokkel'	'1j'	10.00	17.01	7.61	41.55
15021	2001	'Kokkel'	'nb'	0.00	0.00	0.00	0.00
15022	1990	'Kokkel'	'mj'	50.00	602.82	36.19	496.56
15022	2001	'Kokkel'	'nb'	0.00	0.00	0.00	0.00
15023	2001	'Kokkel'	'nb'	0.00	0.00	0.00	0.00
15024	1991	'Kokkel'	'mj'	10.00	59.91	7.08	57.67
15024	1991	'Non'	'nb'	20.00	16.00	-9999.00	-9999.00
15024	1993	'Kokkel'	'mj'	10.00	128.20	8.10	106.86
15024	2000	'Non'	'nb'	9.80	4.90	-9999.00	-9999.00
15024	2001	'Kokkel'	'nb'	0.00	0.00	0.00	0.00
.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.

**Table 3.7.** File with bird sorted to Areaname, jaar and Maand (cf. Section 3.4.5).

Areaname	jaar	SEIZOEN	MAAND	NScholeksters
OSC	1978	1978	7	3617
OSC	1978	1978	8	19431
OSC	1978	1978	9	20375
OSC	1978	1978	10	19299
OSC	1978	1978	11	22589
OSC	1978	1978	12	14213
OSC	1979	1978	1	24253
OSC	1979	1978	2	43189
OSC	1979	1978	3	17973
OSC	1979	1978	4	7087
OSC	1979	1978	5	4336
OSC	1979	1978	6	1578
OSC	1979	1979	7	2241
.	.	.	.	.
.	.	.	.	.

the fished area estimated from the black box data. Note that area name and (surface) area are redundant. The values should be consistent with the spot information file (Section 3.4.3). This is verified.

**Table 3.8.** *Fished areas (Section 3.4.6) are specified per spot ID (cf. Section 3.4.3) and per year. The file contains for each spot also surface area and area name. These two numbers should be consistent with those given in the spot information file (Table 3.5 in Section 3.4.3).*

! stationID	year	Areaname	Area	SumOfBevistOppervalkte
15021,	1994,	'OSW',	267527.21,	2354.00
15022,	1992,	'OSW',	267478.23,	642.00
15025,	1994,	'OSW',	267502.29,	3852.00
15026,	1992,	'OSW',	267477.80,	1926.00
15026,	1994,	'OSW',	267477.80,	2568.00
15027,	1994,	'OSW',	267453.31,	66136.00
15028,	1994,	'OSW',	267428.82,	3852.00
15029,	1992,	'OSW',	267501.86,	95032.00
15029,	1994,	'OSW',	267501.86,	107877.00
15030,	1992,	'OSW',	267477.37,	11129.00
. . .				

**Table 3.9.** *The total amount fished is specified in tons fresh weight per area and per year. See text in Section 3.4.7.*

! based on file /Cees Rappoldt vangst vers.xls/					
! from Yerseke (in miljoen kg)					
! surface & ghostsurface from work by Elze (NOT currently used)					
! year	area	amount	surface	ghostsurface	
1990	, OSW	, 6.21	! open spots in all OS areas (90/91 adaptation)		
1991	, OSW	, 3.2	! open spots in all OS areas (90/91 adaptation)		
1992	, OSC	, 3.111953243	, 1715852,	59064	
1992	, OSO	, 2.67757829	, 1536734,	54998	
1992	, OSW	, 2.810470696	, 2059750,	33598	
1993	, OSC	, 1.139221369	, 1287210,	240322	
1993	, OSO	, 0.680780938	, 1017998,	115346	
1994	, OSC	, 4.340542897	, 3598410,	565174	
1994	, OSO	, 12.38560387	, 5420919,	719682	
1994	, OSW	, 5.393866486	, 4265464,	332128	
1995	, OSC	, 4.197914479	, 2999638,	145306	
1995	, OSO	, 2.112336074	, 1491794,	90308	
1995	, OSW	, 0.469752563	, 438914,	40018	
1996	, OSC	, 2.128898645	, 3188386,	105074	
1996	, OSO	, 1.244012893	, 2771514,	233902	
1996	, OSW	, 2.253761809	, 4473028,	101008	
2001	, OSC	, 1.817024361	, 3171480,	125190	
2001	, OSW	, 5.022978531	, 4849391,	209078	

### 3.4.7 Total amount fished

The name of the file with total amount fished is specified by variable POFishedFile on the control file (see Section 3.1.1). As an example, the Oosterschelde file is given in Table 3.9.



Note that for 1990 and 1991 the “OSW” tons actually refer to the whole Oosterschelde region. This is dealt with in the program. The total columns “Surface” and “Ghost surface” are not currently used. Surface is the total area fished according to the black box data and is redundant (cf. Section 3.4.6). Ghost surface was defined as surface occurring in the black box data as being fished but not included in the prey survey sampling. The amount given, however, has been corrected already for fishing outside the mudflats.

### 3.4.8 Mussel spots Oosterschelde

The name of the file specifying the Mussel spots in the Oosterschelde region is specified by variable `MusselSpotInfo` on the control file (see also Section 3.1.3). Table 3.10 shows the virtual Mussel spots (Section 2.5.1) created for the Oosterschelde region.

The name of the file specifying the Mussel amount in the Oosterschelde region is specified by variable `MusselAmounts` on the control file (see Section 3.1.3). Table 3.11 shows the Mussel amount on the (virtual) Mussel spots in the Oosterschelde region. Note that the surface area is redundant. It is there to emphasize that only the Mussel densities (ratio between tons and area) are used from this file. The surface area column is checked against Table 3.10, however.

### 3.4.9 Mussel spots Wadden Sea

The name of the file specifying the virtual Mussel spots in the Wadden Sea region is given by variable `MusselSpotInfo` on the control file (see also Section 3.1.3). Table 3.12 shows part of an input file.

In the table legend the meaning of the various columns has been described. The data in Table 3.12 form an attempt to reconstruct the amount of mussels and the mussel bed surface areas in the nineties, also for years for which only little data is available. The total amount and surface area have been derived from spring and autumn data by the RIVO. The individual weights are averages from the mussel weights in the RIVO survey files containing also the cockle data. The exposed time fractions actually used are multiple year averages of data on the location of mussel beds.

For each combination of area, year, age class and exposed time fraction a virtual spot is created with the specified fraction of the surface area and mussel amount. The height of this spot is calculated from the desired average exposure time using the inverse of Equation (2.2) for the tidal station of the area where the mussel spot belongs to. Hence, the prescribed mussel bed exposure times are averages. The actual exposure time varies through the simulated season with the tide.

**Table 3.10.** *Virtual Mussel spots with area name year and surface area (cf. Section 2.5.1) created for the Oosterschelde region. The spot ID numbers in column “FETspotIDs” are used only to get exposure times for the created Mussel spots. If several spot ID’s are supplied an equal number of Mussel spots will be created with consecutive numbers. The surface area is then subdivided equally over exposure times derived from the spot ID’s.*

```
! Virtuele mosselspots ; het werkt als volgt
! kolom naam functie
! -----
! 1 SpotID nummer gebruikt in de voedsel file etc.
! 2 Area area name
! 3 Year year belonging to the surface info
! 3 Surface oppervlak in === ha ===
! 4 X, Y must be 0.0 in order NOT to appear on the maps
! 5 FETspotID Fractional Exposure Time reference SpotIDs

! The data in the reference SpotID are used for the FET only.
! If two or more spots are given, new spots with successive numbers
! are generated and the surface is divided equally among all spots.
!
! The height info of the reference spots is neglected. Spot height
! is calculated from an (interpolated) FET using the appropriate
! function for the tidal station belonging to the area.

! Data from Tabel 3.1 "Achtergrond Oosterschelde"

! SpotID Area Year Surface X Y FETspotIDs
! -----
80001 OSW 1988 30.0 0.0 0.0 15059 15060
80001 OSW 1989 54.0 0.0 0.0 15059 15060
80001 OSW 1990 159.0 0.0 0.0 15059 15060
80001 OSW 1991 25.0 0.0 0.0 15059 15060
80001 OSW 1992 26.0 0.0 0.0 15059 15060
80001 OSW 1993 26.0 0.0 0.0 15059 15060
80001 OSW 1994 0.6 0.0 0.0 15059 15060
80001 OSW 1995 0.5 0.0 0.0 15059 15060
80001 OSW 1996 1.0 0.0 0.0 15059 15060
80001 OSW 1998 0.6 0.0 0.0 15059 15060

80003 OSC 1988 331.0 0.0 0.0 15144 15143 15142 15164 15162 15163
80003 OSC 1989 123.0 0.0 0.0 15144 15143 15142 15164 15162 15163
80003 OSC 1990 371.0 0.0 0.0 15144 15143 15142 15164 15162 15163
80003 OSC 1991 76.0 0.0 0.0 15144 15143 15142 15164 15162 15163
80003 OSC 1992 318.0 0.0 0.0 15144 15143 15142 15164 15162 15163
80003 OSC 1994 70.0 0.0 0.0 15144 15143 15142 15164 15162 15163
80003 OSC 1995 30.0 0.0 0.0 15144 15143 15142 15164 15162 15163
80003 OSC 1996 13.0 0.0 0.0 15144 15143 15142 15164 15162 15163
80003 OSC 1998 2.1 0.0 0.0 15144 15143 15142 15164 15162 15163

80009 OSO 1990 239.0 0.0 0.0 15282 15233
80009 OSO 1992 133.0 0.0 0.0 15282 15233
80009 OSO 1993 53.0 0.0 0.0 15282 15233

80011 OSN 1988 40.0 0.0 0.0 15216 15416 15225 15437
80011 OSN 1989 15.0 0.0 0.0 15216 15416 15225 15437
80011 OSN 1991 49.0 0.0 0.0 15216 15416 15225 15437
80011 OSN 1993 26.0 0.0 0.0 15216 15416 15225 15437
80011 OSN 1995 1.4 0.0 0.0 15216 15416 15225 15437
```

**Table 3.11.** Part of file with Mussel densities on the virtual Mussel spots (cf. Section 2.5.1) created using the instructions of Table 3.10. Note that the tons (fresh weight) in column “Ton(FW)” have been taken directly from (Bult et al., 2000, Tabel 3.1). The surface area column is checked against Table 3.10.

```
! Virtuele mosselspots ; het werkt als volgt
! kolom naam functie
! -----
! 1 SpotID nummer gebruikt in de voedsel file etc.
! 2 Year year belonging to the mussel density info
! 3 Species should be Mossel
! 4 Age should be nb
! 5 Ton(FW) Tons fresh weight over all virtual spots
! 6 Surface Surface area in ha total of all virtual spots

! Kolom 5 and 6 together define a ratio, the mussel density
! The input program calculates this ratio. It is done in this
! way just o be able to copy the data from Tabel 3.1.

! Data from Tabel 3.1 "Achtergrond Oosterschelde"

! SpotID Year Species Age Ton(FW) / Surface(ha) ratio
! -----
80001 1988 Mossel nb 891 / 30.0
80001 1989 Mossel nb 1146 / 54.0
80001 1990 Mossel nb 6057 / 159.0
80001 1991 Mossel nb 506 / 25.0
80001 1992 Mossel nb 102 / 26.0
80001 1993 Mossel nb 2854 / 26.0
80001 1994 Mossel nb 152 / 0.6
80001 1995 Mossel nb 49 / 0.5
80001 1996 Mossel nb 127 / 1.0
80001 1998 Mossel nb 105 / 0.6

80002 1988 Mossel nb 891 / 30.0
80002 1989 Mossel nb 1146 / 54.0
80002 1990 Mossel nb 6057 / 159.0
80002 1991 Mossel nb 506 / 25.0
80002 1992 Mossel nb 102 / 26.0
80002 1993 Mossel nb 2854 / 26.0
. . .
```

**Table 3.12.** *Virtual Mussel spots (cf. Section 2.5.1) with area name, year and specifications for seed, “halfwas” and consumption mussels. Per area, per year and per age class an amount is given in millions of kg, an area in hectare and an individual fresh weight in gram. The total amount is then distributed over virtual spots with different exposure times according to 10 fractions given as a percentage. The 10 percentages are fractions of the surface area (and mussel amount) with exposed time fractions of [5%,15%,...85%,95%]. The first 10 fractions refer to the seed mussels and the last 10 fractions refer to both the “halfwas” and the consumption mussels. For each non-zero exposure time class a virtual spot is created with the specified fraction of the surface area and mussel amount.*

!		-----zaad-----			-----halfwas-----			consump	--- 20 percentages ---			
!area	y	milj kg	ha	FW(gr)	milj kg	ha	FW(gr)		zaad		halfwas+cons	
AMS	1994	60.7934	1815.6950	2.15	0.8541	28.4703	8.01	.....	2.8	3.5	...	52.7 13.9 ...
AMS	1995	0.0000	0.0000	2.15	5.9213	511.3150	8.01	.....	2.8	3.5	...	52.7 13.9 ...
AMS	1996	12.6866	513.9280	2.15	1.3170	43.8995	8.01	.....	2.8	3.5	...	52.7 13.9 ...
AMS	1997	0.0000	0.0000	2.15	3.7525	224.4030	8.01	.....	2.8	3.5	...	52.7 13.9 ...
AMS	1998	0.0000	0.0000	2.15	3.1962	127.8484	8.01	.....	2.8	3.5	...	52.7 13.9 ...
AMS	1999	9.2869	969.3870	2.15	1.3099	43.6647	8.01	.....	2.8	3.5	...	52.7 13.9 ...
AMS	2000	1.0217	34.0563	2.15	4.9569	883.1020	8.01	.....	2.8	3.5	...	52.7 13.9 ...
AMS	2001	73.8920	3002.2750	2.15	2.1859	72.8633	8.01	.....	2.8	3.5	...	52.7 13.9 ...
.	.	.	.	.	.	.	.	.	.	.	.	.
BGZ	1994	4.5925	145.9090	2.15	0.0645	2.1507	8.01	.....	3.7	1.8	...	31.6 8.5 ...
BGZ	1995	0.0000	0.0000	2.15	0.9880	32.9342	8.01	.....	3.7	1.8	...	31.6 8.5 ...
BGZ	1996	2.1169	72.4850	2.15	0.2198	7.3250	8.01	.....	3.7	1.8	...	31.6 8.5 ...
BGZ	1997	0.0000	0.0000	2.15	0.5975	19.9179	8.01	.....	3.7	1.8	...	31.6 8.5 ...
BGZ	1998	0.0000	0.0000	2.15	1.8776	62.5874	8.01	.....	3.7	1.8	...	31.6 8.5 ...
BGZ	1999	3.4667	115.5556	2.15	0.4890	16.2993	8.01	.....	3.7	1.8	...	31.6 8.5 ...
BGZ	2000	0.0930	3.0994	2.15	0.4511	18.0446	8.01	.....	3.7	1.8	...	31.6 8.5 ...
BGZ	2001	3.8086	126.9523	2.15	0.1127	3.7555	8.01	.....	3.7	1.8	...	31.6 8.5 ...
.	.	.	.	.	.	.	.	.	.	.	.	.

