Suggestions for an oystercatcher population model

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CONTENTS

1. INTRODUCTION

This report examines the current status of the simulation model "**BOULIMIA**" or "**EFFECTx.x**", where x.x denotes the version number, that was developed for the National Institute of Coastal and Marine Management (RIKZ) of the Dutch Ministry of Transport and Waterways (Min V en W). The primary objective of the report is to make suggestions for improvement with regard to (1) the general structure of the model and (2) parameter estimates. The model aims to predict the effect of man-induced habitat changes on the food intake, distribution and survival of Oystercatchers (*Haematopus ostralegus*) in a local estuary. These habitat changes include complete loss of habitat due to engineering works, as well as reductions in the food supply due to shellfish fisheries. Before we can give suggestions for improvement, what we must ask is how accurate we can expect the predictions from the current version of the model to be? To answer this question we rely heavily on recent investigations of our own, often in cooperation with others.

2 BACKGROUND OF THE BOULIMIA/EFFECTx.x MODEL

2.1 Relationship to other models

The model **BOULIMIA** was originally developed by Bos (1994) following discussions with B.J. Ens and others at a time that the development of a model with similar aims was already well under way. This other "shellfish-shorebird" model is developed for the European Union under contract PEM9303 by a consortium of the Institute of Terrestrial Ecology (ITE), the Royal Society for the Protection of Birds (RSPB) and the Institute for Forestry and Nature Research (IBN-DLO). It aims to extend the "Exe estuary Oystercatcher-Mussel model", to include Cockles and other important Oystercatcher foods, the population dynamics of the shellfish, and the effects of shellfish fishery through disturbance and stock depletion.

The Exe model is the culmination of almost two decades of detailed investigations of John Goss-Custard and his group on Oystercatchers feeding on Mussels in the estuary of the Exe. Version 1 of the Exe model is described by Goss-Custard et al. (1995a&b). Version 2 is addressed in many of the chapters in Goss-Custard (1996a) and an appendix, where Clarke & Goss-Custard (1996) provide a full mathematical definition. The Exe model, and, as a consequence, the shellfish-shorebird model, are very complex simulation models with a huge number of parameters. The primary cause of this complexity is that the population is modeled as being composed of distinct individuals and the fate and whereabouts of each of those individuals is continuously recorded. Each individual is characterized by a vector of properties. Properties that are fixed for a given year include: age class, feeding method, foraging efficiency and global dominance. Variable properties include: local dominance (dependent on the presence of other birds), interference-free intake rate (dependent on feeding method, foraging efficiency and food supply), intake rate (dependent on interference-free intake rate, local dominance and oystercatcher density), energy requirements (dependent on temperature) and body weight (dependent on assimilated intake and previous body weight).

The "shellfish-shorebird" model will incorporate almost every detail that is known on the behavioural ecology of wintering Oystercatchers. Nonetheless, being a complex simulation model, it is not without problems:
(1) It is hard to fully understand how it works, i.e. it is very hard to identify the basic cause of any patterns that emerge. As a result it is hard to know if the model captures the essence of the problem. Correct patterns may emerge for the wrong reason.
(2) Incorporation of the many "known" biological details requires assumptions on unknown relationships. For instance, are foraging efficiency and global dominance correlated or uncorrelated properties of an individual?
(3) With increasing complexity, it becomes increasingly cumbersome to perform a full sensitivity analysis of the model.

(4) It is increasingly easy to make programming mistakes and increasingly difficult to identify such mistakes when the complexity of the model increases.

(5) Running the model requires a lot of computing time and memory space.

(6) Application of the model to a specific case requires measurement of a large number of parameters.

This list makes one wonder if this is really the best way to proceed. According to Goss-Custard (1996b) it is. According to us, there is at the very least room for models that are made as simple as possible. The predictions of these very simple models can then be compared with the predictions of the more complex model. Although the simple models will necessarily ignore much biological detail, they also avoid the problems listed above, so that is not clear a priori which is the better approach. There is certainly much to be learned from a comparison. Convinced by these arguments, Bos (1994) set out to construct a model where it was not necessary to follow the fate of individual birds, even though the basic spirit of the approach was maintained, which Ens, Piersma & Drent (1994) describe as follows:

1.Population processes must be understood from the strategic decisions made by the individuals comprising the population, or "society" as we prefer to call it.

2. Strategic decisions have been shaped by natural selection, i.e. animals are expected to choose those alternatives that yield the highest gains in terms of fitness, or a short-term goal expected to correlate with fitness.

3. The most likely short-term goal during the non-breeding season is maintaining energy balance. At the very least maintaining energy balance is an important constraint: no bird can maintain a negative energy balance indefinitely and a migrant without sufficient energy reserves will not reach its destiny.

However, the resulting model of Bos (1994), although considerably less complex than the Exe model, was not as simple as seemed possible. Partly for this reason, IBN and NIOZ also initiated the development of a simple model, to which we will refer as the **DEPLETE** model. In some respects **DEPLETE** is better described as a family of models, providing a common framework that allows us to explore the effect on the model predictions of changing parts of the structure, like the interference function.

Summarizing, three models dealing with the interaction between shellfish and shorebirds are currently developed:

(1) The complex "shellfish-shorebird" model for the EU of ITE/RSPB/IBN. As not all parts of this model are currently available (the final report will appear early 1997), we will discuss its' precursor version 2 of the Exe model instead, to which we will refer as **EXE2** and which is well documented.

(2) The **BOULIMIA** model of RIKZ of intermediate complexity on which several publications exist. The most recent version of this model is named **EFFECT1.1**.

(3) The very simple **DEPLETE** model(s) of NIOZ/IBN, which we develop ourselves.

Throughout the report, these three model names will be printed in bold capital letters, e.g. **EXE2**, **BOULIMIA/EFFECT1.1** and **DEPLETE**. Names of variables and subroutines that are used in the **EFFECT1.1** source code will be printed in capital letters.

2.2 Additions and alterations of BOULIMIA

BOULIMIA was developed by Bos (1994), as a series of FORTRAN routines. These routines are run within SENECA, a programming environment designed to facilitate the development and use of simulation models couched in terms of differential equations. In this report we will not concern ourselves with SENECA, but only with **BOULIMIA**. Apart from preliminary simulation results, Bos provided an extensive documentation of the conceptual foundations, parameter estimates and the functioning of the model. Bos (1994) stressed the preliminary nature of the model and warned that it could not yet produce reliable predictions. He did feel, however, that it could be used to make general statements on the interaction between shellfishing and Oystercatchers. As Bos did not analyse how sensitive his general conclusions were to the various model assumptions, like the shape of the interference function, we regard this belief as unfounded.

Despite the warnings of Bos that the model was not yet in a shape to be used for particular real-life cases, Kater (1995a) employs the model to study the effect of dredging and other human activities on the carrying capacity of the Westerschelde for Oystercatchers. The modified model is referred to as **EFFECT1.0**. Mistakes may have been introduced when **BOULIMIA** was modified to **EFFECT1.0**, as some simulation results show increasing Oystercatcher numbers in the course of the season, whereas the logic of the model only allows constant or decreasing numbers in the course of the winter (a specified number of Oystercatchers enters the estuary at the start of the winter and these birds may or may not survive). Some of the rather surprising conclusions of Kater (1995a), like the conclusion that turning polders back into mudflats will negatively affect carrying capacity, are probably due to these mistakes in the program.

The mistakes were probably rectified in the version **EFFECT1.1** used by Kater (1995c), as the total number of Oystercatchers no longer increases during the winter in the simulations that are presented. In the first part of the report of Kater a description of the redistribution procedure is given, which we failed to understand. In the second part some real-life simulations are presented, where real-life means that actual Cockle data and actual weather data were used. One of the conclusions is that the model fails to predict the number of Oystercatchers in the Oosterschelde. The criticism that the model should not yet be used for real-life situations still applies. In the final part of the report a sensitivity analysis is performed on the various model paramters and forcing functions. It is concluded that the model is especially sensitive to variation in handling time and basal metabolic rate. It is not investigated how sensitive these conclusions are to changes in the model structure.

Hoen (1996a) reports observations on the prey choice of Oystercatchers in the Oosterschelde and discusses the subroutine DEE.FOR that estimates the daily heat loss for a given combination of wind force, ambient temperature and solar radiation. As far as we can make out this discussion adds very little to the original paper of Wiersma & Piersma (1994) and the model formulation of Bos (1994).

In a second report, Hoen (1996b) discusses the sensitivity of the model for variation in these heat loss parameters. Hoen concludes that the model predictions are very sensitive to those parameters that have not been measured but that were guesstimated by Wiersma & Piersma (1994) to convert the equations that were obtained for Knots to equations that might apply to Oystercatchers. See also appendix B.

In a final contribution, Van Hattum (1996) investigates the effect of using different data files for wind force and ambient temperature. He finds that Oystercatcher populations crash at high wind speeds, as these can dramatically increase the energy demands of the birds.

The source code of the biologically important subroutines of the version 1.1 of **EFFECT** *that we investigated is listed in Appendix A.*

2.3 Conclusions

1. **EXE2, EFFECT1.1** and **DEPLETE** have the same purpose (to predict the effect of man-induced habitat changes on distribution and overwinter mortality of Oystercatchers) and the same general structure. However, **EFFECT1.1** is less complex than **EXE2** and more complex than **DEPLETE.**

2. Recent modifications to **BOULIMIA** mainly involve programming technicalities. Mistakes may have been introduced due to these modifications, but have probably been corrected in **EFFECT1.1**. The lack of a detailed documentation of the various changes does not allow a decisive judgement; the best description of the concepts, the equations and the program underlying **EFFECT1.1** is still provided in the report by Bos (1994) on **BOULIMIA**. As the source code of **EFFECT1.1** is not very long (see appendix A), it would be easy and helpful to incorporate the documentation on the paramaters (meaning, units of measurement, references) in the source code.

3. Much effort has been directed to calibrating the model and a sensitivity analysis of parameters. In our view, this research effort should have been directed to an investigation of the sensitivity of the model to changes in its' structure.

4. The model has been used to make both general statements on the effect of shellfish fisheries on Oystercatchers, as well as to study specific real-life cases. Given the current status of the model, we regard these conclusions as unfounded.

3   GENERAL DESCRIPTION

3.1   Conceptual foundation: the starvation dogma

The belief that starvation is the primary risk that Oystercatchers face during winter is the common thread that runs through many contributions of the recent account of Oystercatcher ecology edited by Goss-Custard (1996a). It leads to the assumption that the birds will often seek to maximize the rate of energy gain whilst feeding. It also leads to the assumption that competition will be mainly for food and that the negative effects of competition can be gauged in terms of by how much the rate of food intake is decreased by an increase in the density of competitors. Finally, it comes as no surprise that, in this view, Oystercatcher numbers in winter are thought, at least in part, to be limited by their food supply. It follows that a decline in the food supply, for whatever reason, should lead to increased mortality and a decline in numbers.

Widely held beliefs are not necessarily true, but there is certainly strong evidence that Oystercatchers often die of starvation. During severe winters, much of the food supply becomes covered with ice, while energy demands of the birds are very high. Several severe winters during the last decades are known to have led to mass mortality among Oystercatchers and other waders (reviewed in Goss-Custard et al. 1996c). The extremely low weights of the dead birds strongly suggest starvation (Swennen & Duiven 1983; Hulscher 1989). It does not necessarily follow, however, that the size of the food supply would have made a difference for their survival: the birds simply can't feed when their food is covered by ice. To survive such difficult periods, the birds accumulate fat reserves in advance (Hulscher 1989; Zwarts et al. 1996d). It may be hypothesized that poor food supplies prevent the birds from accumulating sufficient reserves, making them especially vulnerable to severe winter weather. Remarkably, the evidence that this scenario actually works and that, all else being equal, poor food supplies increase mortality in winter is rather limited. Lambeck, Goss-Custard & Triplet (1996) provide anecdotal information for the Delta estuary in the Netherlands that mortality of Oystercatchers increased when the birds lost part of their feeding habitat due to engineering works. The problem is that the relatively small number of years to which the study was necessarily restricted were characterized by a series of exceptionally severe winters. The most convincing evidence that poor food supplies increase mortality therefore comes from Camphuysen et al. (1996), who were able to draw on a thirty year long series of beached bird surveys along the Dutch coast and a twenty year long series of benthos sampling in the Dutch Wadden Sea (Beukema 1982a, 1982b, 1993). They found that when the effect of winter severity on Oystercatcher mortality was controlled for, more Oystercatchers died on the coast in years with poor food supplies.

While risk of parasitism cannot be ruled out as an important agent in population regulation of Oystercatchers, there are as yet no "positive" signs that it might be important. Thus, it makes sense to stick to the assumption that underlies all current models (**EXE2, EFFECT, DEPLETE**), that starvation

is the primary risk Oystercatchers face during winter. From this it follows that (1) energy need of the individual, (2) intake of energy as a function of food supply and (3) the negative effects of conspecifics on energy intake must be the main elements of a model describing the effect of shellfisheries and other habitat changes on the winter mortality of the Oystercatcher. In this respect we completely agree with the current formulation of **EFFECT1.1**.

3.2 General structure of EFFECT1.1

Since the starvation dogma underlies all current Oystercatcher distribution models, the following description in fact applies not only to **EFFECT**, but to all of these models. Fig. 1 highlights the main steps in the argument.

1. The *simple functional response* describes the relationship between the intake rate of food and a measure of the food supply. This measure of the food supply may be a single variable (like the biomass density of Cockles in the current subroutine FR.FOR of **EFFECT1.1**). More likely a whole range of variables must be measured to characterize the food supply in a given locality: for each potential prey species the density of each size class, the depth distribution per size class, the shell thickness distribution per size class etc. Individual Oystercatchers are known to differ in how efficient they can feed on a given food supply, but such differences are ignored in **EFFECT**.

2. The simple functional response only applies when the focal Oystercatcher is not hindered during feeding by conspecifics. When the area is crowded with other Oystercatchers, *interference* may occur, i.e. the intake rate of the focal bird declines, due to the presence of conspecifics. Individuals may differ in their susceptibility to interference, depending on their dominance status. **EFFECT** assumes a dominance hierarchy where the topdominant bird does not suffer from interference (subroutine DIS-PERS.FOR).

3. To predict the intake rate of an individual Oystercatcher in a given area it is now clear that the simple functional response and interference must be combined in the *generalized functional response*. Mathematically speaken the generalized functional response has always been a single equation.

4. To find the *aggregative response* (the distribution of the birds over the different feeding areas), we need the *ideal free assumption*. This assumption contains the following elements: (1) each individual will choose to feed where it achieves the highest intake rate of food, (2) individuals have a perfect knowledge of the food supply in the different areas and are instantaneously aware of the density of competitors, (3) individuals are free to move, i.e. they pay no fitness cost for moving to a new area, like a reduction in their feeding efficiency, or a reduction in their dominance status. When all individuals suffer equally from interference this leads to the ideal free distribution, where each individual achieves the same intake rate. When dominance affects susceptibility to interference, one possible outcome, depending on the details of the interference function, is that the lowest ranking birds have the same intake rate

everywhere (see later). This is the current formulation in the subroutine
DISPERS.FOR of **EFFECT1.1**.