## 3.5 Output Files

### 3.5.1 FishingYYYY.out

The file “HighTideYYYY.out” reports the fishing carried out by the model for the model run starting in year YYYY. For each fished area it contains a table with fished fractions and fished tons per class of spots with a similar exposure time. Table 3.13 shows an example in which class 9 consists of 13 spots with an exposed time fraction between 40% and 45%. According to the prey survey there were 292.6 ton catchable cockles in this area (above the size limit). According to the black box data these spots were fished for 0.8%. If this is done, the total amount fished exceeds the reported landed amount of 469.8 ton by almost a factor 3, however. The corrected surface fractions are given in the column “Corrected” and the corresponding fished amount in column “Fished”.

**Table 3.13.** *Example of fishing output FishingYYYY.out (cf. Section 3.5.1)*

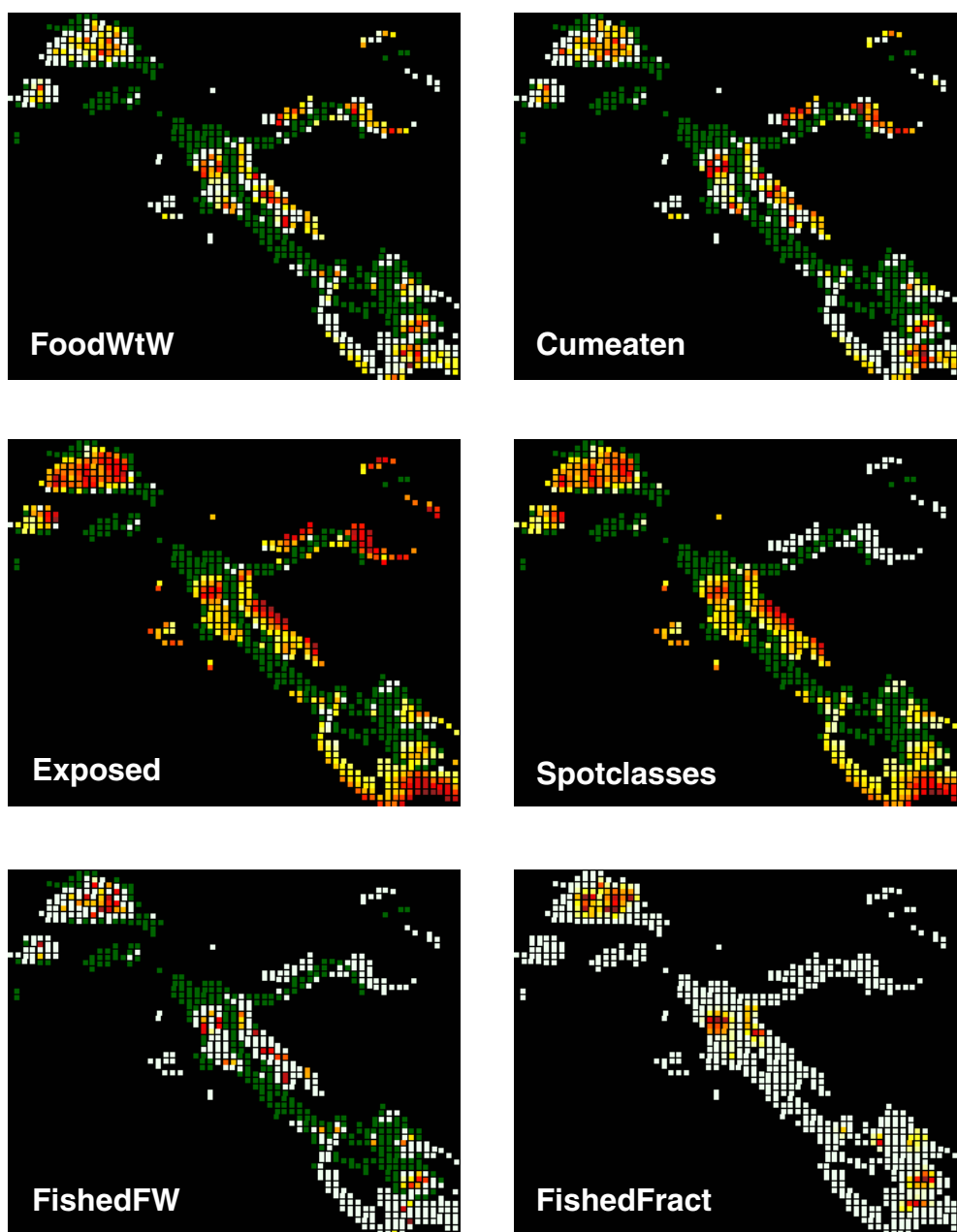
Fishing Report OSW method FIXEDDATEPERCLASS with option LEVELOFF Fishing at 01-October-1995									
		Exposed (%)		Fractional Fished Area			Fresh weight (ton)		
class	spots	from	to	BlackBox	InModel	Corrected	Catchable	Fished	Damaged
1	13	0.0-	5.0	0.000	0.000	0.000	77.2	0.1	0.0
2	2	5.0-	10.0	0.000	0.000	0.000	0.0	0.0	0.0
3	7	10.0-	15.0	0.000	0.000	0.000	36.4	0.0	0.0
4	5	15.0-	20.0	0.001	0.000	0.000	0.0	0.0	0.0
5	5	20.0-	25.0	0.002	0.002	0.001	47.6	0.2	0.0
6	5	25.0-	30.0	0.000	0.000	0.000	46.9	0.0	0.0
7	6	30.0-	35.0	0.023	0.023	0.008	278.5	6.9	0.4
8	7	35.0-	40.0	0.031	0.031	0.011	162.2	6.4	0.4
9	13	40.0-	45.0	0.008	0.008	0.003	292.6	3.0	0.2
10	10	45.0-	50.0	0.049	0.049	0.018	2669.3	331.6	17.5
11	7	50.0-	55.0	0.035	0.035	0.013	1128.9	73.1	3.8
12	8	55.0-	60.0	0.058	0.058	0.021	902.9	48.2	2.6
13	4	60.0-	65.0	0.007	0.007	0.003	105.5	0.5	0.1
14	4	65.0-	70.0	0.000	0.000	0.000	31.3	0.0	0.0
15	1	70.0-	75.0	0.000	0.000	0.000	0.0	0.0	0.0
-----				-----	-----	-----	-----	-----	-----
Area Averages/Totals				0.017	0.017	0.006	5779.1	469.8	24.8
Landed (RIVO data)								469.8	
NOT corrected for Black Box area outside Survey (8.4%)								469.8	
NOTE: no fishing at closed spots (FISHED closed area fraction 0.0%)									

### 3.5.2 HighTideYYYY.out

The file “HighTideYYYY.out” (where “YYYY” stands for the year in which the simulation began) contains for each area a single line of output per tidal period. The file can be easily imported into a spreadsheet and the lines can be sorted to “Area” and the time “SinceStart”. This leads to a quick overview of the results per simulated area. The columns of the file are described in Table 3.14.

**Table 3.14.** *Columns of output file HighTideYYYY.out.*

Variable	meaning
Area	area name
Date	in the form 25/09/1990
Time	high tide time the form 14:16
SinceStart	days since start of the simulation
#Birds	number of birds
Weight	simulated bird weight
SetPoint	preferred weight (Section 5.1)
Liver	liver content (kJ)
UptakeWtW	wet weight uptake during the tidal period passed
HTfr	fraction of uptake realized during high tide
MaxUnlSat	ratio of digestive limit and potential uptake at moment of saturation
DigInt	ratio of digestive limit and potential uptake at high tide
ForagInt	the foraging intensity (Section 2.3.4)
T	the average temperature in the tidal period passed
DigestKJ	digested amount (kJ) in the tidal period passed
UsedKJ	metabolized amount (kJ) in the tidal period passed
EnergyReq	foreseen for the next tidal period
WithWchange	including weight change contribution
MacoFW	fresh weight macoma present (ton)
MossFW	fresh weight mussel present (ton)
Cock_0j	fresh weight 0j cockles (ton)
Cock_1j	fresh weight 1j cockles (ton)
Cock_2j	fresh weight 2j cockles (ton)
Cock_MJ	fresh weight older cockles (ton)
MCock	millions of cockles
Fresh(ton)	fresh weight cockles (ton)
FishdFW	fresh weight fished cockles (ton)
Damaged	damaged by fishing
NatDied	died cockles, not by fishing or birds, fresh weight (ton)
Wet	same but wet weight
KokEatnFW	cockles eaten sofar fresh weight (ton)
KokEatnWW	cockles eaten sofar wet weight (ton)
NonEatnFW	macoma eaten sofar fresh weight (ton)
NonEatnWW	macoma eaten sofar wet weight (ton)
MosEatnFW	mussels eaten sofar fresh weight (ton)
MosEatnWW	mussels eaten sofar wet weight (ton)
OthrEatWW	other preys eaten sofar wet weight (ton)
HiTiEatWW	non-mudflat preys eaten sofar (ton)
2j+mjMayFW	2j+Mj cockles in may of start year (non-dynamic output)
OtherFrac	wet weight fraction of “other” preys eaten
HiTiFrac	wet weight fraction of high tide preys eaten
MeanBirds	mean number of birds since start



**Figure 3.1.** Images produced by the model run for 1996-1997 using historical data for weather, tides, mudflat heights and prey survey. The maps are simple bitmaps representing each spot of the model run with a small square. The colour is a measure for the value. See Section 3.5.3 for some further details. Colour prints of these figures may be inspected in (Rappoldt et al., 2003a, Figs 5.2, 5.3, 5.4 and 5.5).

### 3.5.3 TIFF Files

Figure 3.1 shows the 6 images produced by a model run. In each of the images, the results for the various areas are combined in a single “map” and there is only a single colour scale for the entire Oosterschelde (no scaling per area).

For several maps a logarithmic colour scale white-yellow-red is used. To the maximum value the colour red is assigned. Values less or equal to 1% of the maximum value are white and in between there are yellow spots (with values of about 10% of the maximum). This, at least is the situation in case of 2 decades of colour range. In case of three decades the colour range spans a factor 1000, etc. In case of a linear scale white is zero and red is the maximum value.

The green spots occurring on some images are “ghost spots”, spots occurring in the black box fishing data with a zero exposure time (not part of the mudflats). These ghost spots played a role in an earlier version of the model. They may be neglected now (cf. Section 3.4.7). The following maps are produced. The filenames are equal to the names of the images with a four digit year number added and with extension “tif”.

- FoodWtW. Total wet weight of all prey types at the start of the simulation. The colour scale is logarithmic over 2 decades.
- Cumeaten. Wet wet weight eaten at the end of the simulation.
- Exposed. Actual exposed time during the simulation on a linear colour scale (starting from 0.00 days exposed).
- Spotclasses. The exposure time classes used in the fishing procedure. For a large number of classes this image should be very similar to the image of the actual exposed time. For just 2 or 3 classes (cf. Chapter 7) there are only 2 or 3 colours on this map. Note that Oosterschelde Noord has been a closed area.
- FishedFW. Fresh weight of fished and damaged shellfish.
- Fishedfract. The distribution of the fished fraction of the surface area (cf. Section 3.1.8 and Chapter 7).

### 3.5.4 Movies

By switching on the **Movies** control parameter (Section 3.1.2) the model produces the following multiple frame TIFF files which may be converted into movies (cf. Section 2.1.6).

- BirdDensity. The bird density on the mudflats given for each time step of the model. The colour scale is logarithmic over 3 decades. Frames are only produced for the first few and last few days of the simulated period since otherwise the file (and the number of frames) would be too large to handle.
- EatenWtW. The wet weight of eaten preys for a completed tidal period. The colour scale is logarithmic over 2 decades. The number of frames is equal to the number of completed tidal cycles.



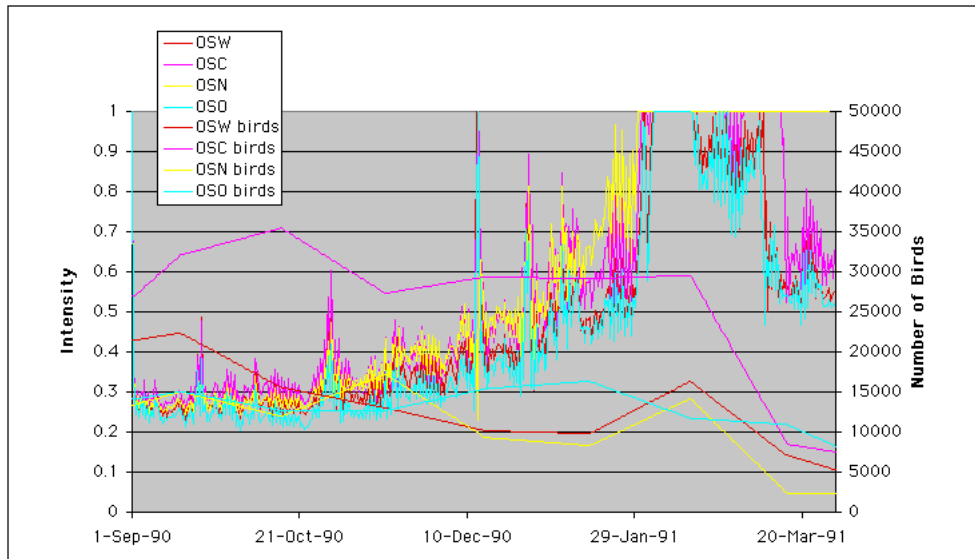
- `RemainCockWtW`. The wet weight of the remaining Cockles. The colour scale is logarithmic over 2 decades. The number of frames is equal to the number of completed tidal cycles.



## Chapter 4

# The stress index

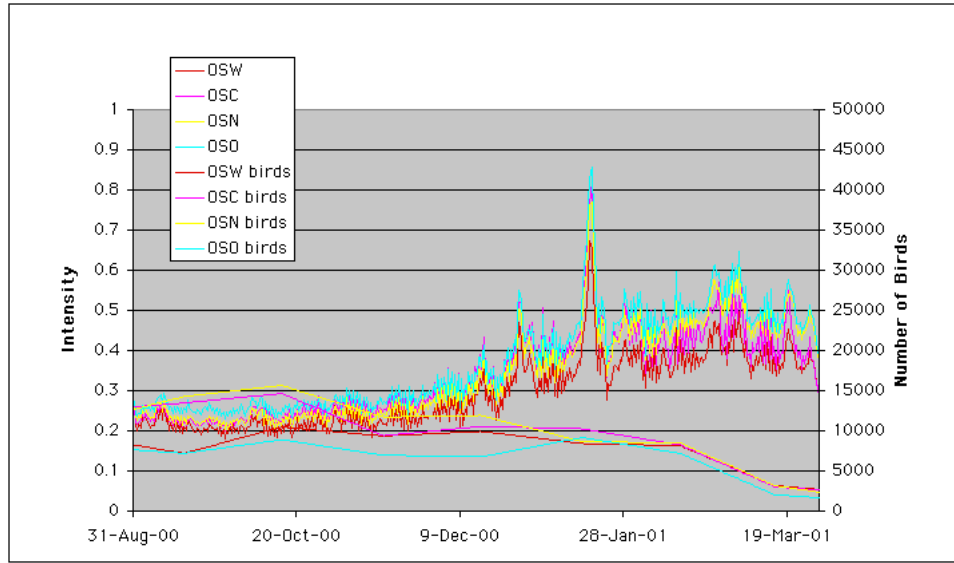
The food situation for the birds in a simulated winter season is evaluated by means of a single index. This index is based on the foraging intensities calculated for the about 170 tidal cycles between december and march. Figures 4.1 and 4.2 show examples of a calculated series of foraging intensities.



**Figure 4.1.** *Foraging intensity as function of time for a simulation of the 1990–1991 winter based on historical bird numbers and prey data. The foraging intensity for the four Oosterschelde areas (North(OSN), West(OSW), Central(OSC) and East(OSO)) is given by the four jiggling lines. The straight lines refer to the right-hand vertical axis and show the interpolated bird counts for the four areas. The frost in february leads to a prolonged period with maximum foraging intensity (and some weight loss).*

The index designed is based on the following considerations.

- Something like a critical intensity threshold does not exist. If there is too little shellfish the birds will tend to feed from inferior prey types as much as possible, lose weight and/or health and experience a higher risk to die during the winter.
- Even if there would be a critical intensity level for each individual, for a pop-



**Figure 4.2.** Foraging intensity as function of time for a simulation of the 2000–2001 winter based on historical bird numbers and prey data. (cf. Figure 4.1. In this mild winter there were no problems for the birds present. Note that the numbers of birds are much lower than in the 1990–1991 winter of Figure 4.1.

ulation there still will be a smooth relation between foraging intensity and average stress level.

- An overall stress index should be dominated by the higher foraging intensities. Low foraging intensities should contribute just a little. Three tidal periods with a foraging intensity of 0.3, for instance, should be no problem compared to a single period with an intensity of 0.9.
- The simplest way to realize such behaviour mathematically is to calculate the square of all intensities and to add them (instead of adding the intensities themselves).

This results into the following definition of a winter stress index  $\sigma$ .

$$\sigma = \frac{1}{\text{number of tidal cycles}} \sum_{\text{tidal cycles}}^{1-\text{dec}, 1-\text{march}} (\text{Foraging Intensity})^2, \quad (4.1)$$

which is simply the mean square foraging intensity. The stress indices for the strong winter in Figure 4.1 are 0.447 (OSW), 0.544 (OSC), 0.575 (OSN) and 0.414 (OSO) with a weighted average of 0.503 (using the wintering number of birds as weights). For the winter in Figure 4.2 these numbers are 0.128, 0.180, 0.177, 0.209 with a weighted average of 0.173. The mortalities in these two winters amounted 7.0% and 0.8% respectively.

The definition in Equation (4.1) is clearly somewhat arbitrary. The stress index is a number which is expected to be *related* to the real stress experienced by the birds. Using the historical record of the Oosterschelde the stress index calculated for a series of years can be *calibrated* against the mortality in those years. This gives us an instrument for the interpretation of model results in terms of an increased risk experienced by the birds.

## Chapter 5

# Bird Parameters

Bird model parameters are present on the model parameter file. The order of the variables on file is not important. The file is a TTUTIL ([van Kraalingen & Rappoldt, 2000](#)) input file.

### 5.1 Bird weight

For both Oosterschelde and Wadden Sea [Zwarts \*et al.\* \(1996c\)](#) give curves describing the bird weight throughout the year. The bird weight in the model follows the prescribed curve unless there is insufficient food intake. The data file contains a weight for a series of day numbers ranging from 1.0 to 367.0.

```
SetPointTable =
  1.0, 562.0, ! (-, gram)
  31.0, 565.0,
  60.0, 560.0,
  91.0, 530.0, ! 31-3  october weight
  244.0, 520.0, ! 31-8
  274.0, 530.0, ! 30-9
  305.0, 550.0, ! 31-10
  335.0, 560.0, ! 30-11
  367.0, 562.0
```

If “InitialWeight” is specified it is used, otherwise the weight is calculated from the interpolation setpoint table above. For the energy requirements a “MinimumWeight” is used, also if the simulated weight is much lower (the birds in the model never die).

```
!!!! InitialWeight = 500.0 ! commented-out initial weight (by ‘!’)
MinimumWeight      = 400.0   ! gram
```

### 5.2 Energy Requirements

There are two types of energy requirements: the costs of thermoregulation and the metabolic requirements. Above a critical temperature, the metabolic expenses

exceed the costs of thermoregulation and the bird does not have to spend additional energy to remain warm. Below the critical temperature the costs of thermoregulation requires additional heat production by the bird.

The costs of thermoregulation  $E_t$  decrease with increasing temperature according tot a linear relation

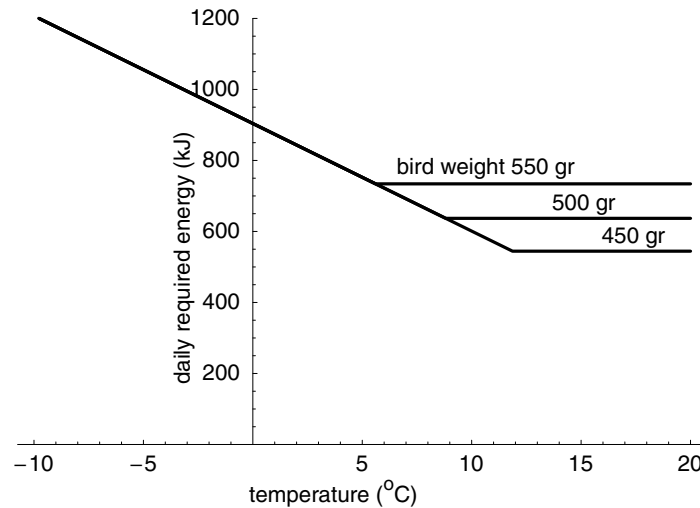
$$E_t = a - Tb$$

in which  $T$  is the temperature in degrees Celsius. Kersten & Piersma (1987) give values for the regression parameters. In the model these parameters are named `ThermoEquatOffs` and `ThermoEquatFact` respectively.

Daily metabolic energy requirement  $E_m$  is described by a power function in the form (Zwarts *et al.*, 1996a)

$$E_m = a \text{ BirdMass}^b \quad (5.1)$$

where parameter  $a$  is named `FysiolEquatCons` in the model and parameter  $b$  `FysiolEquatPowr`.



**Figure 5.1.** Daily energetic requirement as function of temperature for three bird weights.

The birds energy requirement in the model is calculated as the maximum of  $E_t$  and  $E_m$ . This is the energy requirement without body weight changes. Figure 5.1 shows the daily energetic requirement as function of temperature for three bird weights.

### 5.3 Wet weight food intake

The fraction of digested prey actually taken up by the birds body is named `FractionTakenUp` and has a value of 0.85

```
FractionTakenUp    = 0.85      ! Speakman1987, KerstenVisser1996,
                                ! KerstenPiersma1987, ZwartsBlomert1996
```

(Speakman, 1987; Kersten & Visser, 1996; Kersten & Piersma, 1987; Zwarts & Blomert, 1996). Kersten & Visser (1996) give values for the maximum digestion rate and the maximum stomach content.

```

MaxDigestRateWtW = 378.72 ! 0.263 * 60.0 * 24.0 in gram WtW / day
MaxStorageWtW    = 80.0   ! gram WtW
                  ! The digestion rate is 0.263 gr WtW / min
                  ! which is 4.38 mg WtW/s or 0.701 mg AFDW/s

```

[Zwarts \*et al.\* \(1996a\)](#) estimated a leftover fraction of 10% of the prey biomass is not eaten by the bird but remains in the shell.

```

LeftOverKokkel = 0.10      ! ZwartsEnsKerstenEtAl1996
LeftOverNon    = 0.10
LeftOverMossel = 0.10

```

## 5.4 Energy to and from body weight

[Kersten & Piersma \(1987\)](#) reported “body weight reserves” consisting for 85% of fat, for 5% of dry protein and for 10% of water. With the energy content of fat and dry protein from [Smidt-Nielsen \(1975\)](#) this leads to an energy content of 34.3 kJ per gram body weight reserves.

The deposition efficiency is the factor between the body weight reserves and the amount of energy needed to create them. [Kersten & Piersma \(1987\)](#) estimated a deposition efficiency of 88% for Oystercatchers. [De Groote \(1974\)](#) reported deposition efficiencies of 61%, 75% and 84% for domestic fowl. We used an efficiency of 75% which implies that  $(4/3) \times 34.3$  kJ is needed per gram fat reserve. On datafile this reads as

```

BodyGramEnergyCont = 34.295 ! 0.85 * 39.3 + 0.05 * 17.8 in kJ / gram
BodyGramEnergyReq  = 45.66  ! kJ / gram    25% larger

```

The uncertainty in the deposition efficiency will have only minor effects on model results. A seasonal increase in body weight of 50 g costs  $50 \times 45.66 = 2283$  kJ with an uncertainty of, say 200 kJ, which is the metabolic energy required for just about eight hours of life (cf. Section 5.2).

In the model, the energy content of the liver serves as a buffer between energy intake and structural body mass. The only function of this buffer is to prevent energy losses due to conversion of small gains and losses to and from body mass. Therefore, the precise values assumed for standard content and maximum content do not influence any model result. The values below allow the liver content to fluctuate between 0 and 200 kJ which appears to be more than enough to realize the desired smooth behaviour of the simulated bird weight.

```

BestLiverConKJ = 100.0
MaxLiverConKJ  = 200.0

```

## 5.5 Cockle Functional Response Leo Zwarts

The functional response in *WEBTICS* is a capture rate described as a Holling II curve with a prey size dependent handling time. The form of this equation is

$$f(d, s) = \frac{A d}{1 + \lambda(s) A d}, \quad (5.2)$$

where  $f(d, s)$  is the functional response as a capture rate (number of prey per second),  $d$  is the cockle density ( $\text{m}^{-2}$ ) and  $s$  is the prey size (mm).  $A$  is a regression parameters and  $\lambda(s)$  the (effective) handling time as function of prey size, also containing at least 1 regression parameter.

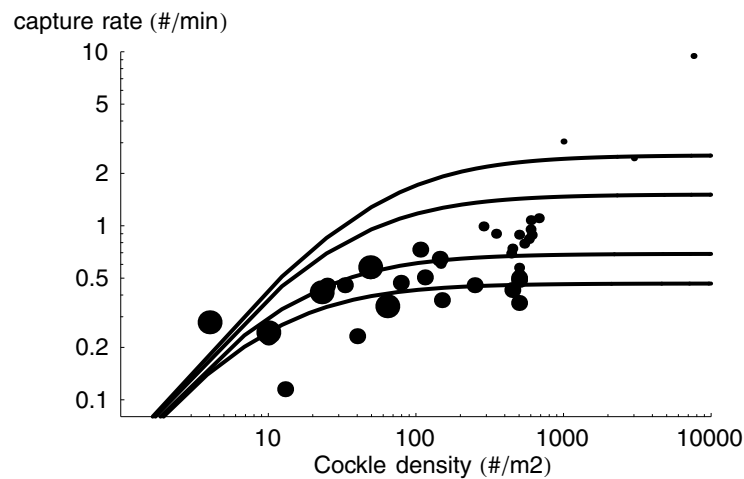
Zwarts *et al.* (1996b) give a review of functional response data for feeding on Cockles from various sources. Assuming a handling time in the form  $\lambda(s) = B s^C$ , a non-linear fit on the capture rate yields (“leoA” is parameter  $A$ , etc)

leoA = 0.000860373  
leoB = 0.220524  
leoC = 1.79206

which implies (cf. Equation (5.2)) for the functional response

$$f(d, s) = \frac{0.000860 d}{1 + 0.0001897 d s^{1.792}}, \quad (5.3)$$

The fit explains 83% of the variance in the data, which is somewhat more than the 67% for the polynomial fit given in Zwarts *et al.* (1996b, Figure 16).



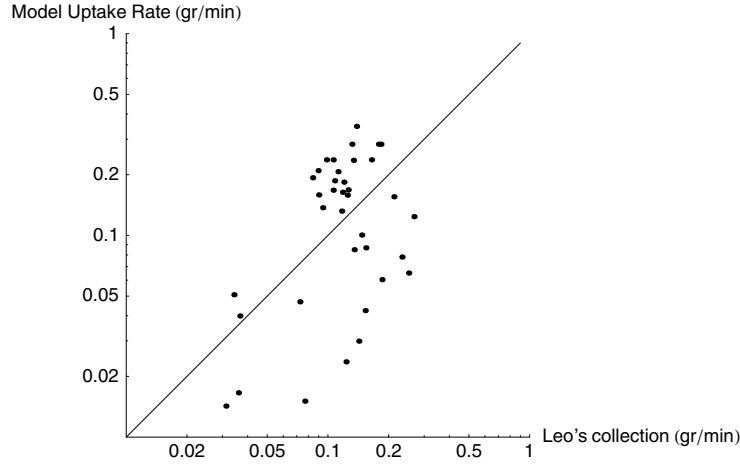
**Figure 5.2.** Functional response data from Zwarts *et al.* (1996b) with regression lines calculated with Equation (5.3) for Cockle sizes corresponding to Cockle weights of 20, 50, 200 and 400 mg (AFDW) (the same values used in Zwarts *et al.* (1996b, Figure 16)).

## 5.6 Cockle Functional Response Norris & Johnstone

Norris & Johnstone (1998) gives a detailed description of Oystercatchers foraging on Cockles by hammering them. The model contains several regression lines for handling times, wasted handling time, etc. These parameters have been included in the Fortran program since it has little use to change them. The program section can be found in Appendix D.

Figure 5.3 shows a comparison between uptake rates calculated with this model and Equation (5.3) derived from the data given in Zwarts *et al.* (1996b). The high uptakes calculated with Norris & Johnstone (1998)’s functional response are much larger than the ones derived from Equation (5.3). This difference was confirmed by





**Figure 5.3.** Uptake rate (gram Wet per minute) according to foraging model of [Norris & Johnstone \(1998\)](#) compared with Equation (5.3) derived for data in [Zwarts et al. \(1996b\)](#).

John Goss-Custard (pers. comm. at EVA conference) who told us that the [Norris & Johnstone \(1998\)](#)’s maximum intake rate (the “plateau” of the functional response) deviates very much from all other values he has seen. Therefore, we no longer use this function and all model results have been obtained with Equation (5.3).