5.   The next question is to find out if intake rates of the birds are sufficient to
     meet their daily energy demands. These energy demands are calculated
     in subroutine DEE.FOR. If some birds cannot meet their daily energy
     demands, they must leave the system, either dead or alive. In the current
     formulation of both **EFFECT1.1** and **DEPLETE** one time unit during which
     energy income does not meet energy expenditure is sufficient to kill the
     birds. In contrast, **EXE2** allows the birds to build up energy reserves, so
     that they can sustain many days with a negative energy balance.

6.   The final question is what determines the *carrying capacity* of the system.
     Because the Oystercatchers eat prey, these prey will decline in numbers
     (included in subroutine DISPERS.FOR). This decline will only take place
     in patches visited by the birds, so some areas are more affected than
     others. For this reason, the birds are allowed to redistribute themselves
     according to the generalized functional response and the ideal free
     assumption at the start of each time unit. This cycle is repeated for every
     day in the winter. It may happen that at some stage due to this depletion
     of the food, some birds no longer succeed in obtaining enough food, so
     that they die (or leave) and carrying capacity is reached. In Fig.1 this is
     depicted as the carrying capacity line being reached due to prey numbers
     declining.
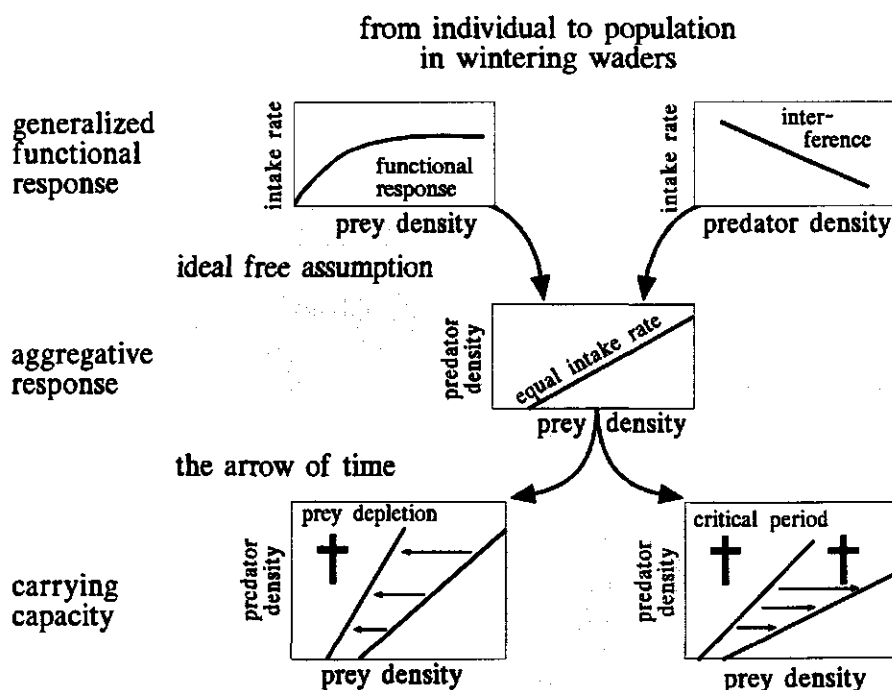
Figure 1.   Scheme showing the major functions and assumptions in the current Oystercatcher distribution models.

However, even if food were not depleted at all due to the birds, energy demands increase in the course of the winter due to colder temperatures and stronger winds, while the total harvestable biomass of prey also declines due to prey mortality not due to Oystercatchers and loss of condition of individual prey (forcing functions in subroutine DIS-PERS.FOR of **EFFECT1.1** which we will not discuss). This may also cause mortality of the birds. This is depicted in Fig. 1 as the carrying capacity line moving to the right. Thus, there are two mechansims by which carrying capacity can be reached: (1) *prey depletion* or (2) a *critical period* that must be survived. In the current version of **DEPLETE** only the first mechanism operate. In **EXE2** and in **EFFECT1.1** both mechanisms operate and it depends on parameter values, which of the two mechanisms is the more important in determining carrying capacity. It is not known which of the two processes is the more important in nature. Perhaps the models can be used to gain an understanding which of the two processes is the more important.

3.3 Conclusions

1.   **EXE2, EFFECT1.1** and **DEPLETE** all assume that the primary risk Oystercatchers face during winter is the risk of starvation. This is considered a sound conceptual foundation in the light of the available empirical evidence.

2.   Carrying capacity may be due to prey depletion or energy needs during a critical period. At present, it is not clear which of the two processes is the more important, both in the models and in nature. It is a topic worthy of further investigation, since we suspect that it may strongly affect how shellfishing and habitat loss will influence Oystercatcher numbers.

3.   We did not examine the validity of the estimates and the assumptions behind the forcing functions in **EFFECT1.1**, that describe how Cockles lose condition and suffer from mortality other than predation by Oyster-catchers.

4   ENERGY NEEDS OF THE OYSTERCATCHER

4.1   Current formulation in EFFECT1.1

In the current formulation of **EFFECT1.1** individual Oystercatchers do not differ in size and they do not build up energy reserves to survive periods of poor feeding conditions. Thus, if the energy intake falls below the required daily minimum during a time period, the birds immediately starve to death. This daily minimum, as well as the daily needs of the average bird, are assumed to depend on the environmental conditions, the feeding activity and the basal metabolic rate (BMR) of the birds. The basal metabolic rate corresponds to the energy expended by an inactive bird at thermoneutral conditions, i.e. at an ambient temperature at which no energy is needed for thermoregulation. BMR is estimated at 2.91 W, which corresponds to the value for an average bird in the study of Kersten & Piersma (1987). Without any sort of biological justification, it is assumed that a bird that barely survives has a BMR of 90% of 2.91 W = 2.62 W. A maximum BMR of 110% of 2.91 W = 3.2 W is also calculated, again without any biological justification. It is not clear to us what the purpose of this maximum BMR is.

Wind speed, ambient temperature and global solar radiation are three environmental variables that determine the cost of thermoregulation. They are included as forcing functions in **EFFECT1.1** and appendix B describes the background to the current complex calculations that yield the maintenance metabolism for a given environment. Maintenance metabolism is defined as the energy expenditure of an inactive bird. Subsequently, it is assumed that during feeding an additional 1.5 BMR must be added to the maintenance metabolism for activity costs.

To find out if food intake is sufficient to cover the daily energy needs, the ingested biomass must be converted to energy that is actually assimilated. For this, it is assumed that the energetic value of the bivalve flesh equals 22 kJ per g AFDM (ash free dry mass) and that the assimilation efficiency of the food equals 85%, i.e. 85% of the energy in the food that is ingested is actually assimilated.

4.2   Other models

The current version of **DEPLETE** resembles **EFFECT1.1** in that it ignores that individuals may differ in size and that they can build energy stores. However, it also ignores that energy expenditure varies as a result of climatic variables, thereby gaining much simplicity and tractability. Mathematically, birds die as soon as they fail to meet the minimum required intake rate. Conceptually, the idea is that birds that consistently fail to meet their energy requirements are bound to perish.

EXE2 resembles **DEPLETE** and **EFFECT1.1** in that effects of size differences between individuals are ignored. The only climatic variable thought to influence daily food needs F_t (g AFDM) on day t is the mean air temperature T_t (°C) on that day (Clarke & Goss-Custard 1996). If T_t 10 < °C then $F_t=26.75+0.19(10-T_t)$. If T_t > 10 °C and not exceeding lethal limits, then $F_t=26.75$ g AFDM. In contrast to both other models, individual Oystercatchers can gain or lose mass. They die when their body mass falls below an age-specific threshold: 300 g for juveniles, 340 g for immatures (2-4 years) and 350 g for adults. This happens when they consistently eat less than needed. When the birds can eat more than they need and are below a target weight, the extra food intake is converted into mass gain until an age- and season-specific target body mass is reached, subject to a maximum possible increase in body mass of 5%.

4.3 Literature review of food intake

Zwarts *et al.* (1996c) provide the most recent review of empirical studies of the food needs of Oystercatchers. They arrive at the following conclusions:
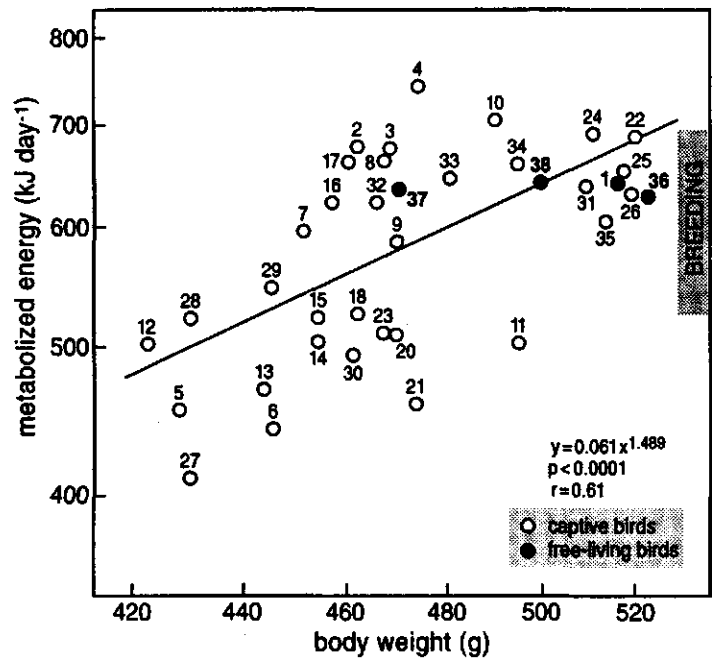
Figure 2. The daily consumption (kJ metabolized energy) as a function of body weight in captive and free-living Oystercatchers according to several data sources given in Table C1. The digit codes in the figure correspond with the source numbers in Table C1. The grey field indicates the variation in daily energy expenditure of adult birds during the breeding season (Kersten 1996: Table 8). The daily consumption was measured at constant body weight and under thermoneutral conditions, and if this was not so, a correction was made (see text and Table C1 in Appendix C). From Zwarts *et al.* (1996c).

(1) Captive Oystercatchers consume daily 25-40 g dry flesh or 550-850 kJ, of which they metabolize 450-700 kJ. Free-living Oystercatchers eat more than captive birds but, contrary to expectation, this is not due to greater activity costs but to a higher body weight (Fig. 2). When body weights are equal, free-living and captive Oystercatchers consume the same amount of food. Appendix C (taken from Zwarts et al. 1996c) summarizes the data, including Table C1 which lists the most pertinent data. Appendix C also explains the analysis upon which the conclusions are based.

(2) The intake rate of Oystercatchers generally varies between 1 and 3 mg dry flesh s^{-1} feeding, but if non-feeding times are included, the crude intake rate usually varies between 1 and 1.5 mg s^{-1}. Extremely high intake rates, above 4 mg s^{-1}, are only observed in birds feeding during a short bout after a long resting period.

(3) According to Kersten & Visser (1996) such high intake rates cannot be sustained for long, because a maximum of 80 g wet flesh, equivalent to 12 g dry flesh, can be stored in the digestive tract and the processing rate does not exceed 4.4 mg wet flesh s^{-1} or 0.66 mg ash-free dry weight (AFDM) s^{-1}. Due to this digestive bottleneck, the birds are forced to spend about 11 h on the feeding area each day. Since the exposure time of their intertidal feeding areas is usually 5-6 h, Oystercatchers generally cannot meet their daily energy requirements in a single low water period, which would often suffice if intake rate was the limiting factor.

(4) For a given length of the feeding period, the bottleneck model predicts the maximum crude intake intake that can be achieved, i.e. the highest intake rate including the non-feeding time. When the birds are able to feed for less than 3 h, the achieved crude intake rate usually remains far below this maximum, suggesting that the rate at which prey are found and eaten determines the intake rate. The consumption is also usually less than would be allowed by digestive constraint when the birds feed for 12 h or longer, because the birds at thermoneutral conditions do not need more than 36 g a day. When the birds spend 3 to 12 h on the feeding area, the average consumption is usually close to, or below the predicted maximum.

4.4 Suggestions for EFFECT

1. It is clear that many variables affect energy expenditure and it is not practical to include them all. While EXE2 is in general the most complex model, EFFECT has the most complex equations for energy expenditure. This means that it is not very useful at this stage to analyze how sensitive the model is to variations in particular parameters. Instead, an analysis is called for where it is investigated which processes and parameters should or should not be included in the model.

2. One way to proceed would be to study if the complex Wiersma & Piersma calculations lead to predicted energy needs that are substantially different from the EXE2 calculations. The goal should be to decrease the complexity in the heat loss calculations as the parameter estimates for the Oystercatcher are not very secure.

3. It may be useful to allow birds to build up energy stores as it is conceptually more sound to let a bird starve to death because its' reserves have fallen to a critical level, than when its' intake rate gets below a critical level. The present assumption in **EFFECT** that daily energy intake may not fall below 90% of the average BMR has no biological basis.

4. Even though there is abundant evidence for the existence of a digestive bottleneck, we do not think it useful to include such a bottleneck in the model.

5. Appendix C provides up to date estimates for several energetics parameters.

5 HANDLING TIME, PROFITABILITY, FUNCTIONAL RESPONSE AND SEASONAL CHANGES IN PREY AVAILABILITY

5.1 Theory

Before we can meaningfully discuss the current formulation of the functional response in **EFFECT** it is necessary to sketch the theory. Fundamental is the assumption that Oystercatchers seek to maximize their rate of energy gain while foraging. Alternative maximization criteria, like the risk of predation, the risk of parasitism or the risk of bill breakage are ignored, as are possible nutritional constraints. When encountering a prey item, the individual must decide whether to ignore or attack the prey on the basis of the expected energy yield per unit time spent handling, compared to the highest possible average intake rate during foraging. The model of intake rate must therefore take into account (1) the weight and associated energy gain E_i (J) from an item of prey type i, (2) the handling time h_i (s) of each prey of type i and (3) search times of different prey types, which can also be characterized by λ_i, the encounter rate (s^{-1}) with prey type i. The multi-species functional response equation, also known as the simple or "classic" optimal prey choice model (Charnov 1976), is based upon these three variables. In the model, prey of different species and sizes are ranked by their profitability, i.e. the rate of energy gain during handling. The ranking may include prey characteristics like prey size, but also shell thickness and burying depth. From the rate at which prey of a given class are encountered during searching, the classes which should or should not be taken to achieve the maximum rate of energy gain during feeding can be calculated. For i prey types:

$$\frac{E}{T} = \frac{\sum \lambda_i E_i P_i}{1 + \sum \lambda_i h_i P_i}$$

where E is total energy intake (J) during observation time T (s) and P_i is the decision variable. P_i represents the probability that the predator takes a prey item of type i after it is encountered. When prey with a profitability below the critical threshold are encountered, it is more efficient to continue searching than to handle and eat those prey, i.e. $P_i = 1$ if $E/T < E_i/h_i$ and $P_i = 0$ if $E/T > E_i/h_i$ (Charnov 1976). The optimal P_i, i.e. the prey choice that maximizes intake rate of energy, can be found if the encounter rates λ_j are treated as fixed constants. Since $\lambda_j = aD_i$, where a is the search rate ($m^2.s^{-1}$) and D_i the density of prey type i (m^{-2}), this will be the case if the birds and the prey always behave the same. Under those conditions the intake rate will increase with prey density to an asymptotic limit set by the profitability of the most profitable prey (the birds spend all their time handling the most profitable prey type and no time on searching), the well-known Holling type II functional response.
A constant search rate implies that the birds do not vary their search speed or searching method (touch or vision). Regrettably, the birds can vary both. Appendix D shows how to modify the equation when search speed is not a

fixed constant, but also a decision variable. It turns out that the optimal search speed for cryptic prey is lower than the optimal search speed for conspicuous prey (Gendron & Staddon 1983).