## 5.7 *Macoma* Functional Response

Figure 5.4 shows the intake rate of Oystercatcher eating *Macoma balthica* as function of the *Macoma* biomass density. The regression line for the intake rate (IR mg AFDW s<sup>-1</sup>)

$$\text{IR}(d) = \frac{0.000625 x}{1 + 0.000213 x}, \quad (5.4)$$

where  $x$  is the biomass density in mg AFDW m<sup>-2</sup>.

The calculations in *WEBTICS* are based on capture rates which are formally derived from encounter rates and handling times. The capture rate CR corresponding to Equation (5.4) is

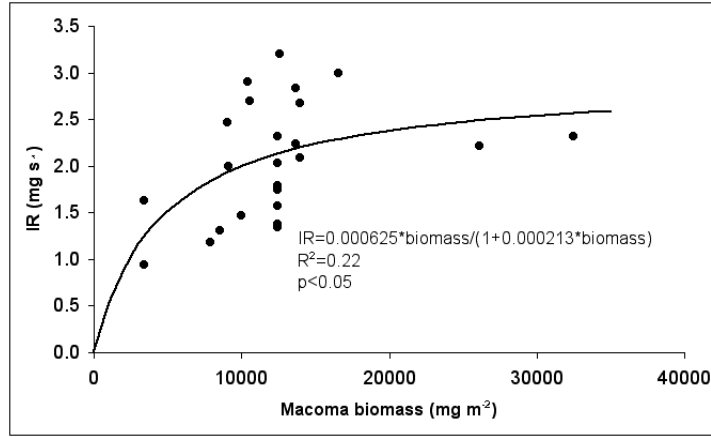
$$\text{CR} = \frac{0.000625 x}{1 + 0.000213 x} \times \frac{1}{1000 \times \text{WetWeight} \times \text{RatioAFDWtoWet}}. \quad (5.5)$$

Expanding the biomass density (in mg AFDW m<sup>-2</sup>) as  $x = d \times 1000 \times \text{WetWeight} \times \text{RatioAFDWtoWet}$  (cf. Section 6.8), where  $d$  is the macoma density, the capture rate in Equation (5.5) becomes:

$$\text{CR}(d) = \frac{0.000625 d}{1 + 0.000213 \times d \times 1000 \times \text{WetWeight} \times \text{RatioAFDWtoWet}},$$

which is equivalent to an encounter rate  $A_{\text{Macoma}}$  given as

$$A_{\text{Macoma}} = 0.000625 d \quad (5.6)$$



**Figure 5.4.** *Functional Response of Oystercatchers feeding on Macoma balthica. The Holling II curve is based on data in Bunscoeke et al. (1996), Hulscher (1982) and Ens(pers. comm.). A fit with Macoma density on the horizontal axis has been published by Hiddink (2003).*

and an apparent handling time  $\lambda_{\text{Macoma}}$  of

$$\lambda_{\text{Macoma}} = \frac{0.000213}{0.000625} \times (1000 \times \text{WetWeight} \times \text{RatioAFDWtoWet}).$$

The data in Figure 5.4 were collected in summer and autumn. In order to account for the decrease of the energetic content of the prey during the winter, the handling time  $\lambda_{\text{Macoma}}$  is calculated in the model for the *initial* prey weight  $\text{WetWeightINI}$ . Hence,

$$\lambda_{\text{Macoma}} = \frac{0.000213}{0.000625} \times (1000 \times \text{WetWeightINI} \times \text{RatioAFDWtoWet}). \quad (5.7)$$

From Equations (5.6) and (5.7) the capture rate  $f(d)$  then becomes

$$f(d) = \frac{A_{\text{Macoma}}}{1 + A_{\text{Macoma}} \times \lambda_{\text{Macoma}}}. \quad (5.8)$$

Multiplying this by the prey weight we get the intake rate of the birds. The plateau of the functional response reached for very high prey density is found by multiplying  $1/\lambda$  by the ash free dry weight of the prey which gives

$$\frac{0.000625}{0.000213} \times \frac{\text{WetWeight}}{\text{WetWeightINI}}.$$

This deviates from the plateau of Equation (5.4) by the weight ratio, which is of course the consequence of using the initial weight of the prey in the handling time.

The datafile contains

```
hiddinkA = 0.000625
hiddinkB = 0.000213
```

## 5.8 Combined Cockle *Macoma* Functional Response

At each spot various sizes of Cockles may occur in combination with *Macoma balthica*. A combined functional response can be calculated by adding as follows the terms in the numerators of the various capture rates

$$f_i(d_i, s_i) = \frac{A_i d_i}{1 + \sum_{i=1}^n \lambda(s_i) A_i d_i}, \quad (5.9)$$

where  $i$  is the prey type counter. This equation implies that there is no preference for specific types of prey. The capture rates and handling times determine the diet.

## 5.9 Mussel Functional Response

The bird distribution algorithm of the model will lead to a fraction of the birds feeding on the virtual Mussel beds and the others feeding on Cockles and *Macoma balthica*.

### 5.9.1 Oosterschelde

In case of the Oosterschelde area there is no information on mussel size available (cf. Section 3.4.8). Goss-Custard *et al.* (2001, Figure 1) showed that the intake rate of Oystercatchers feeding on mussel beds lies between 1.5 and 3 mg AFDW s<sup>-1</sup> and is largely independent of prey density. In *WEBTICS* a value of 2.5 mg AFDW s<sup>-1</sup> is used. This figure, however, refers to relatively heavy Mussels in september. During the winter the prey species lose weight and the maximum intake rate decreases accordingly.

*WEBTICS* keeps track of a numerical prey density at each spot in combination with a prey weight. Therefore, the intake rate of Goss-Custard *et al.* (2001) has to be converted into a capture rate which is done by using a dry mass of 850 mg of a “standard mussel” in september. This gives an effective handling time of 850/2.5=340 s, equivalent to a maximum capture rate of 0.00294 s<sup>-1</sup>.

Although normally no significant depletion takes place on Mussel beds the calculations have to be protected against negative prey densities. An encounter rate of 0.00057 m<sup>-2</sup> s<sup>-1</sup> leads to 95% of the maximum intake at a prey density of about 80 g AFDW m<sup>-2</sup>, which is a very low prey density for a Mussel bed. The resulting capture rate becomes

$$f(d) = \frac{0.00057 d}{1 + \frac{850\text{mg}}{2.5 \text{ mg s}^{-1}} 0.00057 d} \quad (5.10)$$

It can be easily verified that for realistic Mussel densities this equation indeed leads to a capture rate of nearly 0.00294 s<sup>-1</sup>. Multiplied by the september biomass the maximum intake rate of 2.5 mg AFDW s<sup>-1</sup> comes back, but with lower prey weight in winter, the intake rate is reduced.

The datafile contains

```

MosselSeptAFDWrate = 0.0025 ! gram AFDW per second (Goss-Custard)
StandardMosselAFDW = 0.85   ! gram (for 45 mm mussel in september)
MosselA              = 0.00057 ! m2 s-1

```

### 5.9.2 Wadden Sea

In case of the Wadden Sea the virtual spots contain seed mussels, consumption size mussels or sizes in between. Hence, at least some size information is available (cf. Section 3.4.9), which can be used in the functional response calculations.

Like in case of the Oosterschelde, the mussel intake is determined by the plateau of the functional response curve for a large part of the practical mussel density range. This plateau is given as function of mussel size by [Zwarts \*et al.\* \(1996b\)](#), Fig. 12B). The encounter rate is calculated from the same value of the parameter MosselA which has been used for the Oosterschelde region (see Section 5.9.1). The effective handling time is then estimated by calculating the ratio between prey weight and maximum intake rate (plateau value) for that prey size. The plateau value is calculated from the formula in [Zwarts \*et al.\* \(1996b\)](#), Fig. 12B) using the initial (september) weight of the prey. This leads to a slow decrease of the functional response during the winter.

The datafile contains

```

! functional response Mossel (WaddenSea, several types of Mossel)
! y = a xb is intake rate (mg AFDW / s) as function of prey weight x (mg AFDW)
! so this is the plateau of the functional response as function of prey weight
! from Figure 12B ZwartsEnsDurellEtAl1996
MosselIntakeRateA = 0.092
MosselIntakeRateB = 0.506

```

## 5.10 Other prey

The program has the possibility to specify intake of “other” and unknown prey species. By setting a non-zero value for one of the following variables

```

! OTHER preys
MinimumRateAFDW    = 0.00 ! milligram AFDW per second
OtherPreysFraction = 0.10 ! uptake of unspecified preys (WtW only)
                     ! as a fraction of the WtW uptake of regular preys

```

part of the intake is regarded as being from “other” prey. In case of a non-zero `MinimumRateAFDW` each spot gets a minimum intake rate due to intake of “other” prey. This option has not been used. By specifying a non-zero `OtherPreysFraction` the contribution of other prey is set equal to a fraction of the intake of regular prey. The contribution from the regular prey is reduced by the same amount, which implies that the functional response is held constant. In this way, intake of other prey just reduces the depletion rate of regular prey.

Clearly, these variables should be used with caution since their values cannot be justified by any empirical data. There may be reasons, however, to assume that the birds feed to some extent on prey not included in the prey survey.

## 5.11 Interference

[Stillman \*et al.\* \(2002\)](#) describes interference with help of an individual based foraging model. For the Oystercatcher the results of this model are consistent with field studies. The model can be simplified by fitting exponential curves through Stillman's relative uptake values. This has been described in detail in [Appendix A](#).

```
! interference model for Oystercatcher-Cockle pair
! StillmanEtAl2002, Rappoldt2002A
KokkelAttackDistance = 2.0    ! (m)
KokkelInterferenceAlfa = 0.40 ! (-)
MosselAttackDistance = 2.4    ! (m)
MosselInterferenceAlfa = 0.125 ! (-)
```

## 5.12 High Tide Foraging

[Stillman \*et al.\* \(2000\)](#), after Goss-Custard, unpublished data) use a dry mass intake rate of  $0.53 \text{ mg s}^{-1}$  for foraging in fields. This is less than the digestion rate, which means that it cannot be very attractive for the birds. [Stillman \*et al.\* \(2000\)](#) mention that this intake rate is fairly constant through the winter since there is no depletion of prey and that interference effects are absent or negligible.

According to common experience, foraging outside the mudflats only takes place during daylight under circumstances which seem difficult for the birds such as prolonged periods of high water levels. Therefore, in *WEBTICS*, foraging outside the mudflats takes place if

There are no mudflats exposed where the intake rate would be larger,

The average temperature during the last two tidal cycles is above  $0^{\circ}\text{C}$ . Otherwise the soil is assumed to become frozen,

There is daylight (the sun is above  $0^{\circ}$ ),

The foraging intensity (cf. [Section 2.3.4](#)) is above a threshold of 0.4, which means that high tide foraging does not occur if the birds can easily feed on the mudflats,

With a foraging intensity increasing from the threshold to 1.0, the average intake rate increases linearly to  $0.6 \text{ mg s}^{-1}$ .

On the datafile this becomes

```
NonMudThreshold = 0.4    ! intensity threshold
MaxNonMudIntakeRateAFDW = 0.6 ! mg AFDW per second
```

## 5.13 Intake reduction by ice

When the mudflats are covered with ice, the birds cannot reach their prey any more. This happens during prolonged periods of cold weather which occur in some winters. A quantitative description of the historical occurrence of ice is impossible due to a lack of direct observations. Therefore we use a rough approximation of the effect:

If the average temperature during the last two tidal cycles is below  $-5^{\circ}\text{C}$ , the birds can no longer reach their prey. Between  $-5^{\circ}\text{C}$  and  $0^{\circ}\text{C}$ , foraging increases linearly to the ordinary level.

On the datafile this becomes

```
LowTempTable = ! correction of maximum foraging rate
                -50.0 0.0 ! as function of average temperature
                -5.0 0.0 ! is used with average temperature
                  0.0 1.0 ! of previous two tidal periods
                +50.0 1.0
```

## Chapter 6

# Prey Parameters

### 6.1 Cockle Fresh Weight

The Cockle fresh weight (shell + fresh flesh + water in the shell) at September-1 is read from an input file prepared by RIVO. This input file is based on the yearly spring survey and corrected for death and growth of the various size classes during the summer. Fresh weight increases a little in autumn and remains practically constant through the winter period since loss of biomass is compensated for by a larger amount of water inside the shell. During initialization of the program, the fresh weights are converted to wet weights (Section 6.3) and to size (Section 6.7). Wet weight is the weight of the uncooked, non-frozen wet flesh. Size is cockle length.

Fresh weights are further needed for evaluation of the simulated season at the end of the program run and for calculating the number of cockles removed by fishing.

### 6.2 Age classes

In the “RIVO survey” cockle weights are given for four age classes, for 0-th year (‘0j’), 1-st year (‘1j’), 2-nd year (‘2j’) and multiple year (‘mj’) cockles. The 0-th year class, however, cannot be observed in May and therefore does not occur in the input data corrected for summer growth. In reality the 0-th age class are late cockles of the previous year and are treated therefore in the same way as the cockles classified as 1-st year ones.

### 6.3 Fresh to Wet Weight conversion

During initialization of the program the wet weight (non-frozen, uncooked fresh flesh) has to be calculated from the fresh weight measured in the RIVO survey.

### 6.3.1 Cockle

The conversion for Cockles makes use of the following values ([Kesteloo-Hendrikse, 2002a](#)).

```
CockCookedToFW0j = 0.2067 ! (-)
CockCookedToFW1j = 0.1970 ! (-)
CockCookedToFW2j = 0.1701 ! (-)
CockCookedToFWMj = 0.1681 ! (-)
```

for the 0-th, 1-st, 2-nd and higher year class respectively. Here, the zero-th year class refers to the new cockle generation. Hence, the last three numbers are used in the model (cf. Section 6.2).

Conversion of cooked weight to the desired wet weight obviously requires an additional parameter, `RatioCookedToWet` with value given by ([Kesteloo-Hendrikse \(RIVO\)](#), pers. comm.).

```
RatioCookedToWet = 0.90
```

After converting to wet weight, the fresh weight and the wet weight during autumn and winter are simulated independently using two different relative growth curves (cf. Sections 6.4 and 6.5.1).

### 6.3.2 *Macoma balthica*

Wet weight `WW` (gram) is derived from fresh weight `FW` (RIVO survey in gram) by means of

$$WW = A(FW)^B \quad (6.1)$$

with the regression constants from datafile

```
MacomaFWtoWtWA = 0.335 !!!!! = 0.0536 / RatioAFDWtoWet
MacomaFWtoWtWB = 0.917
```

This equation has been derived by taking an equation for the conversion of length to fresh weight ([Ens](#), pers. comm.)

$$FW(g) = 0.0000725 (\text{Length}(mm))^{3.34}, \quad (6.2)$$

inverting it in order to calculate length from fresh weight

$$\text{Length}(mm) = 17.35 (FW(g))^{0.2994}, \quad (6.3)$$

taking an equation for the conversion of length to prey dry weight ([Zwarts, 1991](#), Table 6, month 8)

$$AFDW(mg) = 0.008574 (\text{Length}(mm))^{3.063}, \quad (6.4)$$

and combining the two equations into

$$AFDW(g) = 0.0536 (FW(g))^{0.917} \quad (6.5)$$

which gives, after dividing by `RatioAFDWtoWet` (Section 6.8) the above datafile parameters.