The equation also needs modification when the birds cannot immediately identify the prey type upon encountering it, but must spend some time handling the prey. This happens in Oystercatchers hammering bivalves. Apparently, some hammering time is required to identify if the prey is thin-shelled and therefore profitable, or thick-shelled and therefore unprofitable (see 5.4.6).

5.2 Current formulation in EFFECT and other models

At present, the only prey considered in **EFFECT** are Cockles. These Cockles do have a handling time, but this handling time is not simply measured in time units as one might expect, but in time units per unit biomass. Similarly, the search rate (or attack rate as it is called in the model) is not measured in area searched per unit time, but in biomass units per unit time. The reason for this is that the functional response model is not based on estimates of the parameters in the equation of Charnov (1976), but on a non-linear regression of intake rate against biomass density (see section 6 of this report). Exactly how this regression is performed is nowhere stated, and Bos (1994) is probably the first to admit that the fit of the regression line is not very impressive (see Fig. 4.2 in his report). As the data for the regression come from a single study (Sutherland 1982a,b), it is not a very sound foundation of the model anyway.

While these comments are somewhat critical, these criticisms are not directed against the pragmatism underlying the decision to simply regress the intake rate against a parameter describing the food supply. In **EXE2** a very similar procedure is followed, except that **EXE2** only deals with Mussels. The underlying problem is that confrontations of the optimal prey choice model with reality always yield additional complications. When the complications cannot be solved, it means that it is not known what measurements on the prey should be taken to accurately predict intake rate. Often, complications can be solved, like when it was discovered that for hammering Oystercatchers prey should be classified not only according to size, but also according to shell thickness and coverage with barnacles. However, this means that to apply the model to predict the intake rate in a particular area, all these parameters also need to be measured on the food supply in that area. This can be impractical, necessitating the simplifying regressions that we described above. In this spirit, several authors conclude that the density of *harvestable* prey biomass is the main determinant of the intake rate that a bird can achieve in a given area and the prime candidate for simplistic regressions (many papers by Zwarts, see also Meire 1991; Ens, Piersma & Drent 1994). Following the terminology of Zwarts, prey are considered harvestable when they are *accessible*, *detectable* and *profitable*. Below, we first review prey profitability and then the factors governing intake rate.

5.3 Factors governing handling time and prey profitability

Oystercatchers *Haematopus ostralegus* feed on at least 15 different prey species along the NW. European coast (Cramp & Simmons 1983, Hulscher 1996). On intertidal sand and mudflats, their food consists of Cockles *Cerastoderma edule* and Mussels *Mytilus edulis* and to a lesser degree also of other bivalves, such as *Macoma balthica* *Scrobicularia plana* and *Mya arenaria*, worm species, such as *Arenicola marina* and *Nereis diversicolor*, and the Shore Crab *Carcinus maenas*. On rocky shores, Oystercatchers take Limpets *Patella aspara* and *P. vulgata*, Periwinkles *Littorina littorea* and Dog-welks *Nucella lapillus*, whereas in grassland they select mainly different earthworm species (Lumbricidae) and Leatherjackets (larvae of the crane fly *Tipula paludosa*). For obvious reasons we will not concern ourselves with prey taken on rocky shores.

Zwarts *et al.* (1996b) assembled all information on handling time and prey profitability that is currently available for Oystercatchers from no less than 57 published articles, 6 student reports, 4 unpublished theses and unpublished data files from 9 different scientists. The extracted data and the methods used to extract these data are copied from Zwarts *et al.* (1996b) and given in Appendix E. In sections 5.3.1 to 5.3.4 we excerpt the main conclusions from their paper.

5.3.1 Handling time of armoured prey in relation to prey size, opening technique and burying depth

The smallest armoured prey opened by Oystercatchers are spat Cockles 8 mm long with an AFDM of 3.3 mg (Meire 1996b). The largest prey taken are Giant Bloody Cockles *Anadara* which is the food supply of Oystercatchers wintering on the Banc d'Arguin, Mauritania (Swennen 1990). These birds eat prey that were, on average, 78 mm long containing 3300 mg AFDM. Even larger prey were taken by Oystercatchers in captivity, as well as in the field, when offered large *Mya* 88 mm long with a flesh content of 4200 mg AFDM. However, since these prey usually lie out of reach of the bill (Zwarts & Wanink 1984), they cannot be considered as normal prey for Oystercatchers. Cockle spat could be handled in some seconds, but it took an Oystercatcher 212 s and 265 s, on average, to consume the flesh from the large *Anadara* and *Mya*. Thus, the handling time increases with flesh weight, as is further analysed in this section.

Although prey size explains a substantial part of the variation in handling time, there remains a large residual variation within each size class. In Mussels, a large part of this variation can be attributed to the technique used to open the mussel (Fig. 3, Table 1). Oystercatchers using the stabbing technique take less time than those which hammer Mussels on the dorsal side of the shell. The handling times are especially long when Mussels are torn off the bed, turned upside down and hammered on the ventral side (Cayford & Goss-Custard 1990, Fig. 3, Table 1).
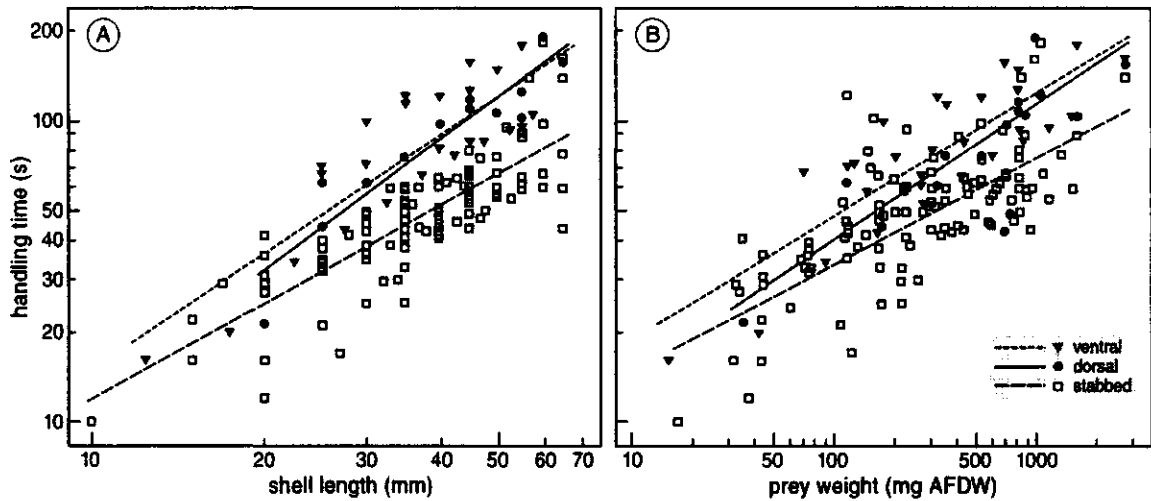
Figure 3.   Handling time as a function of (A) prey length or (B) prey weight in Mytilus opened by Oystercatchers stabbing the bill between the valves. Sources: Blomert et al. (1983), Cayford & Goss-Custard (1990), Ens (1982), Ens et al. (1996b), Hulscher (unpubl.), Koene (1978), Linders (1985), Meire & Ervijnck (1986), Speakman (1984), Sutherland & Ens (1987), Zwarts & Drent (1981). The three regression lines (see also Table 1) differ significantly (P< 0.001) from each other according to covariance analyses: R^2 = .593 for prey length and R^2 = .168 for the three techniques (left); R^2 = .620 for prey weight and R^2 = .100 for the three techniques (right). From Zwarts et al. (1996b).
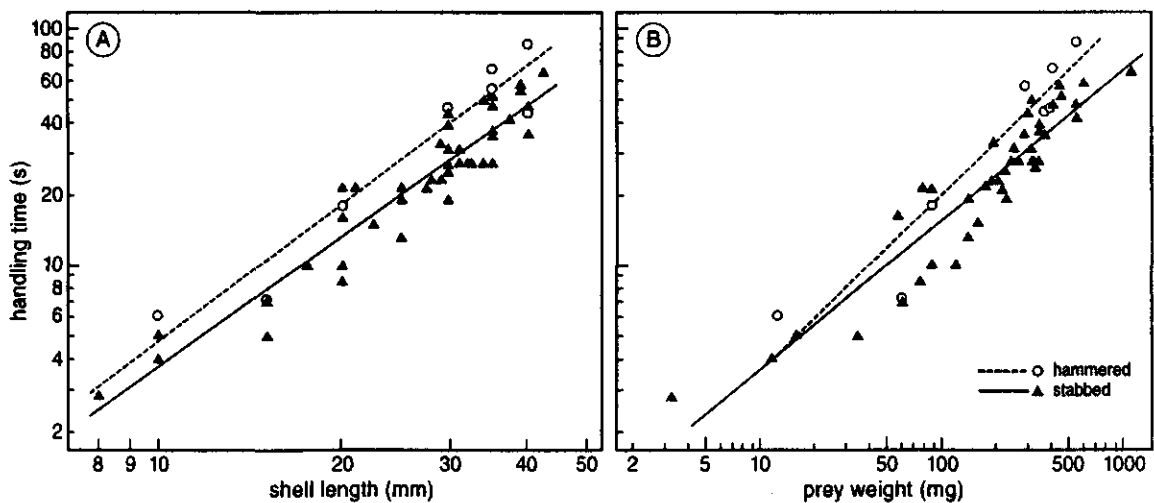
Figure 4.   Handling time as a function of (A) prey length or (B) prey weight in Cerastoderma, given separately for Oystercatchers opening Cockles by stabbing the bill between the valves or hammering the shell. Sources: Hulscher (1976 & unpubl.), Ens et al. (1996b & 1996c), Sutherland (1982c), Swennen et al. (1989), Triplet (1994a,b). The two regression lines (see also Table 1) differ significantly (P =0.002) from each other according to covariance analyses: (A) R^2 = .875 for prey length and R^2 = .024 for both techniques; (B) R^2 = .868 for prey weight and R^2 = .016 for both techniques. From Zwarts et al. (1996b).

Cockles are usually opened by stabbing, or forcing, the bill between the valves, but sometimes by hammering the shell. Ens *et al.* (1996b) found that it took Oystercatchers more time to open Cockles by hammering than by stabbing, just as in Mussels (Fig. 4, Table 1).

Table 1. Handling time as an exponential function of length (L, mm) or weight (W, mg) of the prey. The last column gives the number of the figure where the regression lines are depicted. From Zwarts *et al.* (1996b).

species	category	regression	R	n	Fig.
Mytilus	ventral	$0.712L^{1.313}$	0.86	26	3A
Mytilus	dorsal	$0.443L^{1.432}$	0.93	14	3A
Mytilus	stabbed	$0.975L^{1.081}$	0.82	99	3A
Cerastoderma	hammered	$0.054L^{1.945}$	0.96	8	4A
Cerastoderma	stabbed	$0.053L^{1.846}$	0.95	42	4A
Scrobicularia	field; winter	$0.046L^{1.905}$	0.98	9	5A
Scrobicularia	field; summer	$0.041L^{1.823}$	0.96	7	5A
Scrobicularia	lab; 2cm deep	$0.093L^{1.549}$	0.98	14	5A
Macoma	Aug; lifted	$0.262L^{1.466}$	0.83	7	6A
Macoma	Apr-Jun; lifted	$0.076L^{1.778}$	0.87	16	6A
Macoma	Apr-Jun: in situ	$0.408L^{1.055}$	0.67	5	6A
Mya lab; 2 cm deep		$0.070L^{1.546}$	0.80	44	7A
Mytilus	ventral	$7.258W^{0.411}$	0.84	26	3B
Mytilus	dorsal	$5.114W^{0.451}$	0.92	14	3B
Mytilus	stabbed	$6.549W^{0.355}$	0.78	99	3B
Cerastoderma	hammered	$0.625W^{0.750}$	0.95	8	4B
Cerastoderma	stabbed	$0.817W^{0.637}$	0.93	42	4B
Scrobicularia	field; winter	$1.821W^{0.598}$	0.95	9	5B
Scrobicularia	field; summer	$0.541W^{0.701}$	0.96	7	5B
Scrobicularia	lab; 2cm deep	$0.675W^{0.610}$	0.98	14	5B
Macoma	Aug; lifted	$2.212W^{0.487}$	0.83	7	6B
Macoma	Apr-Jun; lifted	$0.694W^{0.655}$	0.87	16	6B
Macoma	Apr-Jun; in situ	$0.508W^{0.642}$	0.83	10	6B
Mya combined		$0.661W^{0.586}$	0.91	54	7B
Nereis		$0.378W^{0.481}$	0.96	35	8
Arenicola		$0.387W^{0.539}$	0.98	7	8
Earthworms		$1.489W^{0.216}$	0.52	10	8

The handling time also increases with shell length and flesh weight in *Scrobicularia* but it also depends on the depth at which the prey live beneath the surface (Fig. 5, Table 1). Wanink & Zwarts (1985) found that the time needed to handle *Scrobicularia* 37 mm long increased from 18 to 42 s as the burying depth increased from 0 and 5 cm (Fig. 5). Wanink & Zwarts (1996) offered Oystercatchers prey of different size but buried at a depth of 2 cm beneath the mud surface. All size classes were handled rapidly. The handling time of *Scrobicularia* of different size has also been measured in the field, but no attempts have been made to estimate the depth from which the prey are

extracted. It is obvious, however, that most prey in winter are taken after the bill has been inserted fully into the substrate, whereas in summer the majority are taken from nearer the surface. Such a difference is to be expected, since most *Scrobicularia* in winter live out of reach of the Oystercatcher's bill (Zwarts & Wanink 1991, 1993); probably, all prey taken are only just accessible at a depth of 6 cm or 7 cm beneath the surface. In contrast, *Scrobicularia* live at shallower depths in summer, and some prey may be found at a burying depth of just a few cms only. In winter it takes 1.4 times more time as in summer to handle *Scrobicularia* of similar size (Fig. 5). We conclude that the longer handling times in winter are entirely due to the greater burying depth of the prey.
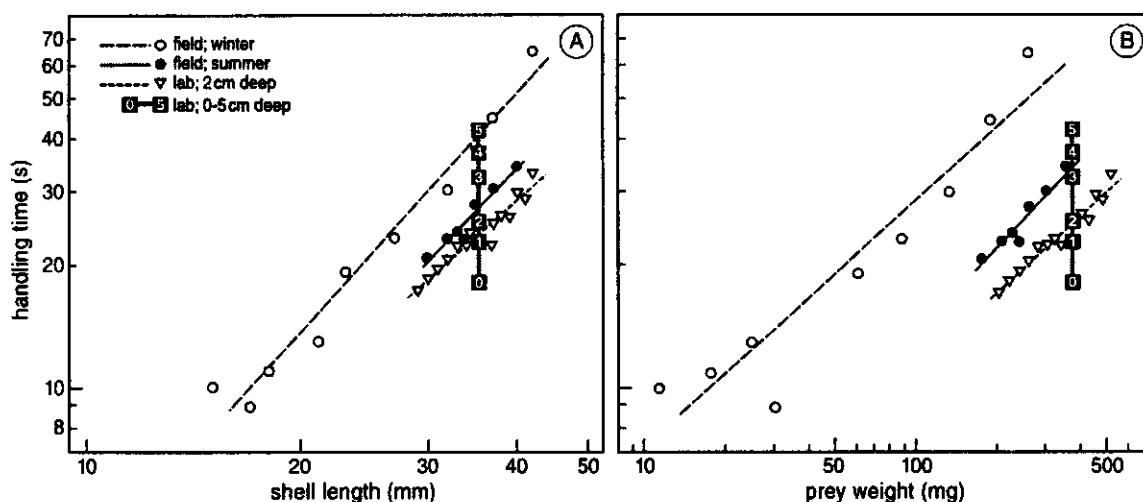
Figure 5.   Handling time as a function of (A) prey length or (B) prey weight in Scrobicularia, given separately for field data collected in winter (Boates & Goss-Custard 1989, Habekotté 1987) or in summer (Blomert et al. 1983) and for captive birds offered prey of similar size at different depths (Wanink & Zwarts 1985) or for different size classes buried to the same depth of 2 cm (Wanink & Zwarts 1996). The three regression lines (see also Table 1) differ significantly (P< 0.001) from each other, according to covariance analyses: (A) R^2 = .848 for prey length and R^2 = .089 for the three groups; (B) R^2 = .674 for prey weight and R^2 = .219 for the three groups. From Zwarts et al. (1996b).
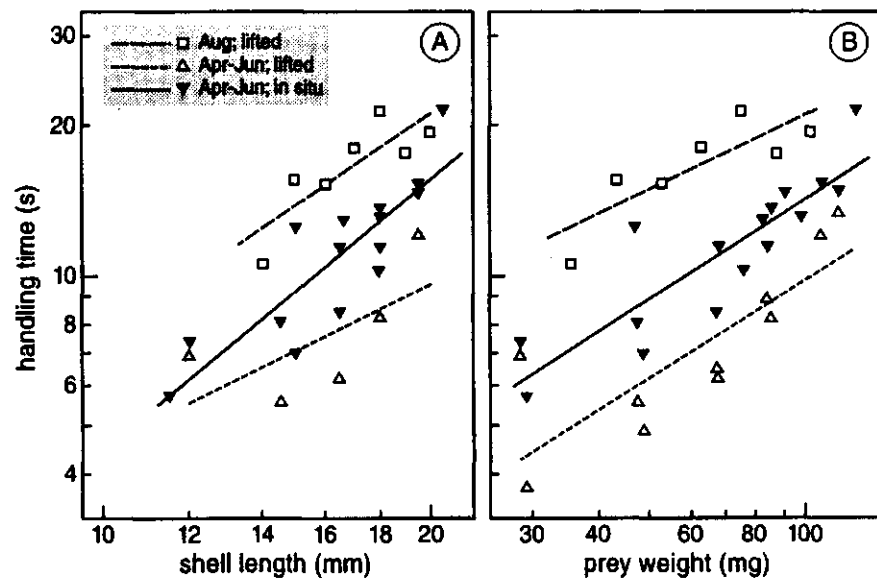
Figure 6. Handling time as a function of (A) prey length or (B) prey weight in Macoma, given separately for prey eaten in situ or lifted to the surface and eaten there; the latter is divided into two periods (April-June, August). Sources: Hulscher (1982 & unpubl.), Hulscher et al. (1996), Blomert et al. (1983), Ens et al. (1996a). The three regression lines (see also Table 1) differ significantly (P< 0.001) from each according to covariance analyses: (A) R^2 = .490 for prey length and R^2 = .326 for the three groups: (B) R^2 = .402 for prey weight and R^2 = .445 for the three groups. From Zwarts et al. (1996b)

The handling times of Macoma also increases with size (Fig. 6A, Table 1). It also seems likely that, just as in Scrobicularia handling time increases with prey depth. Macoma live in the upper three cm of the substrate from April through July, increase their depth from August onwards and live about twice as deep in winter as in summer (Reading & McGrorty 1978, Zwarts & Wanink 1993). No studies are available for Oystercatchers feeding on Macoma in autumn and winter, probably because they are not taken then. However, within the summer half of the year, handling time varies seasonally, being in August 1.5 times as long as in spring and early summer (Fig. 6A); this is presumably due to the greater depth from which the prey are obtained in August. This comparison refers to field studies in which prey were lifted to the surface. However, Macoma are also eaten in situ, and in this case handling times are much shorter (Fig. 6A & B). Captive Oystercatchers lifted deep-living prey more often than shallow prey (Wanink & Zwarts 1985, Hulscher et al 1996), so we assume that prey were eaten more often in situ during summer, whereas in early spring and late summer when they live at greater depth they were more lifted. Bunskoeke et al (1996) provided some tentative support for this idea from free-living birds. As a consequence, the combined handling time of Macoma being lifted and eaten in situ will be short when the prey live close to the surface from April to July, the difference between late summer and early spring being perhaps twofold.
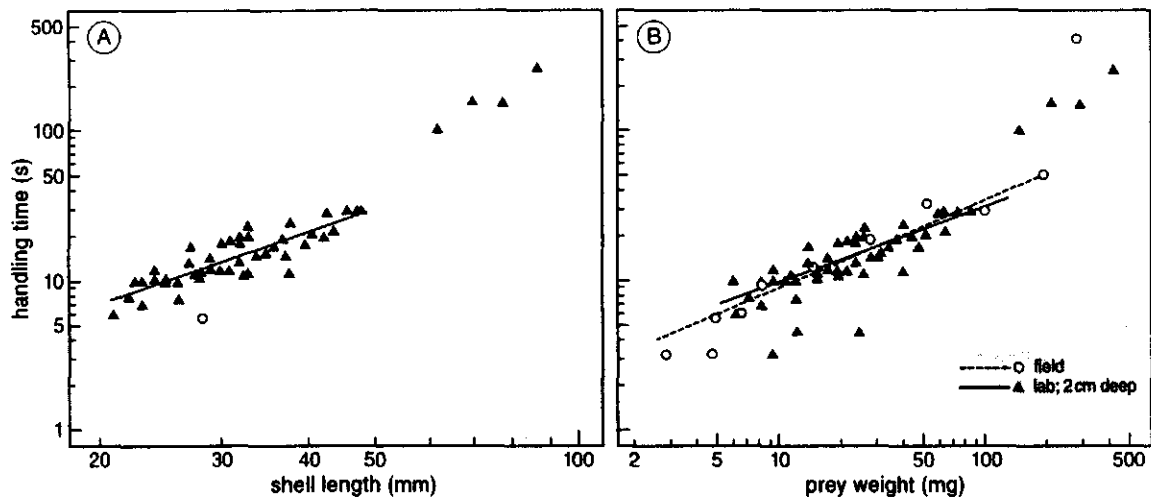
Figure 7.   Handling time as a function of (A) prey length or (B) prey weight in Mya in captive Oystercatchers
feeding on prey lying at a depth of 2 cm (Wanink & Zwarts 1996) or wild birds feeding on clams
from which the flesh is eaten in situ (Zwarts & Wanink 1984, Bunskoeke et al. 1996 & unpubl.).
The regressions are calculated without the four largest clams since their handling times were
untypically long. The handling times as a function of prey weight are not significantly different (P
=0.33 in panel B), so one regression line is given, based on the pooled data. Results of covariance
analyses: (A) R^2 = .853 for prey length; (B) R^2 = .869 for prey weight and R^2 = .002 for the two
groups; Table 1 gives more details. From Zwarts et al. (1996b)

There is no variation in the burying depth of Mya during the year, so we expect
no seasonal, prey depth-related variation in the handling time, as found in
Scrobicularia and in Macoma All the handling times in Fig. 7A were obtained
in the laboratory, except for those obtained in one field study. Fig. 7A shows
the handling time of clams up to 90 mm long. Free-living Oystercatchers never
find Mya larger than 40 mm long, since these large clams live out of reach of
the bill (Zwarts & Wanink 1984, 1989, 1993). All clams in the laboratory
experiments were buried, however, at a depth of about 2 cm and so at an
extremely shallow depth compared to the natural situation, at least for the
larger size classes. This means that, as in Scrobicularia, the handling times
of the larger size classes would be about twice as long if the prey were taken
from a depth of 5 or 6 cm, as would be usual in the field. The single field study
found that, in contrast to the expectation, Oystercatchers handled the prey in
less time than in the laboratory (Fig. 7A). However, while the Oystercatchers
in the laboratory ingested all the flesh from the shell, the birds in the field often
only took the siphon and left behind the remaining part of the body (Zwarts
& Wanink 1984). Another field study (Bunskoeke et al 1996, pers. comm.)
estimated the weight of the flesh extracted from Mya of unknown size, so
more field data were available when handling time was plotted against the
prey weight (Fig. 7B). As Fig. 7B shows, the relationship between handling
time and prey weight was the same as in the laboratory, where all the flesh
from shallow prey was eaten, and field studies, where a variable amount of
flesh was extracted from deep-living prey.

5.3.2   Handling time of bivalves in relation to prey condition

Figures 3 - 7 show the handling times as a function of prey length and of prey weight; the equations of the depicted regression lines are given in Table 1. If most of the handling time is spent in eating the flesh, we expect that the handling time would depend on the amount of flesh ingested and that the close relationship between handling time and prey size is due only to the high correlation between prey size and flesh weight. On the other hand, if handling time consists mainly of time spent in breaking the shell, handling time would be primarily determined by size-related strength of the shell and not by the amount of flesh ingested. Prey weight and prey size are so highly correlated, that it is hardly surprising that it is not possible to tell from Figs. 3 - 7 whether handling time depends on prey weight, and thus indirectly on size, or on prey size, and thus indirectly on the amount of flesh to be ingested.

Although flesh weight and prey size are highly correlated when both are plotted on a log-log scale, the weight variation within each size class is large enough to investigate whether the amount of flesh, independent of prey size, affects the handling time. Most of the species preyed upon by Oystercatchers contain in late winter 40% less flesh than specimens of similar size in early summer (Chambers & Milne 1979, Zwarts 1991, Zwarts & Wanink 1993, Ens *et al.* 1996b). Prey condition has been defined as percent deviation of the average prey weight, such as obtained by regressing log weight against log size, using all data given in Figs. 3 - 7. The increase of handling time with flesh content, such as shown by Ens *et al* (1996b) for his data, is not found when data from different Mussel and Cockle studies are pooled. *Scrobicularia* and *Macoma* are even handled significantly more rapidly if they contain more flesh, but this is because body condition varies seasonally in accordance with burying depth. Thus, a fixed relationship between handling time and prey size can be assumed.

5.3.3   Handling time of soft-bodied prey in relation to prey weight and burying depth

Figure 8 shows the relationship between handling time and prey weight in four soft-bodied prey: Ragworms, Lugworms, earthworms and Leatherjackets. Handling time quadruples as prey weight increases thirtyfold. The handling times are short in these species for several reasons. First, no time is spent in opening, or preparing, the prey, since they are eaten whole. Moreover, soft-bodied prey are ere usually swallowed in one piece and not piecemeal. Further, most of these prey are picked up from, or taken from just beneath, the surface. Handling times are longer when the prey are extracted from the substrate. It takes Oystercatchers, on average, 4 s to remove Leatherjackets from their burrows, 2 - 4 cm deep, and only 1.3 s to mandibulate them (Blomert & Zwarts unpubl.). Hence, depending on the position of the Leatherjacket in its burrow, the handling time varies between 2 and 6 s. We may expect an even larger difference in earthworms. When prey are found at, or just beneath, the surface, they can be grasped easily and transported up the bill in only one catch-and-throw movement (see Gerritsen 1988). But when prey are extracted from the turf, they often break and must therefore

be eaten piecemeal. Whether the prey are at or beneath the surface presu-
mably also explains the average differences in handling time between speci-
es. Lugworms, and the majority of the Ragworms, are grasped while they are
close to the surface and at a shallow depth in their burrows and therefore
handled rapidly. In contrast, the Leatherjackets and earthworms are, at least
partly, extracted from the turf, so that handling takes longer in these grassland
species compared to the estuarine species.
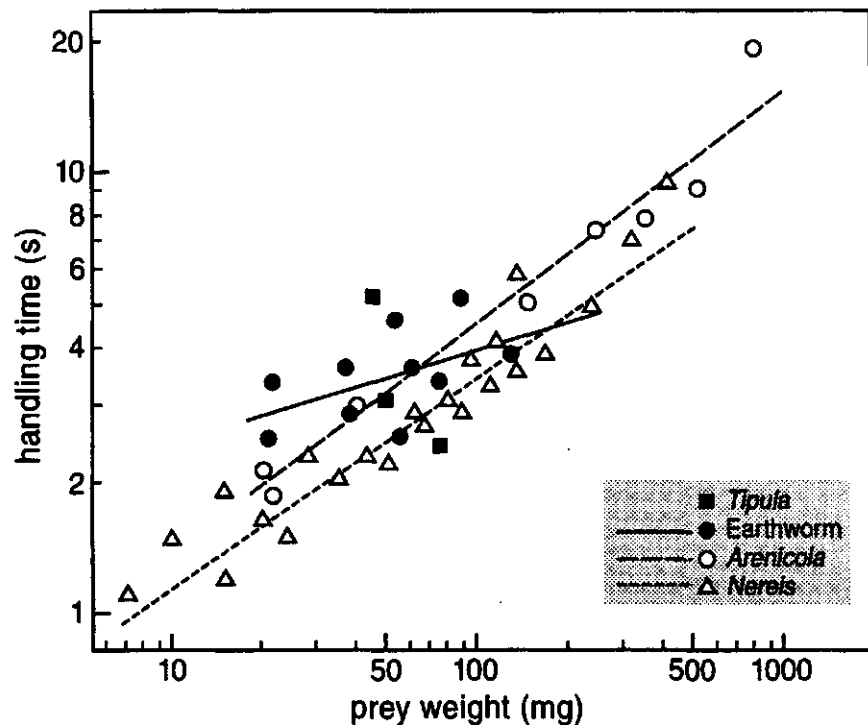
Figure 8.   Handling time as a function of prey weight (mg AFDW) in earthworms (Ens
unpubl.), Nereis (Boates & Goss-Custard 1989, Ens et al. 1996a, Hulscher
unpubl.), Tipula (Blomert & Zwarts unpubl., Ens unpubl.) and Arenicola
(Bunskoeke 1988 & unpubl.). The handling time of the four species differ
significantly according to a covariance analysis (R^2 = .918 for prey weight
and R^2 = .025 for the species). From Zwarts et al. (1996b)