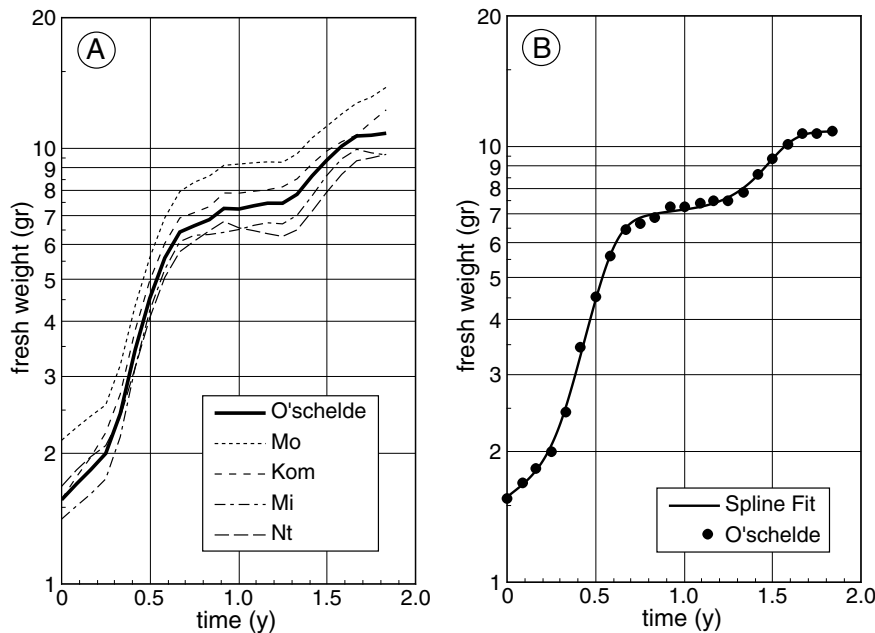
### 6.3.3 Mussel

For the conversion of Mussel fresh weight to wet weight a factor 0.20 is used. Since *WEBTICS* uses a standard Mussel size given by parameter `standardMusselAFDW` (cf. Section 5.9), the fresh to wet weight conversion determines the number of these “standard Mussels” allocated on the beds (fresh weight density is model input). This numerical Mussel density affects the degree of depletion, which is normally insignificant (Goss-Custard *et al.*, 2001). In the model, depletion only takes place if there is no other food available and the birds use the Mussel beds in exceptionally high bird densities.

## 6.4 Cockle Fresh Weight change

For Mussel and Macoma no changes in fresh weight are considered.

Figure 6.1A shows monthly cockle weights for various parts of the Oosterschelde area. The solid curve gives a weighted average. The data show the summer growth of 1-st and 2-nd year cockles. Figure 6.1A uses a logarithmic scale and the vertical distance between the various curves is more or less constant. This means that we can approximate the fresh weight changes by means of a relative growth rate applied to different initial weights.

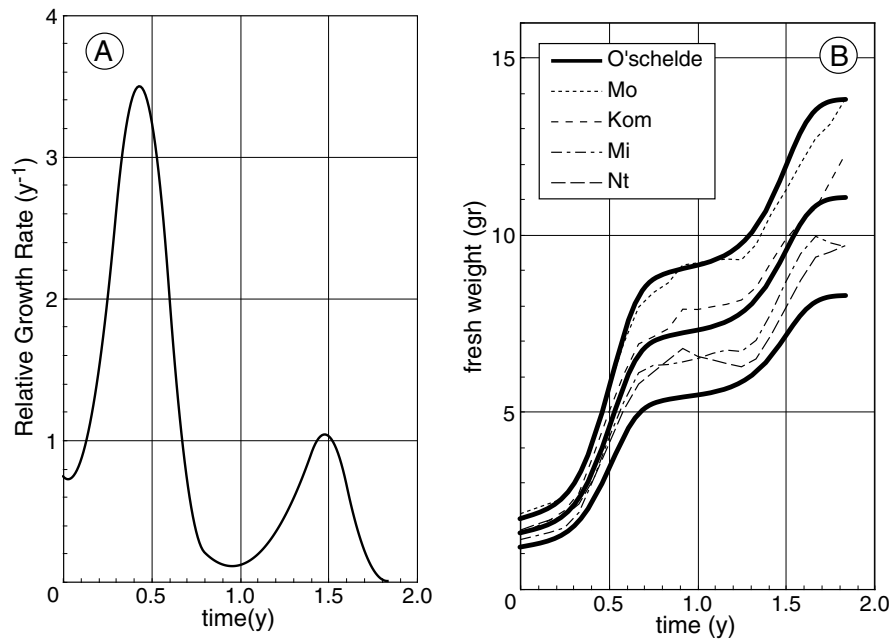


**Figure 6.1.** (A) Monthly values of fresh cockle weight in the Oosterschelde area (Kesteloo-Hendrikse, 2002b). Time is given in years starting at 1-January of the year following the “birth” of the cockles. (B) Least square fit of six third order polynomials on the weighted average fresh weight for Oosterschelde (the solid curve in (A)). The curves (“smoothed cubic splines”) have been calculated for the time intervals  $[0.0, 0.3]$ ,  $[0.3, 0.6]$ ,  $[0.6, 0.8]$ ,  $[0.8, 1.4]$ ,  $[1.4, 1.6]$  and  $[1.6, 1.84]$  using the Fortran library *Math77* (subroutine *SC2FIT* based on de Boor (1972, 1978))

The first step is to derive an approximate curve for for the weighted average in

Figure 6.1A. The datapoints have been redrawn in Figure 6.1B as separate points and a smooth curve has been fitted to the data. The relative growth rate is then found by using  $d \ln(w)/dt = 1/w d(w)/dt$ . Hence, the relative growth rate can be found as the derivative of the logarithmic weight. Figure 6.2A shows the resulting function.

The increase in fresh weight in autumn is rather small. Fresh weight increase has been implemented in the model, however, in order not to overestimate the number of fished cockles. The autumn growth (during September and October) for 1-st year cockles amounts 8.5% following the curve in Figure 6.2A. For 2-nd year cockles this is a mere 2.2%. For multiple year cockles ('mj') and a zero fresh weight increase in autumn is assumed in the model.



**Figure 6.2.** (A) Relative growth rate corresponding to the fit in Fig. 6.1B (B) Simulated fresh weights using the relative growth rate from (A) and starting at three different initial weights. The dashed lines are the original data from Fig 6.1A (now on a linear scale)

In the model the relative growth rate for fresh weight is actually found by linear interpolation between a series of X-Y points read from the curve in Figure 6.2A. The series of points on datafile looks like

```
FWrgrTable =          ! Interpolation table for
0.00000      0.76146  ! relative growth rate (per year) as function of
0.50000E-01  0.74237  ! time expressed in years after 1-Januari of the
0.10000      0.85219  ! year after the "birth" of the cockles
0.15000      1.0909
0.20000      1.4586
0.25000      1.9551
0.30000      2.5806
0.35000      3.1412
. . .          . . .
. . .          . . .
1.6000      0.68574
1.6500      0.42501
```

1.7000	0.22846
1.7500	0.09610
1.8000	0.02792
1.8356	0.01849

Relative growth rates calculated with this list have been used to simulate the fresh weight curves in Figure 6.2B. The three curves have been calculated by just choosing three different starting values (note the *linear* y-scale). The thin lines depict again the Oosterschelde data from Figure 6.1A.

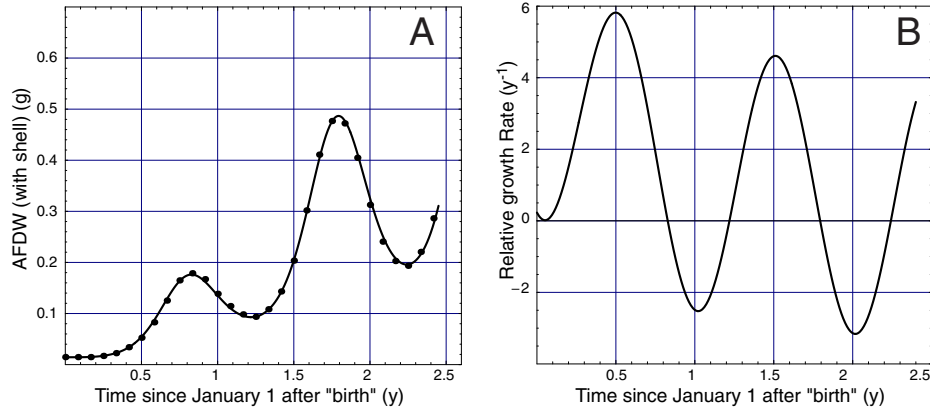
## 6.5 Wet Weight change

### 6.5.1 Cockle

The wet weight of the cockles is simulated using a start weight and a relative growth rate. The relative growth rate depends on the time of the year and can be specified in two ways, depending on the value of the variable `CockleCurveType`

**CockleCurveType='Klepper'**. The curve used for wet weight is, up to a constant factor `RatioAFDWtoWet`, equal to the curve for the ash free dry weight AFDW given by Klepper (1989, Figure 7.2). This curve is shown in the form of points in Figure 6.3A. The curve in the graph is a fitted function given by:

$$\text{AFDW}(t) = 0.0136285 \text{Exp}\left[\frac{5.13146 t}{1.28867 + t} + 0.59952 \sin(3.05164 + 2 \pi t)\right], \quad (6.6)$$



**Figure 6.3.** (A) Ash-free dry weight as function of time in years since 1-January 00:00 of the year following the “birth” of the cockles. The “datapoints” have been read from the curves given by Klepper (1989, Figure 7.3). The curve was fitted through the points and is given by Equation (6.6). (B) Corresponding Relative growth rate with mathematical expression given in Equation (6.7). This curve is used to calculate the wet cockle weight during the winter starting from September,1. The unit of the relative growth rate is  $y^{-1}$ . Numbers have to be divided by the average length of a year (365.25 days) in order to get a relative growth rate per day.

where  $t$  is the time in years since 1-January 00:00 of the year following the “birth” of the cockles. The relative growth rate corresponding to the weight curve in Fig-

ure 6.3A is

$$\frac{1}{\text{AFDW}(t)} \frac{d \text{AFDW}(t)}{dt} = \frac{6.61274}{(1.28867 + x)^2} + 3.76689 \cos(3.05164 + 2 \pi x). \quad (6.7)$$

Figure 6.3B shows a graph of this function. Using this *relative* growth rate function, a weight curve can be constructed from any initial weight and from any start day. This is what we do for the initial wet weights at 1-September.

The first period of autumn growth and winter weight loss in Klepper's weight curve is used for the 0-th and 1-st year class of the survey. The second one is used for all higher year classes. No growth curve for higher year classes is available but after 1-September there is mainly loss of weight and it is assumed that this weight loss takes place in the same way for class 2 and higher.

Note that the Equations (6.6) and (6.7) should *NEVER* be used for extrapolation of the cockle weight or the cockle growth rate outside the range  $0 < t < 2.4$ . This leads to serious errors in the calculated weights.

**CockleCurveType='Tables'**. As an alternative for Klepper's curve the weight loss can be specified as an interpolation function between day 1.0 and 367.0. This requires specification of the following tables:

```
Wgain_0j_Table = 1.0, -0.00385, 367.0, -0.00385 ! (constant decrease)
Wgain_1j_Table = . . . . .
Wgain_2j_Table = . . . . .
Wgain_3j_Table = . . . . .
```

The unit of the relative growth rates in the tables is day<sup>-1</sup>.

### 6.5.2 Mussel

The decrease in Mussel weight given by Goss-Custard *et al.* (2001, Figure 2) corresponds to a fractional weight loss of about 0.0025 per day relative to the initial (september) wet weight. On datafile:

```
StandardMosselWtWgain = -0.0025 ! gram per day per gram startweight
! (Figure 2 Goss-Custard for 45 mm mussel)
```

### 6.5.3 *Macoma balthica*

The same value as for Mussel has been used. On datafile:

```
MacomaWtWgain = -0.0025 ! mussel value taken
```

## 6.6 Prey death

Prey death by causes other than predation by birds and fishing is taken into account as an additional monthly death rate of about 1% of the prey population.

This leads to

```

CockleDeathRate      = 0.00033  ! per day (1% per month)
StandardMosselDeathRate = 0.00033
MacomaDeathRate      = 0.00033

```

Note that a death rate of 1% per month was also used by [de Vlas \(2002\)](#). The results of the Cockle balance calculations in [Rappoldt \*et al.\* \(2003b\)](#), Figs. 3.14 and 4.2) suggest that 1% per month may be *somewhat* too small, but this does not cause important deviations during the simulation of a single wintering season when starting with measured stocks ([Rappoldt \*et al.\*, 2003b](#), Figs. 3.12 and 3.13).

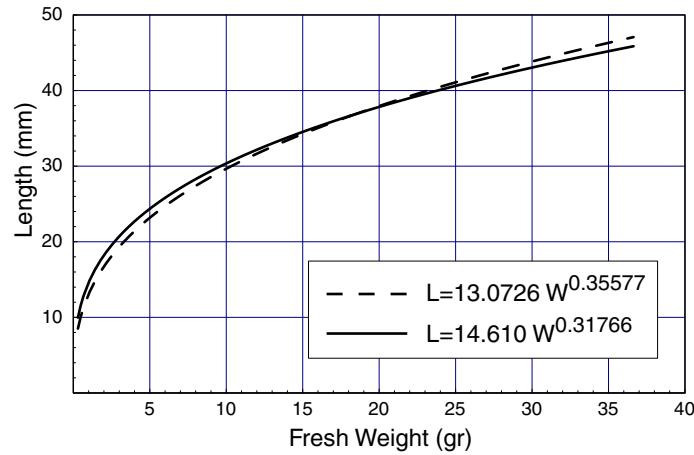
## 6.7 Cockle Fresh weight to Length conversion

This conversion is needed to distinguish between cockles removed and not removed by fishing. Cockle length is also a parameter of the functional response model described in Section 5.5.

There are two sets of data available. In both cases the conversion is based on a linear relation between the logarithm of the length  $\ln(L)$  and the logarithm of the fresh weight  $\ln(W)$ , which is the same as a power law relation between  $L$  and  $W$ .

[Kamermans & Kesteloo-Hendrikse \(2001\)](#) report the regression equation  $W = 0.7280L^{2.8108}$  where  $W$  is in milligram and  $L$  in mm. Inversion the equation and expressing  $W$  in gram gives

$$L = 13.0726 W^{0.35577} \quad (\text{mm} = a(\text{gram})^b) \quad (6.8)$$



**Figure 6.4.** Comparison between Equation (6.8) and Equation (6.9) for the calculation of Cockle length from Cockle weight.