5.3.4 Comparing the profitability of armoured and soft-bodied prey

Figures 3 - 8 show the relation between handling time and prey weight in five
armoured and four soft-bodied prey species. The profitability, the amount of
flesh consumed per unit time handling, was calculated for these species, also
including Anadara and Uca, and plotted against their prey weight (Fig. 9).
Worms and Leatherjackets were, on average, 4.43 times more profitable than
armoured prey of similar size. Although there was a large scatter in the
profitability of the armoured prey, it is clear that the profitability of soft-bodied,
as well as armoured prey, increases with prey weight. The large scatter in
the profitability of armoured prey could largely be explained by the species

concerned and the technique used to open them. Taking the ratio shell weight to flesh weight as a measure of the amount of armour, profitability is directly related to prey armour (Fig. 10). Clearly, profitability is least for the most heavily armoured prey.
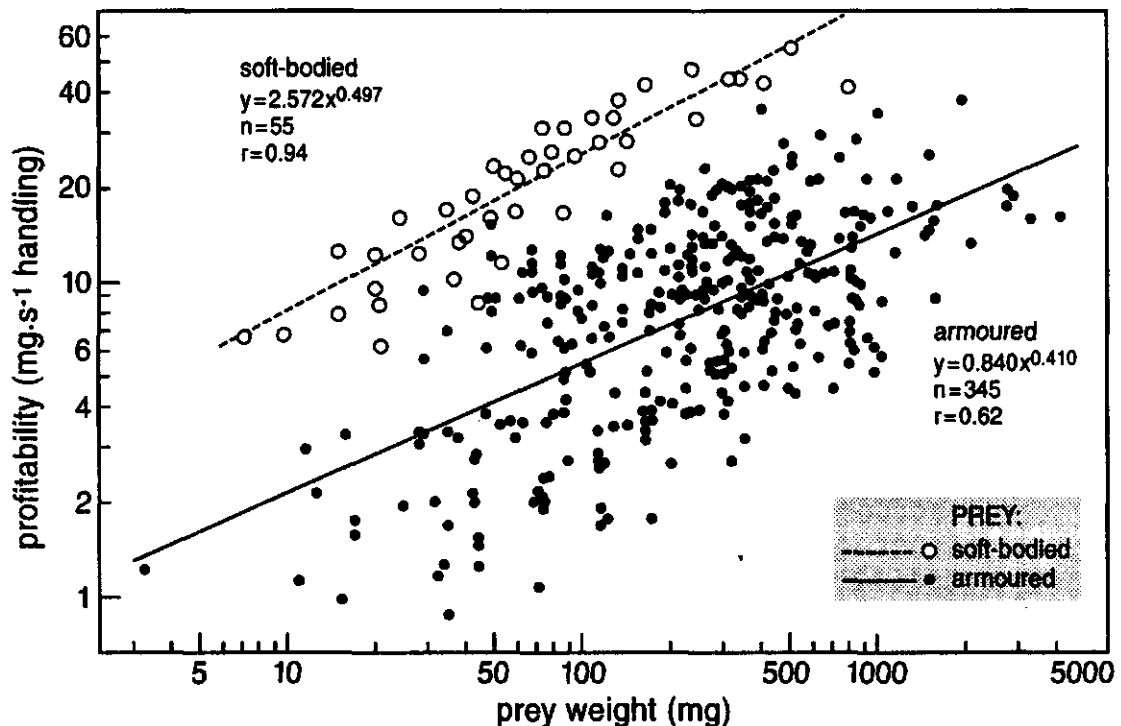
Figure 9.   Profitability (mg s⁻¹ handling) as a function of prey weight (mg AFDW), given separately for soft-bodied prey (same data as Fig. 8) and armoured prey (in addition to the data given in Figs. 3 - 8, also Anadara (Swennen 1990), Littorina (Boates & Goss-Custard 1992), Patella (Safriel 1967) and Uca (Ens et al. 1993 & unpubl.)). The regression lines are shown separately for soft-bodied and armoured prey. A multiple regression analysis revealed that non-parallel regression lines did not explain more variance than parallel ones (R^2 = 0.515 and .514, respectively). Hence a common exponent (0.421) may be used with different intercepts: 0.788 for armoured prey and 3.490 for soft-bodied prey. From Zwarts et al. (1996b)

Since handling time tends only to be reported for prey that are consumed, the calculations are based on the time actually taken to handle prey. This ignores the waste handling time spent on rejected prey. If waste handling times due to prey being rejected or stolen prey could be included, the graph for the soft-bodied prey would not change much because few such prey are refused and waste handling time is therefore very short (Ens et al. 1996a). In contrast, waste handling time have a significant effect on prey profitability in armoured prey, such as Mussels hammered on the dorsal or ventral side (Meire & Ervynck 1986, Cayford & Goss-Custard 1990, Ens & Alting 1996a, Meire 1996c). As a consequence, the difference in profitability between soft-bodied and armoured prey at the surface is even larger than shown in Fig. 10.
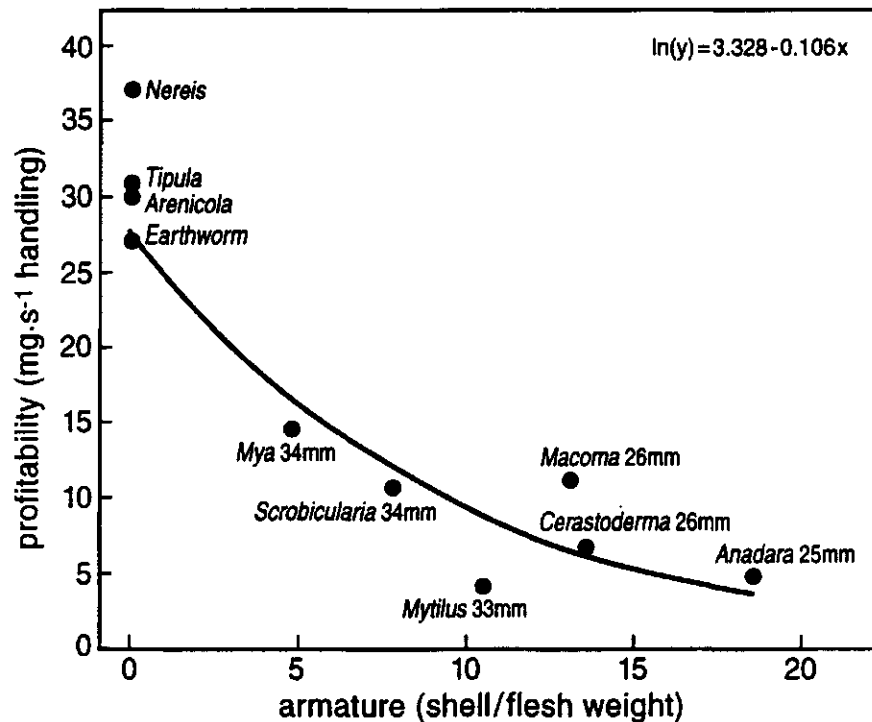
Figure 10. Profitability as a function of the armour index in estuarine prey containing 200 mg flesh. The corresponding shell length of the bivalves is indicated. The fitted curve is highly significant (r = -0.91, P =0.0003). Profitability of the different prey species was standardised for a prey of 200 mg. Armature index is defined as the ratio shell to flesh weight for the size classes concerned. Shell weights from Wolff et al. (1987), Zwarts & Blomert (1992); flesh weights from Zwarts (1991) and Zwarts & Wanink (1993). From Zwarts et al. (1996b)

5.3.5 Summary of the rules governing profitability

Summarizing the results of Zwarts et al. (1996b), four rules govern profitability. First, within each species large prey are more profitable than small prey, because flesh content increases more steeply with prey size than handling time. Second, soft-bodied prey, such as worms and Leatherjackets, which can be swallowed whole, are much more profitable than armoured prey, such as bivalves, which Oystercatchers have to open before the flesh can be extracted from the shell. Third, heavily armoured surface-dwelling prey, like Mussels and Cockles, are the least profitable prey of all, even if the armour is bypassed through stabbing the bill between the valves. Fourth, within the burying prey species, the profitability of prey decreases with depth. Hence burying bivalve species that bury in winter at larger depth than in summer, are in winter, if not out of reach of the bill, anyway less profitable.

5.4 Functional response

This section on the functional response is largely based on the paper by
Zwarts, Wanink & Ens (1996) who estimate the parameters in the prey choice
model and analyze ten years of data on food supply, as well as distribution
and prey choice of Oystercatchers feeding along the Frisian coast. A funda-
mental problem in such a study is how to deal with spatial heterogeneity in
the food supply and temporal variability in the searching behaviour of the bird?
Two observations help us out. First, the prey species of the Oystercatcher
usually occur in different patches within the tidal zone. For instance, the birds
have to decide whether to go to a mussel bed to feed on Edible Mussels
Mytilus edulis or to a mudflat to feed on the clam *Scrobicularia plana*. Second,
even if Oystercatchers feed on a mudflat where two prey species, for instance
Edible Cockles *Cerastoderma edule* and *Scrobicularia*, occur together, they
may be forced to adapt their searching behaviour depending on which species
they exploit. For instance, it is sufficient to bring the bill tip into contact with
the mud surface to encounter *Cerastoderma* but the birds have to probe their
full bill into the mud to find *Scrobicularia*, so searching for surface prey and
deep-living prey is not easily compatible. For the same reason, Oystercat-
chers have to compromise if they search simultaneously for conspicuous and
cryptic prey. They search slowly if they feed on prey hidden in the substrate,
but speed up their walking rate if they feed on easy prey, such as Ragworms
Nereis diversicolor that graze at the surface around their burrow (Ens *et al.*
1996a).

Zwarts, Wanink & Ens therefore assume as a first approximation that, with
one exception, searching for a particular prey species implies a zero encoun-
ter rate with all other prey species. To find under these conditions the prey
choice that maximizes intake rate, one first has to calculate the optimal prey
selection within a prey species. This will yield a profitability threshold for each
prey species and an associated intake rate. One then chooses the highest
one among these intake rates and identifies this prey and the associated
selection criteria as the optimal choice for that sampling date. The one
exception that is currently allowed is where the bird can choose between
Scrobicularia and the Baltic Tellin *Macoma balthica*, both of which live buried
in the mud.

5.4.1 Scrobicularia

Assuming that Oystercatchers probe their bill at random in the mud when they
search for buried bivalves, it is possible to predict the searching time from the
prey density (Hulscher 1976, 1982). To make precise predictions on intake
rate, it is necessary to divide the prey into different depth categories and to
measure the effect of burying depth on handling as well as on searching time
(Wanink & Zwarts 1985). One also needs to know the relationship between
burying depth and prey weight since the accessible shallow-living bivalves
may represent marginal prey compared to the prey of similar size living at
larger depths (Zwarts & Wanink 1991). The encounter rate λ = aD, where a
is the instantaneous rate of discovery ($m^2 s^{-1}$) and D (m^{-2}) the density of the
prey. The searching time is the inverse of the encounter rate, which is the

product of three variables: (1) the time needed to thrust the bill a certain distance into the mud, (2) the number of probes that has to be made to encounter a prey and (3) the proportion of the searching time spent in probing. All three relationships were measured:

(1) the relation between probing time T (s) and probing depth P (cm) was quantified using a high-speed film:

T = exp(0.39P - 2.49) (Wanink & Zwarts 1985);

(2) the encounter rate was derived from the prey density and the "effective touch area", i.e. the surface area S (cm^2) of the prey as a function of prey length L (mm):

S = 0.154 $L^{2.09}$ (Zwarts & Blomert 1992),

enlarged with the surface area of the bill tip (Hulscher 1982, Zwarts *et al.* 1996a: Table 2.1);

(3) the probing time appeared to be a fixed proportion of the total searching time, 30% independent of the prey density of *Scrobicularia* (Wanink & Zwarts 1985).

Wanink & Zwarts (1985) offered a captive bird *Scrobicularia* 35-36 mm long, buried at different depths and predicted the intake rate, using the multi-species functional response equation (Charnov 1976). Extrapolation of this model to free-living birds was possible because the relationship between effective touch area and prey size has been quantified for different bivalve species (Zwarts & Blomert 1992), as well as the relationship between handling time and prey weight for the same prey species (Zwarts *et al.* 1996b). Based on this information, Wanink & Zwarts (1996) have estimated the encounter rate of free-living Oystercatchers feeding on *Scrobicularia* using the six-year data base of the bimonthly depth measurements (Zwarts & Wanink 1989, 1993). The handling time H (s) of *Scrobicularia* as a function of burying depth B (cm) and prey length L (mm) was based on the empirical relationship:

H = (0.093 $L^{1.549}$ / 23.4) - (3.7B + 24.9).

The flesh weight of all mm classes was known per cm depth class, so it was possible to calculate the intake rate under the assumption that Oystercatchers probe their bill at random into the mud. The calculation was repeated for birds probing 2, 3, ... 8 cm deep. If all prey were deeply buried, the birds would achieve the highest intake by probing as deeply as possible, but if many live close to the surface, the optimal depth selection could be attained by ignoring all deep-living *Scrobicularia*.

5.4.2 Macoma

The intake rate of Oystercatchers feeding on *Macoma* could be predicted in the same way as in *Scrobicularia*. However, whereas the relationships between handling time and burying depth and shell length were available for *Scrobicularia*, this must be estimated for *Macoma*. The only clue was the relationship between handling time and prey weight for two periods where prey depth could be estimated, i.e. spring and late summer, when the animals lived 2 and 4 cm, on average, beneath the surface of the mud, respectively (Fig. 5 in Zwarts *et al.* 1996b). From that figure it could be concluded that prey weight correlated better with handling time than prey length, so that for practical reasons prey weight, instead of prey length was used to predict the handling time. To obtain the handling time of *Macoma* as function of prey weight W (mg) for other burying depths, linear interpolation was performed, resulting in the following equation:

$$H = 0.231B \times 0.602W^{0.571} = 0.139B \times W^{0.571}$$

Since Oystercatchers never take *Macoma* <11 mm long (Hulscher 1982, Zwarts *et al.* 1996a), the calculations of Zwarts, Wanink & Ens were based on the assumption that the birds took all *Macoma* ≥ 11 mm that they encountered.

5.4.3 Scrobicularia + Macoma

Scrobicularia and *Macoma* occurred in the same habitat, reaching the highest density on the mid-shore and living buried in the substrate. Hence, Oystercatchers encountered both prey if they probed the mud with their bill. Assuming that Oystercatchers took all *Scrobicularia* and *Macoma* ≥ 11 mm, it was possible to calculate the intake rate for both species combined. There were 53 sampling days out of a total of 88 during which both prey species were common. In this period, Oystercatchers rarely raised their intake rate by taking both species. They even lowered their intake rate on seven days by adding *Macoma* to a diet of *Scrobicularia*; in contrast, it hardly affected their intake rate when they added *Scrobicularia* to a diet of *Macoma*. However, the intake rates predicted for birds feeding on *Macoma* or on both species did not differ much.

5.4.4 Mya

In principle, a similar depth-related model might be developed to predict the intake rate for Oystercatchers feeding on *Mya*. However, in this prey, the siphon holes are sometimes visible at the surface, by which they may be located by sight. This makes a model based on randomly probing the mud less appropriate. *Mya* are only harvestable by Oystercatcher during a short period of their lives, being too small to be profitable before the second growing season and buried too deeply to be accessible after the third (Zwarts & Wanink 1984). Hence, the prey was harvestable by Oystercatchers during only 2 of the 10 years of observation. The intake rate was actually measured in one of these two winter half years.

The birds achieved an intake rate of 1.86 mg s^{-1} in October 1980 (correcting for the 30% overestimation of prey weight by Zwarts & Wanink 1984; see Zwarts et al. 1996c). The birds continued to feed on Mya in the following months but the intake rate was not measured. The body condition of the prey decreased gradually by 20% from November to February, but the decline in intake rate would have been larger because the Oystercatchers depleted their food. The birds eliminated 80% of all the Mya, and 90% of the shallow, most profitable prey. Consequently, the search time must have increased during these months of heavy exploitation. The decrease in intake rate could be estimated, because the Mya-eating Oystercatchers in autumn foraged in 73 plots where the prey density was known. The feeding rate was significantly correlated with prey density (r = 0.27, n = 80 observation periods of 10 min, p = 0.01) and decreased from 4 clams min^{-1} at 100-250 clams m^{-2} to 2.2 clams min^{-1} at 50 clams m^{-2}. When the linear regression was extrapolated downwards to below 50 clams m^{-2}, the feeding rates must be too high. A third-degree polynomial was used to describe the sigmoidal function of feeding rate F (Mya min^{-1}) against prey density D (Mya m^{-2}):

$$F = -0.21 + 0.66D - 0.00033D^2 + 0.00000056D^3$$

The density of the harvestable clams was reduced to only 15 clams m^{-2} at the end of the winter. Hence, by extrapolation downwards the intake rate must have dropped from 1.86 mg s^{-1} in October to the extremely low level of about 0.30 mg s^{-1} some months later.

5.4.5 Cockles

Cockles live close to the surface. Therefore, when the birds hunt by touch, it is sufficient to know the density and frequency distribution of the size classes to calculate the encounter rate with the prey, using the random touch model of Hulscher (1976). However, as Hulscher (1976) also showed, in daylight Oystercatchers hunt visually for Cockles. Moreover, he could show that the birds became more selective at high prey densities by ignoring the closed bivalves that could not be opened in a single stabbing movement. That is why random touch models could not be used to predict the intake rate of cockle-feeding Oystercatchers. Instead, the intake rate was predicted from the empirical relationship between intake rate I (mg s^{-1}), prey density D (n m^{-2}) and prey weight W (mg AFDM). The function was based on a multiple regression, performed on the 38 data points extracted from 10 out of 12 available studies (Zwarts et al. 1996b); as discussed by Zwarts et al. (1996b) intake rate was presumably overestimated by Goss-Custard (1977), while Triplet (1994a) does not present sufficient details to be included in the analysis. A problem is that W refers to the mean prey weight of the prey that were actually taken in the plot, whereas D refers to the density of the Cockles that were actually present. As a result, large variation in size within a plot may cause problems. In several studies only one year class of Cockles was present, that did not vary too much in size. In studies where two or more year classes were present, it often happened that the smaller size class was completely ignored. In that case D only refers to the size class that was taken. The effect of prey weight was highly significant (R^2 = .577, P < 0.001) as was

the effect of prey density (R^2 = .093, P = 0.004), with a highly negative correlation between ln(D) and ln(W) (r = -0.72). Intake rate I can be predicted from prey weight W and prey density D as follows:

$$I = exp(0.476W + 0.238D - 0.0124D^2 - 2.727)$$

Fig. 11 shows the intake rates predicted by this multiple regression analysis as a function of prey density for Cockles weighing 50, 200 and 400 mg. These curves can be compared directly with the 38 measurements, since the prey weight has been indicated by four different symbols. It is obvious that intake rates are well predicted at high prey density but not at low.
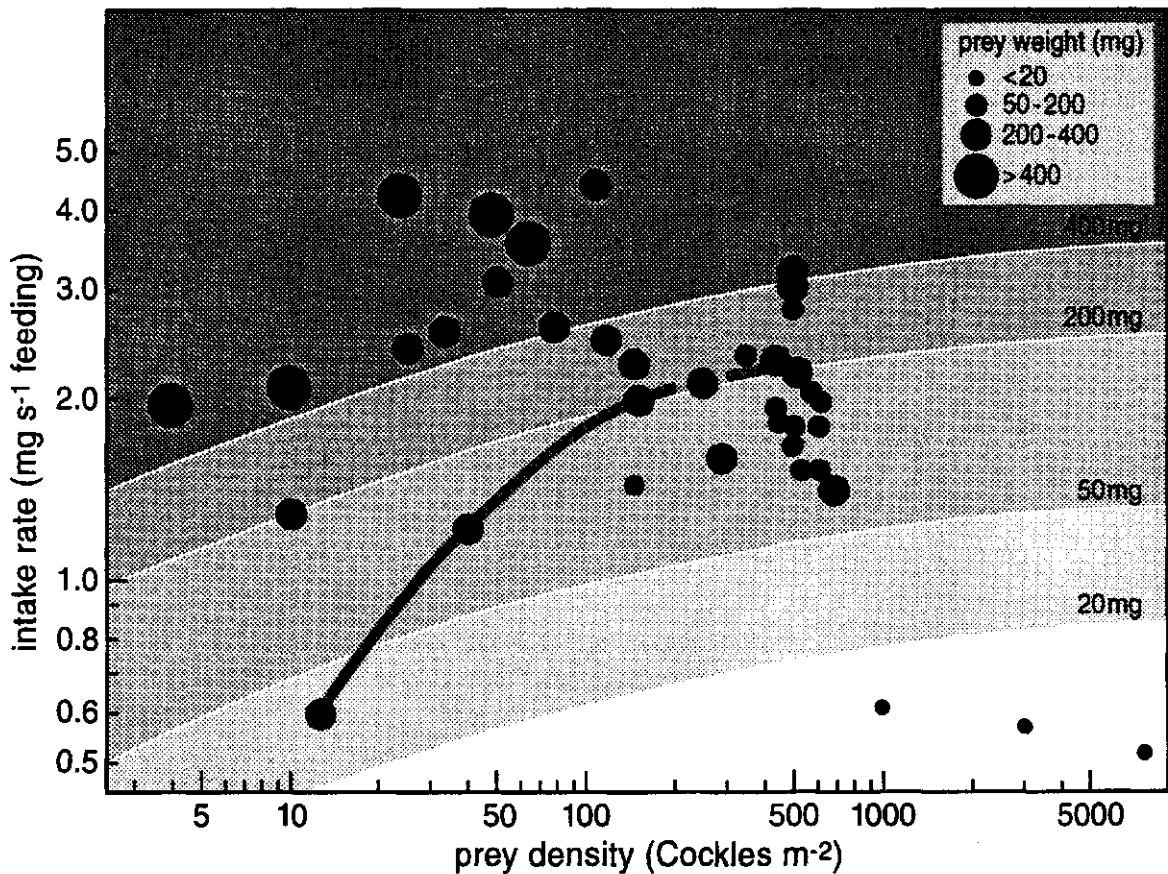
Figure 11.   Intake rate of Cockle-feeding Oystercatchers as a function of prey density (n m^{-2}) assembled from ten studies. Hulscher (1976) and Leopold et al. (1989) offered caged birds different prey densities. Drinnan (1957), Sutherland (1982a,b,c), Ens et al. (1996b,c), Meire (1996b), Exo et al. (unpubl.), Hulscher (unpubl.) and Hulsman (unpubl.) observed birds in the wild. The four curves are based upon the multiple regression equation:
Y = 0.238X$_1$ - 0.012X^2$_1$ + 0.476X$_2$ -2.727 (R^2 = 0.670, n = 38, P < 0.001)
with Y = ln(intake rate), X$_1$ = ln(prey density) and X$_2$ = ln(prey weight). The grey line connects the measured intake rate of a captive Oystercatcher offered Cockles of 313 mg in different densities (Hulscher 1976). From Zwarts et al. (1996b).

This may be due to the inevitably larger sampling error when prey density is low. Moreover, there are no studies of birds feeding on small Cockles occurring in low densities. Hence the curves for small Cockles at low prey densities must be considered as extrapolations. The regression analysis may systematically overestimate the intake rate at low prey densities because the samples refer to average density within a plot, whereas the birds would presumably select the richer patches within a plot. This typical problem for field studies was absent in Hulscher's (1976) experimental study in which Oystercatchers fed in a small plot with homogeneous prey density. As would be predicted, the intake rate at low prey densities in that study is indeed below the prediction of the regression model based on all the studies (Fig. 11). Sometimes Oystercatchers can feed on Cockles that have recently died, e.g. due to frost bite after a cold spell. In these circumstances the birds simply extract the flesh from the gaping valves and achieve intake rates well exceeding 3 mg s^{-1} (Hulscher & Zwarts unpubl.).

5.4.6 Mussels

When Oystercatchers feed on Mussels, they regularly reject prey after spending some time handling this prey. This happens especially often in Oystercatchers hammering Mussels. This requires that the optimal prey choice model be modified to include the time wasted on prey that are subsequently not taken. For this reason, Meire & Ervynck (1986) adapted the optimal prey choice model in the following way:

$$\frac{E}{T} = \frac{\sum \lambda_i E_i P_i (1 - R_i)}{1 + \sum \lambda_i (h_i (1 - R_i) + W_i R_i) P_i}$$

where w_i (s) represents the time wasted in handling a prey item of type i that is subsequently rejected, and R_i the probability of rejecting a prey item of type i. This notation is slightly different from Meire & Ervynck (1986), to make clear that P_i still remains the decision variable whether to attack a prey item that is encountered ($P_i=1$) or ignore it ($P_i=0$).
From search speed S (m s^{-1}) and the density of prey type i, D_i (m^{-2}), Meire obtained a relative measure of encounter rate, following Thompson (1983):

$$\lambda_i = 1/100 \sqrt{(1/D_i)/S}$$

For ventral hammerers they estimate S at 0.085 m s^{-1}, while probability of rejection and waste handling time depended on lenth L (mm) in the following way:

R_i = 1.127 - 0.016L_i for 10 < L_i <70
w_i = -4.04 + 0.679L_i for 10 < L_i < 55
As they observed that Mussels overgrown with barnacles were rarely attacked, such Mussels were not included in the estimate of prey density D_i.

Apart from ventral hammerers, Cayford & Goss-Custard (1996) employed this model also for dorsal hammerers and stabbers. Their estimates for rejection rates and waste handling times can be read from the graphs in their paper; rejection rates and waste handling times are smallest for stabbers. They estimate search speed at 0.17 m s^{-1} for stabbers, 0.083 m s^{-1} for ventral hammerers and 0.073 m s^{-1} for dorsal hammerers.

The reason that ventral hammerers reject many Mussels is that the shells are too thick. Meire (1996c) investigates the possibility that the birds can gauge after a few blows to the shell how many more blows they would need to open it. Thicker shells require a greater number of blows to open, so handling time can be predicted from shell thickness. This means that profitability is determined by both shell length and shell thickness, while shells covered in barnacles are still classified as "inedible". The implication is that a complete measurement of the food supply entails measurement of all these variables, i.e. the density D_{ijk} of Mussels in length class i, thickness class j, and barnacle coverage class k, for all i,j,k must be known, as well as the biomass content.

The alternative to these highly sophisticated functional response models are simplistic regressions. According to the reviews of Zwarts et al. (1996a,b), prey size is more important than prey density in determining intake rate. They find that the intake rate I (mg AFDM per s feeding) is related to mean prey weight W (mg AFDM) as follows:

$$I = 0.082W^{0.523}.$$

In **EXE2** intake rate of a stabber of average feeding efficiency feeding singly, I_s, is predicted from the biomass density of mussels Q (g AFDM m^{-2}) as follows:

$I_s = 3.2367Q - 0.00422Q^2$ for Q$\leq$ 383 g AFDM m^{-2}
$I_s = 621$ for Q > 383 g AFDM m^{-2}

Similarly, in **EXE2** intake rate of a hammerer of average feeding efficiency feeding singly, I_h, is predicted from the biomass density of Mussels Q (mg AFDM m^{-2}) as follows:

$I_h = 4.9041Q - 0.00639Q^2$ for Q $\leq$ 384 g AFDM m^{-2}
$I_h = 941$ for Q > 384 g AFDM m^{-2}

Clarke & Goss-Custard (1996) do not specify the units of I_s and I_h, but knowing that observation periods in the Exe study usually last 5 min, we expect that I_s and I_h are measured in mg AFDM per 5 min feeding.

5.5 Suggestions for EFFECT

1. For each of the major prey of the Oystercatcher, handling times in relation to length and weight have been estimated. These estimates, in combination with the energy content of the prey, allow the calculation of profitability. They can then be incorporated in **EFFECT**, which currently only deals with Cockles.

2. For each of the bivalve prey, parameters of the functional response are provided, which can be incorporated in **EFFECT**. Which of the prey are actually included must depend on the estuary of interest.

3. In some cases, more than one functional response equation is provided. In that case, the choice which equation to incorporate in **EFFECT** may be guided by the type of prey data that are actually available, or that can be most easily collected.

4. In rare cases, the average intake rates provided by Zwarts et al. (1996b) may be used to estimate the intake rate of a scarce alternative prey (table 2).

5. It is suggested that the assumption that Oystercatchers can search for only one prey species at a time is not too far from the truth. It simplifies incorporation of the multi-species functional response enormously.