Another set of data (Ens, pers. comm.) has been described by the regression equation  $\ln(W) = 3.148\ln(L) - 8.442$  (units gram and mm). Inverting gives

$$L = 14.610 W^{0.31766} \quad (\text{mm} = a(\text{gram})^b) \quad (6.9)$$

The data underlying Equations (6.8) and (6.9) may have been collected in different areas or in different seasons. Figure 6.4, however, shows that the difference between the two equations is probably of little importance.

The regression parameters  $a$  and  $b$  (in  $L = a \times W^b$ ) are present on the input file as the variables CockFWtoSizeA and CockFWtoSizeB respectively:

```
CockFWtoSizeA = 14.610      ! param a in:  L = a FW^b  (mm = a gram^b)
CockFWtoSizeB = 0.31766     ! param b in:  L = a FW^b  (mm = a gram^b)
```

## 6.8 Shellfish energy content

The ash free dry weight (AFDW) per gram wet weight and the energy content per gram AFDW are given by ([Zwarts \*et al.\*, 1996b](#))

```
RatioAFDWtoWet    = 0.16    ! -
AFDWenergyContent = 22.5     ! kJ / gram
```

## Chapter 7

# Fishing Parameters

Fishing in *WEBTICS* means removal of cockles from spots. The amount of cockles landed in the various years are known and from the black box data a fished fraction has been derived for each spot. Different “fishing methods” can be designed for removing the fished cockles from the spots in the model.

### 7.1 Fishing method

Currently, two removal methods have been implemented, both “fixed date methods”. Hence the fished amount is removed at a certain date, for instance at 1-October. The fishing method is chosen on data file by

```
FishingType = 'FixedDatePerClass' ! Fishing method ; one of these:
                                     ! NoFishing          => No fishing
                                     ! FixedDatePerSpot   => B Box data per spot
                                     ! FixedDatePerClass => B Box data per class
```

The option `FixedDatePerSpot` leads to fishing precisely as specified by the fished area fractions derived from the black box data. There is no normalization. Hence the actual amount removed may differ from the data on landed cockles.

The option `FixedDatePerClass` uses the exposure time data to make classes of spots. For each class the black box fished areas are grouped into a fished area fraction for that class. Then, within the class, fishing takes place at the richest spots. The class width is set by the variable `SpotClassSize` as a percentage of exposure time.

The date at which the fishing takes place in the model is set by

```
FixedFishingDOY = 274.0      ! 1-October as fixed date for removal
```

Within the method `FixedDatePerClass` there are two ways of “fishing in a class of spots” and the choice is made by setting `PerClassOption` in

```
PerClassOption = 'LevelOff' ! FixedDatePerClass option for rich spot fishing
                                     ! LevelOff => reduce rich spots to some FW density
                                     ! Empty    => reduction to zero of richest spots
```

The option `Empty` empties all spots, starting with the richest, until the required area fraction is reached. This usually leads to an overestimate of the fished amount and the actual fishing is reduced in such a way that the landed amount is matched. The option `LevelOff` leads to a reduction of the (average) cockle density in the richest spots to a certain level. This level is calculated in such a way that the fished area fraction for the class is matched. Then again the actual removal is normalized to match the landed amount.

### 7.1.1 Threshold cockle size

The minimum width  $w$  of cockles caught is 19.62 mm (van Stralen, 1990, Minimum length). The relation between Cockle width  $w$  and fresh weight  $W$  (van Stralen, 1990, length versus weight) is

$$W = 0.6162 w^{2.9582} \quad (\text{mg Fresh} = a (\text{mm})^b) \quad (7.1)$$

Equation (7.1) gives a minimum fresh weight of 4109 mg. With Equation (6.8) the minimum length then becomes 21.61 mm. On datafile

```
ThresholdSize = 22.0 ! mm
```

## 7.2 Collateral damage

Collateral is described by two model parameters

```
DamageRemaining = 0.10 ! fraction dead of undersized cockles
FishingEfficiency = 0.95 ! landed fraction of removed cockles
```

The variable `DamageRemaining` describes the fraction killed of the undersized cockles. The fraction of cockles killed during fishing (removed but not landed) is  $1 - \text{FishingEfficiency}$ .

The figures used here are rough estimates suggested by de Vlas (pers. comm.) during a workshop in Yerseke. There is a lot of debate, however, about the damage done by the suction dredge to the undersized shellfish and the figures used may be too low. In that case the effect of fishing will be underestimated by the model. The required food reservation calculated in Rappoldt *et al.* (2003a,b) will not be sensitive to the error, however, since it is calibrated on the return of the birds in the next year.



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# Appendix A

## Stillmans interference curves approximated with a one parameter model

### Summary

#### Statistical description of interference

Different types of dominant and subdominant behaviour of individuals will play a role in the interference between the birds of a foraging flock. The overall result of the process is not necessary complicated from a descriptive point of view, however. Studying results of the detailed behavioural model of Richard Stillman, I observed that the decrease of the average intake rate is very close to an exponential decrease. An exponential decrease also results from a simple analytical model based on a few assumptions. If the effect of interaction is proportional to the probability that individuals come within a certain distance from each other, and if the distribution of scattered individuals is random, at least at low densities, the probability of an interaction depends exponentially on the value of the product  $\rho \times D_A^2$ , where  $\rho$  is the density of the individuals and  $D_A$  a characteristic distance belonging to the interference process considered, Stillman's attack distance for instance. The product  $\rho \times D_A^2$  is dimensionless, which means that interference processes at very different spatial scales are characterized by the same sort of values of this product. From the very definition of the dimensionless quantity  $\rho \times D_A^2$  it can be immediately inferred that a threshold bird density  $\alpha_{95}$  (the density belonging to an uptake reduction of 5%), will depend quadratically on the attack distance according to  $\alpha_{95} \propto D_A^{-2}$ , which is precisely what Stillman found in his simulations.

## Introduction

Stillman *et al.* (2002) describes interference with help of an individual based foraging model in combination with rules for stealing prey. The resulting interference strength is largely dominated by the so called attack distance, the distance between a kleptoparasitic bird and its victim. The attack distance itself appeared to be a function of the handling time of the prey.

Applying Stillman's "quick prediction" in a food exploitation model is not as easy as it looks like, however. Even using his parameter values for Oystercatcher and Cockles for instance, we have nothing more than a graph describing the result of theoretical calculations.

This note is an attempt to understand some of the relations Stillman *et al.* (2002) give and to derive an approximate expression for their interference curves.

## An approximate interference model

Stillman *et al.* (2002, Figure 2) show that the profitability of stealing is larger than the profitability of independent foraging. This means that the presence of a suitable victim determines the frequency of kleptoparasitic behavior. And indeed, their model results suggest that interference is largely determined by a distance, the attack distance  $D_A$ . If there is a dominant bird within attack distance a prey stealing event takes place.

The distance to neighbouring birds is undoubtedly the result of a complicated game played by dominant and subdominant birds. In the end, however, there must be some relation with bird density. In a denser flock it will always be more difficult to avoid a stealing neighbour than in a sparse one. In order to understand this a little better, we start studying the *statistical distribution* of the nearest neighbour distance  $D$ .

## From distance distribution to interference model

Clearly, this distribution will depend on the average bird density  $\rho$ . In general, a 4 times larger bird density leads to 2 times smaller distances. Therefore it is advantageous to use the product  $\rho D^2$  as the stochastic variable instead of the distance  $D$  itself. The (stochastic)  $D^2$  is multiplied by the average bird density  $\rho$  in order to get dimensionless nearest neighbour distances, which are the same numbers for sparse and dense flocks.

For mathematical reasons we multiply the dimensionless numbers by  $2\pi$  and define our dimensionless distance variable  $x$  with

$$x = 2\pi\rho D^2.$$

The attack distance  $D_A$  characterizes a certain predator-prey combination and corresponds to a dimensionless distance  $x_A$  defined by

$$x_A = 2\pi\rho D_A^2. \tag{A.1}$$

Note that this  $x_A$  becomes larger for increasing bird density, reflecting that a increasing fraction of the distances comes within attack range.

In case of a random bird distribution, the dimensionless quantity  $2\pi\rho D^2$  has a Chi-square distribution with 2 degrees of freedom. The probability  $p$  that the actual distance  $D$  is *above* the attack distance  $D_A$  (and *no* stealing can take place) is the same as the probability that  $x$  is larger than  $x_A$ . It is given by an integral over the probability density of  $x$  according to

$$p = \int_{x_A}^{\infty} \chi^2(2, x) dx$$

where  $\chi^2(2, x)$  is the Chi-square probability density function of  $x$  with 2 degrees of freedom. Although this looks complicated, after substitution of the equation for the  $\chi^2$  distribution, the integration is easy and

$$p = e^{-x_A/2}. \quad (\text{A.2})$$

We now associate  $p$  with the relative uptake  $U$ , the uptake divided by the uptake without interference. However, this would leads us to  $U=p$ , which cannot be correct for several reasons. In the first place the distances within attack range should refer to subdominant neighbours, which will not always be the case. Secondly, prey stealing events take place in time and their frequency cannot be described as a static probability derived from a distance distribution. In an attempt to account for these complications we put a “calibration constant”  $\alpha$  in Equation A.2 and write

$$U(x_A) = e^{-x_A\alpha/2}. \quad (\text{A.3})$$

Note that Equation A.3 satisfies a few elementary conditions. For  $x_A = 0$ , there is no interference and the relative uptake is 1. For large values of  $x_A$  the relative uptake approaches zero. There are certainly many functions with this behaviour. The exponential function, however, appears in the above analysis of distances and it is interesting to see how far we can come with it.

The exponent in Equation A.3 may be seen as the actual argument of the relative uptake function (here exponential). It is a dimensionless number and we therefore call it the interference number  $\mathcal{I}$  defined by

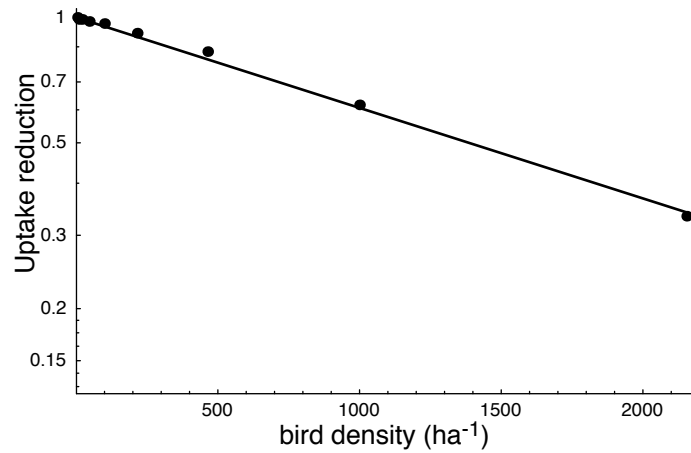
$$\mathcal{I} = x_A\alpha/2 = \pi\rho D_A^2 \alpha. \quad (\text{A.4})$$

This definition clearly implies

$$U(\mathcal{I}) = e^{-\mathcal{I}}. \quad (\text{A.5})$$

### The relative uptake as function of bird density

The shape of the uptake curves in [Stillman \*et al.\* \(2002, Figures 4a and 5a\)](#) is compared with the approximate model derived above. The parameter  $\alpha$  is found by fitting the approximate model to Stillman’s curves.



**Figure A.1.** The Oystercatcher-Cockle model results (black points) in [Stillman et al. \(2002, Figure 4a\)](#) redrawn using a linear bird density axis. The straight line is given by Equation A.6 using  $D_A = 2.0\text{ m}$  ([Stillman et al. \(2002, Table 3\)](#)) and  $\alpha = 0.40$  (fitted to the points).

We begin with substituting Equation A.1 in Equation A.3. The resulting equation predicts a simple exponential decrease with increasing bird density  $\rho$ . Using a linear horizontal axis for bird density and a vertical logarithmic axis for the uptake reduction, we expect to find a straight line relationship between  $\rho$  and  $U$ .

$$U(\rho) = e^{-\pi\rho D_A^2 \alpha} \quad (\text{A.6})$$

Figure A.1 shows the Oystercatcher model results in [Stillman et al. \(2002, Figure 4a\)](#) as black points. The line is given by Equation A.6 with  $D_A = 2.0\text{ m}$  ([Stillman et al. \(2002, Table 3\)](#)) and  $\alpha = 0.40$ , which was found by fitting the line to the Stillman's points.

The message of Figure A.1 is that the results of Stillman's detailed foraging and interference model can be described by means of a simple descriptive model in which the main interference parameter of the Stillman's model, the attack distance  $D_A$ , is retained and used in combination with one additional parameter, the fitted  $\alpha$ .

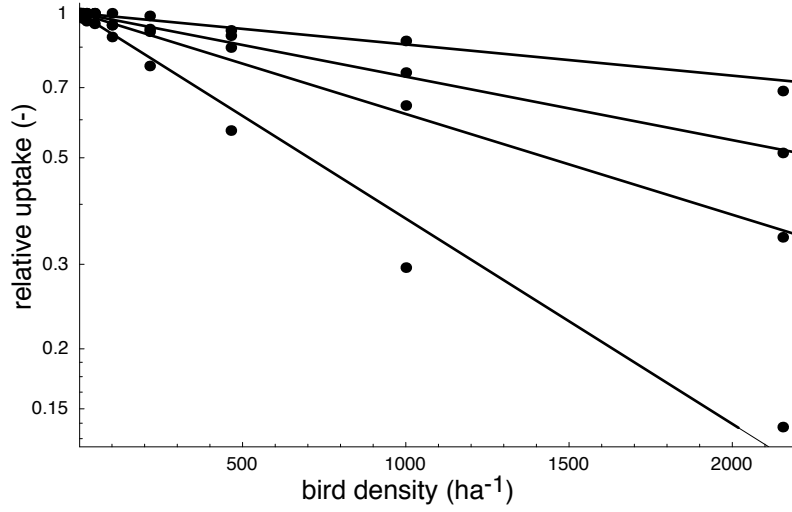
Also the other curves in [Stillman et al. \(2002, Figures 4 and 5\)](#) appear to become almost straight lines by using a linear density axis. Figure A.2 shows the points of [Stillman et al. \(2002, Figure 5b\)](#) combined with exponential uptake lines calculated for Stillman's  $D_A$  values and fitted  $\alpha$  values. The  $\alpha$  values used in the various lines are given in Table A.1 where they are compared with values calculated in the next section in a different way.

### The 95% threshold density

Also in the approximate model the 95% threshold density is a function the attack distance. This function is fitted to the threshold densities in [Stillman et al. \(2002, Figures 6a and 7a\)](#). Further, values of  $\alpha$  are derived from Stillman's 95% thresholds which are then compared to the ones found above.

According to Equation A.5 the uptake reduction  $U$  reaches 0.95 for interference





**Figure A.2.** The *Oystercatcher* model results (black points) in [Stillman et al. \(2002, Figure 5b\)](#) with exponential uptake lines based on  $D_A$  values from [Stillman et al. \(2002, Table 2\)](#) and the fitted  $\alpha$  values given in [Table A.1](#).