Table 2.   Average intake rate (mg AFDM s^{-1} ± SD) and prey weight per prey species; n is number of studies (given in Appendix E). Eleven studies with a feeding period < 1 h and two studies with extremely low intake rates (no 196 & 197 in Appendix E) have been excluded. From Zwarts et al. (1996b).

species	mg s^{-1}	SD	mg	n
Anadara	1.85		1637	1
Arenicola	2.96	1.64	216	2
Cerastoderma	2.17	0.93	230	48
Earthworms	1.18	0.53	71	5
Littorina	1.24	0.27	138	8
Macoma	2.34	0.59	67	12
Mya	3.14	0.64	172	3
Mytilus ventral	2.04	0.92	418	26
Mytilus dorsal	2.10	0.93	513	27
Mytilus stab	2.05	0.69	409	48
Nereis	2.00	0.95	67	23
Patella	2.35		120	1
Scrobicularia	1.74	0.75	178	11
Tipula	1.34	0.48	53	18
Uca	1.78		786	1
all species	2.00	0.85		240

6 INTERFERENCE

6.1 The EFFECT model and general theory on interference

6.1.1 Scramble and contest competition

The major goal of the EFFECT model was to predict the density-dependent winter mortality of oystercatchers in relation with habitat loss and shellfish fisheries. Habitat loss and fisheries most likely reduce resources that are used by birds. These resources, for example food or space, may be the limiting factor governing mortality. It is therefore evident that knowledge about the way birds share a limited resource is of utmost importance (Nicholson 1954; Lomnicki 1988). A simple example of food limitation will illustrate this. Suppose that at the start of the winter one hundred prey items are available. An oystercatcher needs five of these prey items to survive the winter. What will happen when twenty-five birds arrive in the area at the start of the winter? Sharing all food equally (this is called scramble competition) the birds would get four prey items each (assuming that no other predators eat this kind of prey). That is not enough for survival and all birds would die (assuming that the birds cannot go elsewhere and alternative food is not available). In contrast, if some animals are more equal than others, it might turn out that twenty birds get what they need and five wretches get nothing and die (this is called contest competition). This simple example shows that one should know whether the intra-specific competition for winter food is of the scramble type or of the contest type: it matters a lot whether all twenty-five birds die or only five. Of course, contest and scramble competition are only the extremes of a continuum. In the example, the number dying might be somewhere in between five and twenty-five. In the harsh reality of life, it is also most unlikely that pure scramble or pure contest competition occurs. Generally, a graph of the density-dependence of mortality and how it changes in response to fisheries or habitat loss, is a beautiful way to summarise the results of a model like the EFFECT model (Houston 1996).

6.1.2 Exploitation and interference competition

Intra-specific competition may work in two different ways. Indirectly through a reduction in food stocks (this is called exploitation competition) or directly through interference between predators. Interference occurs through a) food stealing (called kleptoparasitism), b) wasting time in "social" interactions, such as fighting, avoidance behaviour, vigilance or c) via a reduction in foraging efficiency, i.e. through a reduced searching rate or an increased handling time when there are more predators around. This reduction in foraging efficiency may be due to a behavioural response of the prey organisms: crabs and shrimps may return to their holes, worms may bury deeper in the sediment, and bivalves may close their shells when there are more predators around. In practice, it might be difficult to distinguish b) from c). Searching rate may drop as a result of subtle changes in vigilance during searching.

Pure exploitation competition is of the scramble type. At a given moment the food supply is dissipated and all birds will die. As was said earlier, this is very unlikely to happen in true life. So, interference effects will play a role. Models like the **EXE2** and the **EFFECT** model indeed assumed that interference among predators occurs. These models have incorporated that food intake rate of a bird decreases as a result of interference. The exact formulation, however, differs. We will see below that these differences may have great impact on the model outcome.

6.1.3   Spatial and temporal scales and the ideal free distribution

Animals will only respond to competitors in their neighbourhood, the ones that they get in touch with. In order to avoid a detailed modelling of the exact searching routes of each individual, the models mentioned above divide the spatial environment into a group of patches. It is assumed (implicitly or explicitly) that each patch has a random prey distribution (more precisely, prey intensity is constant at each point in space). Encounters between searching birds within a patch also occur randomly. Birds in another patch are (in the short term) not of importance.

Modelling the movement between patches is based on the idea that the birds are "ideal" and "free". "Ideal" means that each bird is able to choose the patch that maximises its intake rate. "Free" means that there are no costs associated with moving between or entering a patch. In the models the birds redistribute themselves each day, in such way that no individual bird can increase its intake rate by moving. During the day the birds eat, the prey distribution changes, and the next day the birds redistribute themselves again.

Both the spatial and the temporal scale in the models thus have two components: homogeneous patches (of a given size) in an area (of a given size) and days in a winter time. The relevance of the choice for a particular spatial and temporal scale (Are patches homogeneous? Do birds redistribute themselves once a day?) that was made in the **EFFECT** model may be further examined. The same holds for the consequences of the choice in terms of model output.

6.1.4   Some animals are more equal

Originally, ideal free theory assumed that animals are all alike. The various oystercatcher models discussed here, however, assume that birds differ. This is in agreement with empirical data. Ens and Goss-Custard (1984) observed that individual oystercatchers differed in their susceptibility to interference. When the intake rate was plotted on predator density, dominant birds showed hardly any decrease, whereas subdominants did show a decreasing encounter rate with increasing density of conspecifics. In the models, therefore, individuals differ in their susceptibility to interference. Again, the precise way in which these differences are incorporated in the model structure differs considerably. And so again, we will see below that these differences may have great impact on the model outcome.

6.1.5 Basic model structure

The basic structure of models like the **EXE2** and the **EFFECT** model is the same. The intake rate W of an individual of dominance class j is a function of the density of the various prey classes n_k and the various dominance classes p_j of its competitors in the patch. The ideal free distribution is reached when the intake rate is the same for all patches $i=1...I$:

$$W_{ij}=f(n_{i1}...n_{iK},P_{i1}...P_{ij})=c_j,$$

where c_j is a constant. The aim then is to find predator densities p_{ij} such that the above similarity holds and each c_j is maximized. For simple models (no differences in competitive abilities among predators; W always increases with increasing p) a unique solution that obeys these criteria can be found analytically. For more complex models simulations, in which the fate of each individual is kept track of, are used to find the solution. Usually, the animals are initially distributed between sites in a regular way (Parker and Sutherland 1986; Sutherland 1992; Sutherland and Parker 1992). Subsequently the animals are allowed to move one-by-one to a site where they can achieve a higher intake rate. The order of movement depends on the gain in intake rate that an individual can achieve (Sutherland 1992). A steady state solution is reached when no individual can increase its intake rate by moving to another patch. In the steady state each individual of a given level of competitive ability obtains (more or less) the same intake rate in all patches it inhabits. Yet such steady-state solution does not necessarily exist. Animals may keep on moving. Neither is it certain that such steady-state solution will be reached, when it exists.

Nevertheless, each of the three models (**EXE2**, **EFFECT** and **DEPLETE**) uses some rule to stop the distribution process. Once distributed, the animals exploit the patch of their choice during the time of a day. The prey depletion is recorded. The next day the animals redistribute themselves in accordance with the new prey distribution. Below we will see in more detail what (simplified) procedure is used in the **EFFECT** model.

6.2 Current formulation in EFFECT

In the **EFFECT** model it is assumed that there is a linear hierarchy in competitive ability between the birds in a patch. The major strength of the model is the notice that the assumption that the individuals with the lowest rank in each patch do have equal intake rates, directly yields the distribution of the birds! The idea has been worked out in appendix II of the Bos report. Below, we will repeat the argument, but in a slightly different form (original notation between brackets).

Suppose that the intake rate of the individual with the lowest rank in patch i equals

$$W_i = W_i^{max}\left(1 - q\frac{P_i}{D_i}\right)$$

where W_i^{max} is the interference-free intake rate in patch i (PINTAKE), q an interference coefficient (CONSTIF), P_i the number of predators in the patch (N) and D_i the surface area of the patch (SURFACE). So, there is a linear decrease in intake rate with an increase in the density of predators. Considering two patches, we may state that $W_1 = W_2$ and $P_1 + P_2 = P$, where P is the total number of predators in the system (N(10)). So

$$W_1^{max}\left(1 - q\frac{P_1}{D_1}\right) = W_2^{max}\left(1 - q\frac{P - P_1}{D_2}\right),$$

which leads after simple algebraic rearrangement to an explicit solution for P_1 (and thus for P_2 as well):

$$P_1 = \frac{\dfrac{\left(W_1^{max} - W_2^{max}\right)}{q} + \dfrac{W_2^{max}}{D_2}P}{\left(\dfrac{W_1^{max}}{D_1} + \dfrac{W_2^{max}}{D_2}\right)}.$$

That was Appendix II of the Bos report. Yet, a more general solution is possible (Van der Meer and Ens submitted). In **EFFECT** it is assumed that the interference-free intake rate is related to prey abundance by Holling's disc equation. So

$$W_i = \frac{an_i}{1 + ahn_i}\left(1 - q\frac{P_i}{D_i}\right)$$

where a is the searching rate, n_i prey density in patch i and h handling time. In a multiple patch situation, we may state that W_i is the same for each patch. Thus $W_i = c$ for all patches i, where c is a constant depending on P. Re-writing leads to an expression where predator density is a function of prey density:

$$\frac{P_i}{D_i} = \frac{1 - ch}{q} - \frac{c}{aq}\frac{1}{n_i}.$$

This expression immediately shows what sort of aggregative response should be expected: a maximum predator density

,

$$\frac{P_i}{D_i} = \frac{1-ch}{q},$$

that is asymptotically reached at high prey densities ($n_i \to \infty$); and a threshold prey density equal to

$$\frac{1}{a\left(\frac{1}{c}-h\right)},$$

below which predator densities are zero. The value for c can be derived (numerically) from the equation:

$$c = \frac{1-q\sum_{i=j}^{l}\frac{d_i}{D^*}p_i}{h+\frac{1}{a}\sum_{i=j}^{l}\frac{d_i}{D^*}\frac{1}{n_i}}.$$

This analysis reveals that the aggregative response as obtained by simulations with **EFFECT** and as presented in Fig. 4.5 on p 35 of the Bos report could have been obtained analytically. May that be true, we now arrive at a more important issue, you might even say that we come to the heart of the matter. Van der Meer and Ens also explored a variety of other models of interference and derived (analytically) the accompanying aggregative responses. It appeared that these responses differed considerably. One remarkable result of the **EFFECT** model was presented in Fig. 4.5 of the **EFFECT** report. The figure showed that good patches are getting more and more crowded in the course of time and poor patches are rather quickly deserted. In other words the variance between patches in terms of predator densities tended to increase in time. This result could not be repeated by many other models. For example, the well-known interference relation of Hassell and Varley (where it is assumed that the log of the searching rate a linearly decreases with increasing log predator density) showed an opposite result. Good patches were readily exploited and in the course of time all patches tend to become similar. The variance among patches decreased with time. Hence the remark on page 16 of the Bos report that "the debate on whether or not the logarithm of the x and or y-axis should be taken ... can be ignored as long as only qualitative trends are investigated" is unfortunately not true.

Another point of concern with the **EFFECT** approach is that arguments why it is allowed to look only at the lowest rank animals in order to obtain the distribution of the birds are not clearly given (see p. 32 of the Bos report). The following line of thought provides the proper argument (in other words the approach of Bos was right but he did not prove it, therefore we will do it below). We first consider the situation that all predators are alike. In that case W_i as

defined above is the intake rate for each individual, and evidently the approach followed above (setting W_i equal for all (two) patches) is appropriate. Now consider the linear hierarchy system. The most dominant animal will go to the best patch, whatever other animals do. One might say, that in its perception no other animals exist. The second most dominant animal will compare the encounter rate in the second best patch with one individual, itself, with the encounter rate in the best patch with two animals, itself and its

superior. Thus, it will go to the best patch if $W_1^*\left(1-q\dfrac{2}{D_1}\right) > W_2^*\left(1-q\dfrac{1}{D_2}\right),$

and willgo to the second best patch otherwise. Here is the point: precisely the same decision would have been made if the first animal was not dominant, but equal to the second one. The distribution would have been 'both in patch one' if ,

$W_1^*\left(1-q\dfrac{2}{D_1}\right) > W_2^*\left(1-q\dfrac{1}{D_2}\right),$, and 'one in patch one and one in patch two'

if not. Similarly, for the third animal it does not really matter whether the first two are more dominant or are equal to itself. And so on. The distribution that is obtained after the least dominant competitor has made its choice, is exactly similar to the ideal free distribution, that would have been obtained when all animals were supposed to be equal. That is to say, the number of animals per patch is identical. The example also shows that the intake rate of the least dominant animal in each patch are generally not exactly similar between patches (due to the fact that in a strict hierarchy no animals are equal). Yet, simulations that we performed showed that the approximation that the intake rates of the least dominant animal in each patch are exactly equal, works reasonably well.

The similarity between the **EFFECT** model and a model with equal competitors (e.g. **DEPLETE**) may even hold for the mortality rate! In **DEPLETE** it is assumed that when the phase is reached that birds cannot achieve their requirements, just enough birds die such that the remaining birds are able to meet their energy requirements. In **EFFECT** the same thing happens, but the birds that die are the lowest ranked birds, whereas in **DEPLETE** they are, as it were, simply randomly selected. The number of birds that die are, however, the same in both approaches.

A final point concerns the assumption of a linear hierarchy. Other assumptions on the way differences in competitive ability should be incorporated in the relation between intake rate and predator densities, e.g. those made by Sutherland and Parker (1985) reveal a totally different distribution than is obtained by applying the linear hierarchy assumption. Sutherland and Parker's model predict the so-called "truncated phenotype distribution". This distribution says that all strong competitors share the good patches, and that they leave the poor patches to the weaklings. Although an underlying mechanism is lacking in their approach (but that is not unique), the radically different distribution that their models predict, compared to the **EFFECT** model, is a

warning that the final distribution of the birds is not very robust against minor differences in the precise formulation of differences in competitive ability.

6.3 Suggestions for EFFECT

Above we showed that there are some assumptions made in **EFFECT** that need further study (spatial and temporal scales; linear decrease in intake rate with increasing predator numbers; linear hierarchy). One aspect of studying these assumptions concerns the reliability of these assumptions. Unfortunately, in spite of 15 year research on oystercatchers the required detail on how interference exactly works is still lacking. A second direction, however, is within reach and that concerns the robustness of the model output (the density dependence of mortality) to different assumptions. Is the density dependence relation strongly influenced by the spatial scale that is used for the patches? Do the results severely deviate when interference is modeled differently? We strongly advocate that such analysis should be performed. The usual validation and sensitivity procedures are only concerned with the parameter uncertainty. Yet the uncertainty about the model structure cannot be ignored.