**Table A.1.**  $\alpha$  values found by fitting an exponential decrease through the model points in [Stillman et al. \(2002, Figure 5b\)](#) compared with  $\alpha$  values calculated from one uptake point, the threshold densities at 95% relative uptake in [Stillman et al. \(2002, Figure 6a\)](#)

predator-prey case	$D_A$	fitted $\alpha$	$\alpha$ from threshold
Oystercatcher & Large Spisula	3.6	0.242	0.251
Oystercatcher & Small Mussels	2.5	0.246	0.177
Oystercatcher & Small Spisula	1.7	0.335	0.367
Oystercatcher & Earthworms	1.5	0.234	0.212
Black-tailed godwit & Ragworms	1.7	0.293	0.277
Black-tailed godwit & Earthworms	0.8	0.283	0.328
Black-tailed godwit & Scrobicularia	0.7	0.180	0.228

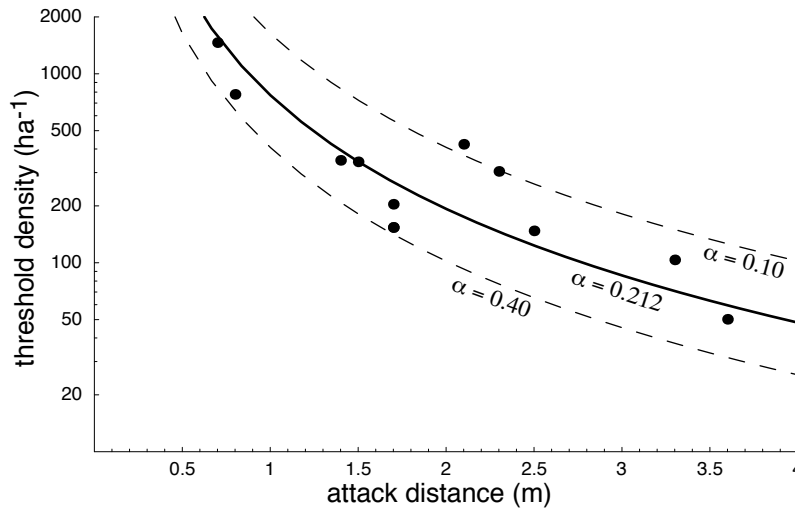
number  $\mathcal{I} = 0.05129$ . The corresponding threshold bird density  $\rho_{95}$  follows by rearranging Equation [A.4](#) leading to

$$\rho_{95}(D_A) = \frac{0.05129}{\pi D_A^2 \alpha}. \quad (\text{A.7})$$

This is an inverse quadratic function of the attack distance, which allows us to determine an “overall” value for  $\alpha$  from Stillman’s 95% threshold densities.

The points in [Figure A.3](#) show these threshold densities (read from [Stillman et al., 2002, Figures 6a and 7a](#)). The middle curve is the inverse quadratic function of Equation [A.7](#) with  $\alpha = 0.212$  as fitted parameter. This one parameter fit describes 73.3% of the variation in the points, which is slightly better than Stillman’s linear fit with 2 parameters. The dashed curves in [Figure A.3](#) give the function  $\rho_{95}(D_A)$  for  $\alpha = 0.1$  and  $\alpha = 0.4$ .

Also for each individual 95% threshold density a value for  $\alpha$  can be calculated. This means that for each predator-prey combination the exponential uptake function is drawn through 1 point: the point at threshold density  $(\rho_{95}, 0.95)$  (in combination



**Figure A.3.** The 95% threshold density as function of the attack distance  $D_A$ . The model results (black points) were taken from [Stillman et al. \(2002, Figures 6a and 7a\)](#). The curves have been calculated with Equation A.7 using three values of  $\alpha$ : 0.10, 0.212 (fitted to the points) and 0.40.

with the trivial point  $(0, 1)$ ), whereas in Figures A.1 and A.2 the uptake function was fitted through a series of uptakes values. The values of  $\alpha$  obtained from Stillman's threshold densities will be denoted as  $\alpha_{95}$  and are calculated as (e.g. Equation A.7)

$$\alpha_{95} = \frac{0.05129}{\pi D_A^2 \rho_{95}}. \quad (\text{A.8})$$

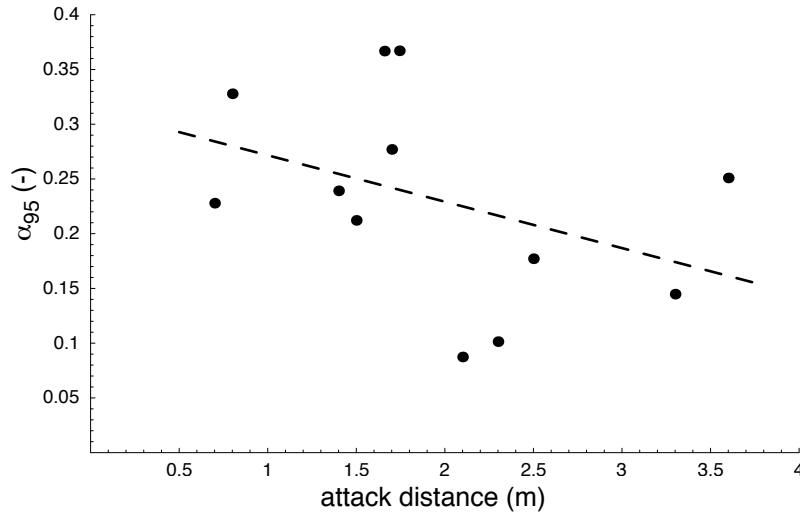
In Table A.1 seven out of twelve  $\alpha_{95}$  values are compared with the  $\alpha$  values obtained in the previous section from the seven uptake curves in [Stillman et al. \(2002, Figures 5\)](#). There is a reasonable agreement between the two sets, which means that the exponential uptake model works satisfactory: the exponent derived from a single point (with just 5% uptake reduction) is about the same as the slope derived from a series of points.

The 12 numbers  $\alpha_{95}$  represent parameter values for the 12 predator-prey cases in [Stillman et al. \(2002, Table 2\)](#). Since  $\alpha$  summarizes the influence of a lot of parameters on the behaviour of Stillman's interference model, we might ask if  $\alpha$  is related in a simple way to measurable properties of the predator-prey combination. A quick search with the parameters in [Stillman et al. \(2002, Table 2\)](#) yielded a weak relation with, again, the attack distance (see Figure A.4). It may be worthwhile to investigate this a little better.

## The strength of interference

In the approximate model Stillman's "strength of interference"  $m_{1000}$  is calculated as function of the attack distance. The result is compared to the  $m_{1000}$  values in [Stillman et al. \(2002, Figures 6b and 7b\)](#).

According to Stillman's definition the strength of interference derived from Equa-



**Figure A.4.**  $\alpha$  values calculated from the 12 threshold densities in [Stillman et al. \(2002, Figures 6a and 7a\)](#) plotted as function of the attack distance  $D_A$ . The decrease is not significant.

tion [A.6](#) becomes ( $1000 \text{ birds ha}^{-1}$  is  $0.1 \text{ m}^{-2}$ )

$$m_{1000}(D_A) = -\frac{\rho}{U} \frac{dU}{d\rho} \Big|_{\rho=0.1} = \pi \rho D_A^2 \alpha \Big|_{\rho=0.1} = 0.1 \pi D_A^2 \alpha \quad (\text{A.9})$$

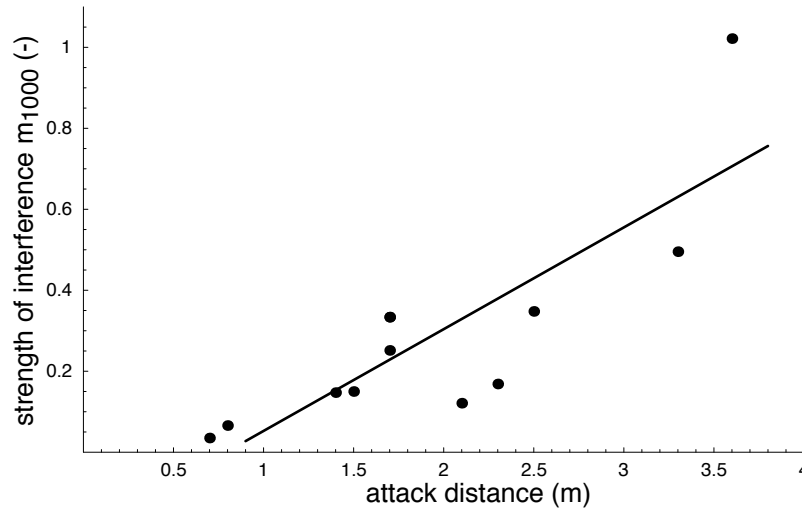
Note that this is precisely the interference number  $\mathcal{I}$  at a bird density of  $1000 \text{ ha}^{-1}$ . Equation [\(A.9\)](#) predicts a quadratic relation between the strength of interference and the attack distance (if  $\alpha$  is not correlated with the attack distance for the cases considered).

For Stillman's 12 predator-prey cases we calculated  $m_{1000}$  from Stillman's attack distances and the  $\alpha_{95}$  values derived from the threshold densities in the previous section. Figure [A.5](#) shows the result as function of the attack distance. The most striking difference with [Stillman et al. \(2002, Figure 7\)](#) is that the values predicted by the exponential model are smaller, especially for the larger attack distances.

In order to understand this we have to realize that  $m_{1000}$  is the slope of the relative uptake curve (at  $\rho = 1000$ ) on double logarithmic paper. Apparently, these slopes are steeper in Stillman's detailed model than in the approximate exponential model. This probably is a real difference between the two models. For larger densities the relative uptake curve tends to be a little steeper than predicted by the exponential model on the basis of the threshold bird density (cf. Figures [A.1](#) and [A.2](#)).

## Discussion

The usefulness of a simple exponential interference model depends on the purpose of the calculations. In a specific situation, like in the Oystercatcher-Cockle case (Figure [A.1](#)), the approximation is sufficiently accurate and does not require simulations of the foraging process. The approximate model still requires, however, a value of  $\alpha$  fitted to either field data or results of a detailed foraging model.



**Figure A.5.** The strength of interference  $m_{1000}$  as function of the attack distance (at  $\rho = 1000$ ) calculated with Equation A.9 using the attack distances  $D_A$  from Stillman et al. (2002, Table 2) and the  $\alpha$  values derived from 95% threshold densities. The regression line is given by  $-0.199 + 0.251D_A$ .

It is interesting to speculate on out why the 95% threshold density in the model fits so well to Stillman’s results and the strength of interference fails to do so. The exponential expression in Equation A.5 can be replaced by any function that continuously decreases from 1 to 0 on  $[0, \infty]$ . As long as the uptake reduction depends solely on  $\mathcal{I}$  there is a single value of  $\mathcal{I}$  at which 95% uptake is reached. This single value implies the quadratic behaviour of  $\rho_{95}$  in Equation A.7. Hence, the fit with Stillman’s data is independent of the precise shape of the relative uptake curves, as long as it is a unique function of  $\mathcal{I}$ .

This does not hold for the strength of interference as function of  $D_A$ . That relation does depend on the *shape* of the uptake reduction function since it is the slope of the relative uptake on double logarithmic paper. One of the reasons for

Values of  $\alpha$  can also be calculated from the  $m_{1000}$  values in Stillman et al. (2002, Figure 6b). This means, however, that  $\alpha$  is found from the slope at  $\rho=1000$  and we should realize that we want approximate uptake values rather than slopes of uptake curves. Therefore we estimated  $\alpha$  values from uptake curves and from threshold densities (points on uptake curves).

## Appendix B

# Model parameter file

The datafile given here contains the parameters discussed in Chapters 5, 6 and 7. The file below is the one used for the historical runs in the period 1990–2001.

The datafile is a TTUTIL ([van Kraalingen & Rappoldt, 2000](#)) input file. Every value is identified with a name and the order of the variables on datafile is arbitrary. Values can be either a character string, an integer value, a real value, a date or time, or a logical value. Note that anything behind an exclamation mark is comment added to the datafile.

```
! BIRD parameters (for current input reading same for all areas)
! =====
! bird weight
! weight set point during the year as function of day number [1,367]
!
! Oosterschelde (Fig 15) ZwartsHulscherEtAl1996
!
SetPointTableOS =
  1.0, 562.0, ! (-, gram)
  31.0, 565.0,
  60.0, 560.0,
  91.0, 530.0, ! 31-3  october weight
  244.0, 520.0, ! 31-8
  274.0, 530.0, ! 30-9
  305.0, 550.0, ! 31-10
  335.0, 560.0, ! 30-11
  367.0, 562.0

!
! Wadden Sea (Fig 15) ZwartsHulscherEtAl1996
!
SetPointTableWS =
  1.0, 615.1 ! average of january and december
  16.0, 617.7 ! average of december and february
  46.0, 623.0
  75.0, 575.3
  106.0, 566.3
  136.0, 540.0
  167.0, 529.7
  197.0, 535.2
  228.0, 550.0
  259.0, 547.8
  289.0, 555.7
```

```

320.0, 593.7
350.0, 612.4
367.0, 615.1 ! average of january and december

! InitialWeight = 500.0 ! read from table unless activated
MinimumWeight = 400.0 ! gram (technical limit, bird is dead)

! energy requirement
!
FysiolEquatCons = 0.061 ! param a in: KJ/day = a (gram)^b ZwartsEnsKerstenEtAl1996
FysiolEquatPowr = 1.489 ! param b in: KJ/day = a (gram)^b ZwartsEnsKerstenEtAl1996

ThermoEquatOffs = 904.0 ! (kJ / day) KerstenPiersma1987
ThermoEquatFact = 30.3 ! (kJ / day / deg) KerstenPiersma1987

FractionTakenUp = 0.85 ! Speakman1987, KerstenVisser1996,
! KerstenPiersma1987, ZwartsBlomert1996

MaxDigestRateWtW = 378.72 ! 0.263 * 60.0 * 24.0 in gram WtW / day KerstenVisser1996
MaxStorageWtW = 80.0 ! gram WtW KerstenVisser1996
! The digestion rate is 0.263 gr WtW / min
! which is 4.38 mg WtW/s or 0.701 mg AFDW/s

BestLiverConKJ = 100.0 ! buffer between body weight and daily intake + usage
MaxLiverConKJ = 200.0 ! buffer between body weight and daily intake + usage

BodyGramEnergyCont = 34.295 ! 0.85 * 39.3 + 0.05 * 17.8 in kJ / gram
BodyGramEnergyReq = 45.66 ! kJ / gram 25 % larger ?????? $$$$$$

LeftOverKokkel = 0.10 ! ZwartsEnsKerstenEtAl1996
LeftOverNon = 0.10
LeftOverMossel = 0.10
LeftOverothers = 0.00 ! n.v.t.

! functional response
FRtype = 'LeoZwarts' ! type of functional response
! LeoZwarts => regression from Leo Zwarts data
! Norris&Johnstone => NorrisJohnstone1998
!
! CaptureRateN = 0.000860373 * density /
! (1.0 + 0.220524 * Size**1.79206 * 0.000860373 * density)
!
leoA = 0.000860373 ! based on data in ZwartsEnsDurellEtAl1996
leoB = 0.220524 ! fit in Matematica notebook C. Rappoldt 2002
leoC = 1.79206 ! density (#/m2) ; Size (mm) ; CaptureRate (#/s)

! functional response Macoma (OS run 60 and higher, alle WZ runs)
hiddinkA = 0.000625
hiddinkB = 0.000213

! functional response Mossel (Oosterschelde, 1 type of Mossel)
MosselSeptAFDWrate = 0.0025 ! gram AFDW per second (Goss-Custard)
MosselA = 0.00057 ! estimated by assuming 95% of max uptake at
! 80 gram AFDW/m2 (= 80.0/StandardMosselAFDW) #/m2 (Goss-Custard Fig 1b)
! max capture rate (MosselSeptAFDWrate/StandardMosselAFDW)
! which implies handling time h=(StandardMosselAFDW/MosselSeptAFDWrate)
! =340 seconds
! Then MosselA=0.95/0.05/h/(80.0/StandardMosselAFDW)=
! (0.95*MosselSeptAFDWrate)/(0.05*80)=0.00057 (m2/s)

! functional response Mossel (WaddenSea, several types of Mossel)
! y = a x^b is intake rate (mg AFDW / s) as function of prey weight x (mg AFDW)
! so this is the plateau of the functional response as function of prey weight
! from Figure 12B ZwartsEnsDurellEtAl1996
MosselIntakeRateA = 0.092

```

```

MosselIntakeRateB = 0.506

! OTHER preys
MinimumRateAFDW = 0.00 ! milligram AFDW per second
OtherPreysFraction = 0.10 ! uptake of unspecified preys (WtW only)
! as a fraction of the WtW uptake of regular preys

! non-mudflat uptake
NonMudThreshold = 0.4 ! intensity threshold
MaxNonMudIntakeRateAFDW = 0.6 ! mg AFDW per second

LowTempTable = ! correction of maximum foraging rate
-50.0 0.0 ! as function of average temperature
-5.0 0.0 ! is used with average temperature
0.0 1.0 ! of previous tidal period
+50.0 1.0

! interference model for Oystercatcher-Cockle pair
InterferenceType = 'ApproximateStillman'

! interference model for Oystercatcher-Cockle pair
KokkelAttackDistance = 2.0 ! (m) StillmanEtAl2002
KokkelInterferenceAlfa = 0.40 ! (-) Rappoldt2002A

! interference model for Oystercatcher-Mossel pair (used for Oosterschelde vanaf 60)
MosselAttackDistance = 2.3 ! same as for WaaddenSea consumption size
MosselInterferenceAlfa = 0.210 !

! interference model for Oystercatcher-Mossel pair (used for WaddenSea)
MZaadAttackDistance = 2.5 ! (m) StillmanEtAl2002 for small mussels
MZaadInterferenceAlfa = 0.254 ! (-) regression on Stillman's model results
MHalfAttackDistance = 2.5 ! (m) StillmanEtAl2002 for small mussels
MHalfInterferenceAlfa = 0.254 ! (-) regression on Stillman's model results
MconsAttackDistance = 2.3 ! (m) StillmanEtAl2002 for large mussels
MconsInterferenceAlfa = 0.210 ! (-) regression on Stillman's model results

! Reduced intake rate during "Above Digestion Rate" time window
RIRandSpread = .true. ! reduce intake rate and spread birds
RIRoffsetTime = 1.0 ! (hour) time offset after reaching ADR time window

! measuring the numerical response
NumRespWindow = 1.0 ! hour (around time of low tide)

! PREY parameters
! =====
! Wet weight change
CockleCurveType = 'Klepper' ! option for Wet Weight change
! Klepper => use Klepper's curves for relative rates
! Tables => use interpolation table below

! this interpolation table (Relative_Growth_Rate (per day) versus Day_Of_Year DOY)
! gives a factor 0.5 loss in 180 days
Wgain_0j_Table = 1.0, -0.00385, 367.0, -0.00385 ! table for 0j cockles
Wgain_1j_Table = 1.0, -0.00385, 367.0, -0.00385 ! table for 1j cockles
Wgain_2j_Table = 1.0, -0.00385, 367.0, -0.00385 ! table for 2j cockles
Wgain_mj_Table = 1.0, -0.00385, 367.0, -0.00385 ! table for mj cockles

! Fresh weight change
FWrgrTable = ! Interpolation table for
0.00000 0.79129 ! relative growth rate (per year) as function of
0.50000E-01 0.75207 ! time expressed in years after 1-Januari of the
0.10000 0.84790 ! year after the "birth" of the cockles
0.15000 1.0788
0.20000 1.4448
0.25000 1.9458

```

0.30000	2.5819
0.35000	3.1536
0.40000	3.4613
0.45000	3.5051
0.50000	3.2849
0.55000	2.8008
0.60000	2.0527
0.65000	1.2773
0.70000	0.71118
0.75000	0.35434
0.80000	0.20679
0.85000	0.17182
0.90000	0.15276
0.95000	0.14959
1.0000	0.16233
1.0500	0.19097
1.1000	0.23550
1.1500	0.29594
1.2000	0.37228
1.2500	0.46452
1.3000	0.57266
1.3500	0.69670
1.4000	0.83664
1.4500	0.94189
1.5000	0.96179
1.5500	0.89635
1.6000	0.74555
1.6500	0.56408
1.7000	0.40655
1.7500	0.27297
1.8000	0.16333
1.8500	0.77636E-01
1.9000	0.15888E-01
1.9500	-0.21916E-01
2.0000	-0.35774E-01
2.0500	-0.30909E-01
2.1000	-0.12536E-01
2.1500	0.19344E-01
2.2000	0.64731E-01
2.2500	0.12363
2.3000	0.19603
2.3500	0.28193
2.4000	0.38135
2.4500	0.45748
2.5000	0.47353
2.5500	0.42949
2.6000	0.32538
2.6500	0.16118
2.7000	-0.63101E-01
2.7500	-0.25644
2.8000	-0.32782
2.8500	-0.27724
2.9000	-0.10469
2.9178	-0.13815E-01

! conversion FreshWeight to Size  
! using  $\ln(\text{FW}) = 3.148 \ln(\text{Size}) - 8.442$  (Ens, Personal Communication)  
! (which leads to  $B=1/3.148=0.3177$  and  $A=\text{EXP}(8.442/3.148)=14.61$ )  
!  
CockFWtoSizeA = 14.610 ! param a in:  $L = a \text{ FW}^b$  (mm = a gram<sup>b</sup>)  
CockFWtoSizeB = 0.31766 ! param b in:  $L = a \text{ FW}^b$  (mm = a gram<sup>b</sup>)

! conversion FreshWeight to WetWeight  
CockCookedToFW0j = 0.2067 ! (-) KestelooHendrikse2002A  
CockCookedToFW1j = 0.1970 ! (-) ,,



```

CockCookedToFW2j = 0.1701 ! (-) ,,
CockCookedToFWMj = 0.1681 ! (-) ,,
RatioCookedToWet = 0.94 ! (-) Kesteloo (metingen 12 december 2002)

! Mossel conversion for WaddenSea FreshWeight (gram) to Size (mm)
! using Size(mm) = a FW^b (values inverse of mean curve Ens, pers.comm)
MosFWtoSizeA = 19.6929
MosFWtoSizeB = 0.333968

! Mossel conversion to wet weight
! using BIndex (Rob Dekker, Bert Brinkman)
! this is gram ADW / L^3 (L in mm)
! value for september is mean of august and oktober values
MosBIndexSept = 5.82E-06

! conversion Macoma FreshWeight to Length (Bruno Mokbaai data, studentenverslag)
! FW(gr) = a L(mm)^b : a=7.25E-5 b=3.34
! L(mm) = A FW^B : A=17.35 B=0.2994
!
MacomaFWtoSizeA = 17.35
MacomaFWtoSizeB = 0.2994

! conversion Macoma Length to AFDW weight (Leo proefschrift Table 6, month 8)
! ln(mg) = -4.759 + 3.063 ln(mm) ==>
! mg = 0.008574 * mm^3.063 ==> (combined with FreshWeight to Length)
! mg = 0.008574 * (17.35 FW^0.2994)^3.063
! mg = 53.600 * FW^0.917 (mg AFDW)
! gram = 0.0536 * FW^0.917 (gram AFDW)
! gram = (0.0536 / RatioAFDWtoWet) * FW^0.917 (gram WtW)
!
MacomaFWtoWtWA = 0.335 !!!!! = 0.0536 / RatioAFDWtoWet
MacomaFWtoWtWB = 0.917

! natural death rate Cockles
CockleDeathRate = 0.00033 ! per day (1% per month)

! prey energy content
RatioAFDWtoWet = 0.16 ! - ZwartsEnsDurellEtAl1996
AFDWenergyContent = 22.5 ! kJ / gram ZwartsEnsDurellEtAl1996

! standard mussel parameters (Oosterschelde)
! volgens Waddenzee data (variabelen MosFWtoSize en MosBIndexSept)
! komt de standaard mussel van 0.85 gr AFD overeen met 19 gram FW ; 52 mm
! dat levert een WtW/FW verhouding van (0.85/0.16) / 19 = 0.28
StandardMusselAFDW = 0.85 ! gram (Goss-Custard for 45 mm mussel in september)
StandardMusselWtWtoFW = 0.28 ! rough estimate for september

! weight gain and death rate
MusselWtWgain = -0.0025 ! gram per day per gram startweight
! (Figure 2 Goss-Custard for 45 mm mussel)
MusselDeathRate = 0.00033 ! per day (1% per month)
MacomaWtWgain = -0.0025 ! mussel value taken
MacomaDeathRate = 0.00033 ! per day (1% per month)

! FISHING parameters
! =====
FishingType = 'FixedDatePerClass' ! Fishing method ; one of these:
! NoFishing => No fishing
! FixedDatePerSpot => B Box data per spot
! FixedDatePerClass => B Box data per class

PerClassOption = 'LevelOff' ! FixedDatePerClass option for rich spot fishing
! LevelOff => reduce rich spots to some FW density
! Empty => reduction to zero of richest spots

```

```

SpotClassSize   = 5.0      ! percentage of exposed time fraction
GhostCorrection = .false.

FixedFishingDOY = 274.0    ! 1-October as fixed date for removal
ThresholdSize   = 22.0     ! mm

DamageRemaining = 0.10     ! fraction dead of undersized cockles
FishingEfficiency = 0.95   ! landed fraction of removed (or killed) cockles

```

## Appendix C

# The power of a linear trend test

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A trend is fitted by a simple linear (least-squares) regression. Since the test of the regression slope is, in fact, a one-sample  $t$ -test, the power can be relatively simply calculated by using the cumulative Students  $t$ -distribution function ( $\text{TCF}(n, t)$ , with  $n$  degrees of freedom), where the effect size  $d$  is expressed as the size of the trend (the slope of the regression) divided by its standard error (which follows from the estimated error variance and the number points  $n$ ).

The power  $P$  belonging to a certain significance level  $\alpha$  is the probability that a true effect  $d$  (the average effect over many experiments) is actually detected as a significant slope in a one-sample  $t$ -test. With a significance level  $\alpha$  corresponds a two-sided  $t$  value of  $t_\alpha$ , say. Then the probability  $P$  that a value drawn from a  $t$ -distribution around  $d$  lies either above  $t_\alpha$  or below  $-t_\alpha$  becomes

$$P = 1.0 - \text{TCF}(n - 2, t_\alpha - d) + \text{TCF}(n - 2, -t_\alpha - d) \quad (\text{C.1})$$

The type-ii error is the probability that the statistical test with significance level  $t_\alpha$  does not lead to a significant result although there actually is an effect of size  $d$ . Hence, the type-ii error is equal to  $1 - P$ .

## Appendix D

# The Norris & Johnstone functional response

This is a Fortran program section. It is probably a better summary of [Norris & Johnstone \(1998\)](#)'s method than a more abstract description. The original paper is not easy to read and it is somewhat questionable whether or not a unique transcription into a program text is possible or not. Therefore just the source code.

```
BillTipWidth      = 0.179  ! cm
BillTipLength     = 1.1    ! cm
ProbingRate       = 5.5    ! s-1
ReductionInSitu   = 0.438  ! -
ReductionWasteInSitu = 0.266 ! -
OpenedFractionInSitu = 0.75  ! -

TakenList = (/1.000, 1.000, 1.000, 1.000, 0.773, 0.024/)

ShellArea(ip) = (0.479 * Prey(ip)%Size**2.003) / 100.0
TouchArea(ip) = BillTipWidth * BillTipLength + ShellArea(ip) + &
    2.0 * (BillTipWidth + BillTipLength) * SQRT(ShellArea(ip)/PI)
EncounterRate(ip) = ProbingRate * Prey(ip)%Number * TouchArea(ip) / 10000.0
CockleSizeClass(ip) = (Prey(ip)%Size + 2.5) / 7.0
ProbTaken(ip) = TakenList(MIN(NINT(CockleSizeClass(ip)),5))
HandlingTimeCarried(ip) = 3.339 + 8.615 * CockleSizeClass(ip)
WasteHandlingTimeCarried(ip) = 22.380 - 3.015 * CockleSizeClass(ip)

if (Prey(ip)%Size > 22.0) then
    ProbCarried(ip) = 1.0
else
    ProbCarried(ip) = 0.441
end if

OpenedFractionCarried(ip) = 1.0 / (1.0+Exp(0.384*CockleSizeClass(ip)-2.57))
OpenedFraction(ip) = ProbCarried(ip) * OpenedFractionCarried(ip) + &
    (1.0-ProbCarried(ip)) * OpenedFractionInSitu
HandlingTime(ip) = HandlingTimeCarried(ip) * &
    (ProbCarried(ip) + (1.0-ProbCarried(ip)) * ReductionInSitu)
WasteHandlingTime(ip) = WasteHandlingTimeCarried(ip) * &
    (ProbCarried(ip) + (1.0-ProbCarried(ip)) * ReductionWasteInSitu)

denom = denom + EncounterRate(ip) * (HandlingTime(ip) * OpenedFraction(ip) + &
    (1.0-OpenedFraction(ip)) * WasteHandlingTime(ip)) * ProbTaken(ip)
```

```

! eaten numbers and wet weight per bird per day (day as unit of time)
do ip=1,np
  Prey(ip)%EatenN = EncounterRate(ip) * OpenedFraction(ip) * &
                    ProbTaken(ip) / denom * 86400.0
  Prey(ip)%EatenWtW = Prey(ip)%EatenN * Prey(ip)%WetWeight
end do

```