7 CONCLUSIONS

The model **EFFECT1.1** does not differ significantly from the model **BOULI-MIA** developed by Bos (1994). Bos concludes the abstract of his report with the statement that "some important aspects are to be studied first, before the model can produce reliable predictions". Subsequent workers have interpreted this to mean that some paramters required better estimation and concentrated on sensitivity analyses of the various parameters. In this report we hope to have convinced the reader that the model is still in need of a thorough analysis of its' structure. Basic questions that need to be addressed are:
- should individuals be allowed to build up energy stores?
- is it necessary to include the complex calculations on heat loss?
- how should interference be modelled?
- is prey depletion limiting Oystercatcher numbers, or should we think in terms of a critical period?
In the absence of this analysis, general conclusions like "it is predicted that limited cockle fishery will have the least negative effects on the wintering population of Oystercatchers, if it is spread over the best cockle beds of the estuary" (Bos 1994) must be regarded as premature. Furthermore, at this stage of the development of the model, research effort should be directed to the proposed analysis of the program definition, instead of sensitivity analyses.

While we consider **EFFECT1.1** not yet fit for application to real-life situations, it is clear that this must be the ultimate goal. In this report we have presented the best available estimates of energy needs, as well as handling times, profitability, seasonal changes in availability and other aspects of the functional response of the most important prey. This information can be incorporated.

The ideal free assumption figures prominentely in **EFFECT1.1**. It is necessary to calculate at each time step how the birds will distribute themselves. However, the ideal free assumption only makes sense when the geographical scale is relatively small. When the geographical scale becomes large, the assumption is no longer tenable and a metapopulation structure is needed. This will almost certainly require a completely new model structure.

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APPENDIX A: FORTRAN SOURCE CODE OF EFFECT1.1

FORTRAN source code of the relevant subroutines of the EFFECT1.1 model that was investigated.

```
C###############################################################
C SENECA 2.0                                        (C) NIOO-CEMO/DGW
C File: XSTART.FOR
C Date: 1-12-92
C This file contains the user initialization routine (XSTART)
C and the user termination routine (XEND).
C###############################################################
      SUBROUTINE XSTART(TIME)
C
      IMPLICIT REAL(A-Z)
C Parameter:
      REAL TIME
C
C This routine will be called once at the begin of a simulation run,
C after all initializations but before the first results at TIME = 0
C are stored.
C----------------------------------------------
C Declarations:
      INCLUDE 'EFFECT.DCS'
      INCLUDE 'EFFECT.DCP'
      INCLUDE 'EFFECT.DCV'
      INCLUDE 'XSIMO.DEX'
C
C----------------------------------------------
C Statements:

      do 10 i=1,xncomp

* controle op invoer
      if ((nprey(i).eq.0).and.(biom(i).gt.0)) then
          STOP 'fout in biomassa en dichtheid invoer'
      endif

      if (nprey(i).gt.0) then
          wprey(i)=xdiv(biom(i),nprey(i))
          yavg(i)=xdiv(wprey(i)*100,fwcockle(time))
      endif


   10 continue

      END
C End of XSTART
C
C
C*************************************************** ******************
      SUBROUTINE XEND(TIME)
C
```

```
      IMPLICIT REAL(A-Z)
C Parameter:
      REAL TIME
C
C This routine will be called once at the end of a simulation run.
C after the last calls to the submodel routines but before the last
C results are stored.
C───────────────────────────── ──-
C Declarations:
      INCLUDE 'EFFECT.DCS'
      INCLUDE 'EFFECT.DCP'
      INCLUDE 'EFFECT.DCV'
      INCLUDE 'XSIMO.DEX'
C
C─────────────────────────────-
C Statements:
C
      END
C End of XEND
C***********************************************************************
```

```
C######################################################################
C SENECA 2.0                                            (C) NIOO-CEMO/DGW
C File: XFORC.FOR
C Model: EFFECT
C Creation date: 27-6-1995
C This file contains all Forcing functions declarations.
C######################################################################
C
      REAL FUNCTION FWIND(TIME)
      REAL TIME
      EXTERNAL XTIMSER
      FWIND = XTIMSER(3,1,0,TIME)
      RETURN
      END
C of FWIND
C
      REAL FUNCTION FTEMP(TIME)
      REAL TIME
      EXTERNAL XTIMSER
      FTEMP = XTIMSER(3,2,0,TIME)
      RETURN
      END
C of FTEMP
C
      REAL FUNCTION FRAD(TIME)
      REAL TIME
      EXTERNAL XTIMSER
      FRAD = XTIMSER(3,3,0,TIME)
      RETURN
      END
C of FRAD
C
```

```
      REAL FUNCTION FNCOCKLE(TIME)
      REAL TIME
      EXTERNAL XTIMSER
      FNCOCKLE = XTIMSER(3,4,0,TIME)
      RETURN
      END
C of FNCOCKLE
C
      REAL FUNCTION FWCOCKLE(TIME)
      REAL TIME
      EXTERNAL XTIMSER
      FWCOCKLE = XTIMSER(3,5,0,TIME)
      RETURN
      END
C of FWCOCKLE




C#################################################################
C SENECA 2.0                                        (C) NIOO-CEMO/DGW
C File: "submodel".FOR
C Date: 1-3-93
C#################################################################
      SUBROUTINE DEE(TIME)
C
C Submodel subroutine
C
      IMPLICIT REAL(A-Z)
C Parameter:
      REAL TIME
C the parameter TIME contains the simulation time
C the simulation time is expressed in the model's Time Unit
C and is relative to the start date/time of the simulation period
C so at the start of the simulation, when this subroutine is
C called for the first time, TIME equals 0.0
C after every integration step TIME is increased with the amount
C of the integration step size.
C----------------------------------------
C Declarations:
      INCLUDE 'EFFECT.DCS'
      INCLUDE 'DEE.DCP'
      INCLUDE 'DEE.DCV'
      INCLUDE 'XSIMO.DEX'
C
C----------------------------------------
C Statements:
C
*  Daily Energy Expenditure Module
*  calculates the DEE
      DO 10 i=1,3
      IF (i.eq.1) THEN
            bmr=bmrmin*avgbmr
      ELSEIF (i.eq.2) THEN
            bmr=avgbmr
```

```
          ELSEIF (i.eq.3) THEN
                  bmr=bmrmax*avgbmr
          ENDIF
*         energiebehoefte tijdens eten (j=1) en rusten (j=2)
*         eten 2* 6 uur, rusten 2* 6 uur
          DO 20 j=1,2
          IF (j.eq.1) THEN
                  windfac=heightcorr
          ELSE
                  windfac=windfact
          ENDIF
          heatloss=(condmwind+windcond*(windfac*fwind(time))**power)*
     &            (btempm-ftemp(time))-radcond*frad(time)
          tempex=btempm-heatloss/condpwind
          IF (tempex.ge.lct) THEN
                  mmaint=bmr/(equ3a+equ3b*tempex)
          ELSE
                  IF (tempex.le.teql) THEN
                     mmaint=(oyst*(btempo-tempex))/equl
                  ELSE
                     mmaint=(oyst*(btempo-tempex))/(equ2a-equ2b*tempex)
                  ENDIF
          ENDIF

          IF (j.eq.1) THEN
                  deefeed=((bmr*act+mmaint)*tm)/(enval*asef)
          ELSEIF (j.eq.2) THEN
                  deeroost=((bmr*act+mmaint)*tm)/(enval*asef)
          ENDIF
20        continue

          IF (i.eq.1) THEN
                  mindfi=deefeed+deeroost
          ELSEIF (i.eq.2) THEN
                  avgdfi=deefeed+deeroost
          ELSEIF (i.eq.3) THEN
                  maxdfi=deefeed+deeroost
          ENDIF

10        continue

          END
C***********************************************************************




C#######################################################################
C SENECA 2.0                                              (C) NIOO-CEMO/DGW
C File: "submodel".FOR
C Date: 1-3-93
C#######################################################################
          SUBROUTINE FR(TIME)
C
C Submodel subroutine
C
```

```
C       IMPLICIT REAL(A-Z)
C Parameter:
        REAL TIME
C the parameter TIME contains the simulation time
C the simulation time is expressed in the model's Time Unit
C and is relative to the start date/time of the simulation period
C so at the start of the simulation, when this subroutine is
C called for the first time. TIME equals 0.0
C after every integration step TIME is increased with the amount
C of the integration step size.
C-----------------------------------------------
C Declarations:
        INCLUDE 'EFFECT.DCS'
        INCLUDE 'FR.DCP'
        INCLUDE 'FR.DCV'
        INCLUDE 'XSIMO.DEX'

        INTEGER L
C
C-----------------------------------------------
C Statements:
C
* FUNCTIONAL RESPONS MODULE


        do 10 i=1,noacomp
                helpmass(i)=biom(i)
10      continue

*       sorteren

        L=noacomp/2+1
        IR=noacomp

100     CONTINUE
        IF(L.GT.1)THEN
          L=L-1
          RHELPMASS=HELPMASS(L)
          RPOINTER=POINTER(L)
        ELSE
          RHELPMASS=HELPMASS(IR)
          RPOINTER=POINTER(IR)
          HELPMASS(IR)=HELPMASS(1)
          POINTER(IR)=POINTER(1)
          IR=IR-1
          IF(IR.EQ.1)THEN
            HELPMASS(1)=RHELPMASS
            POINTER(1)=RPOINTER
          goto 199
          ENDIF
        ENDIF
        I=L
        J=L+L
120     IF(J.LE.IR)THEN
          IF(J.LT.IR)THEN
            IF(HELPMASS(J).GT.HELPMASS(J+1))J=J+1
```

```
                ENDIF
                  IF(RHELPMASS.GT.HELPMASS(J))THEN
                  HELPMASS(I)=HELPMASS(J)
                  POINTER(I)=POINTER(J)
                  I=J
                  J=J+J
                  ELSE
                    J=IR+1
                  ENDIF
          GO TO 120
              ENDIF
              HELPMASS(I)=RHELPMASS
              POINTER(I)=RPOINTER
              GOTO 100
      199     continue


*  _____
* uitschakelen klassen zonder biomassa

              do 250 k=1.noacomp
                      i=pointer(k)
                      if (biom(i).le.0.0) then
                              noacomp=noacomp-1
                      endif
      250     continue


*  _____-
* berekenen functionele respons

              do 300 k=1.noacomp
                      i=pointer(k)
                      pintake(i)=(ar*biom(i))/(val+(ar*ht*biom(i)))
                      if (k.eq.1) then
                              surf=surface(i)
                              pint=pintake(i)
                      endif
      300     continue

          END


C***********************************************************************




C######################################################################
C SENECA 2.0                                                 (C) NIOO-CEMO/DGW
C File: "submodel".FOR
C Date: 1-3-93
C######################################################################
          SUBROUTINE DISPERS(TIME)
C
C Submodel subroutine
C
          IMPLICIT REAL(A-Z)
```

```
C Parameter:
        REAL TIME.potn
C the parameter TIME contains the simulation time
C the simulation time is expressed in the model's Time Unit
C and is relative to the start date/time of the simulation period
C so at the start of the simulation, when this subroutine is
C called for the first time, TIME equals 0.0
C after every integration step TIME is increased with the amount
C of the integration step size.
C-------------------------------------
C Declarations:
        INCLUDE 'EFFECT.DCS'
        INCLUDE 'DISPERS.DCP'
        INCLUDE 'DISPERS.DCV'
    INCLUDE 'XSIMO.DEX'
C
C-------------------------------------
C Statements:
C
        j=noacomp
  5     CONTINUE
        dubprod=0
        relsur=0

        DO 10 k=2.j
                i=pointer(k)
                hulpf=surface(i)/surf
                dubprod=dubprod+xdiv(pint.pintake(i))*hulpf
                relsur=relsur+hulpf
  10    CONTINUE

        hulpe=ntot*constif/surf-relsur+dubprod
        sf=xdiv(hulpe.(val2+dubprod))
        loin=-sf*pint+pint
        i=pointer(j)
        IF ((loin.gt.pintake(i)).or.(mindfi.gt.pintake(i))) THEN
                j=j-1
                goto 5
        ENDIF

  *  ----
  * berekenen aantallen en dichtheden
  * van de klassen waar de loin lager ligt dan de potential intake


        sum=ntot

        DO 20 k=1.j
        i=pointer(k)
  * berekenen potentieel aantal vogels
        soif(i)=xdiv((pintake(i)-loin).pintake(i))
  c     write (*,*) i. soif(i). pintake(i). loin
        n(i)=(soif(i)/constif)*surface(i)
  * is dit aantal vogels nog aanwezig ?
  * JA
```

```
             if (sum.ge.n(i)) then
** kan iedere vogel de MDF halen?
**ja
             if (loin.ge.mindfi) then
                n(i)=(soif(i)/constif)*surface(i)
                nha(i)=soif(i)/constif
                sum=sum-n(i)
** nee
             else
                n(i)=n(i)-n(i)*xdiv((mindfi-loin).(pintake(i)-loin))
                nha(i)=n(i)/surface(i)
                sum=sum-n(i)
             endif
* NEE
         else
** kan iedere vogel de MDF halen?
**ja
             if (loin.ge.mindfi) then
                n(i)=sum
                nha(i)=n(i)/surface(i)
                sum=sum-n(i)
** nee
             else
*** bereken eerst of de hoeveelheid vogels zorgt voor een overschrijding van
*** de MDF
                potn=n(i)-n(i)*xdiv((mindfi-loin).(pintake(i)-loin))
*** als potn groter is dan sum kunnen alle vogels erop
                if (potn.ge.sum) then
                       n(i)=sum
                       nha(i)=n(i)/surface(i)
                       sum=sum-n(i)
                else
                       n(i)=potn
                       nha(i)=n(i)/surface(i)
                       sum=sum-potn
                endif
             endif
         endif


    20   CONTINUE


* vaststellen aantallen vogels in klassen waar de minimale opname niet
* gehaald kan worden:

         IF (j.lt.xncomp) THEN
                DO 30 k=(j+1).xncomp
                i=pointer(k)
                nha(i)=0
                n(i)=0
                soif(i)=0
    30          CONTINUE
         ENDIF

*  totaal aantal vogels in het systeem
```

```
                    ntot=ntot-sum
        * berekening vogeldagen
                    vogeldag=vogeldag+ntot


        * depletieberekeningen

                    DO 40 i=1,noacomp
                    IF (n(i).eq.0) THEN
                       depl(i)=0
                    ELSE
                            IF (pintake(i).gt.maxdfi) THEN
                                    hulpd=avgdfi*n(i)
                            ELSE
                                    hulpd=n(i)*((pintake(i)+loin)/fac4)
                            ENDIF
                            IF (biom(i)*fac*surface(i).lt.hulpd) THEN
                                    depl(i)=biom(i)
                            ELSE
                                    depl(i)=hulpd/(fac*surface(i))
                            ENDIF
                    ENDIF
        40          CONTINUE


        * herberekeningen
                    DO 50 i=1,noacomp
                            nprey(i)=nprey(i)-xdiv(depl(i),wprey(i))
                            nprey(i)=nprey(i)-nprey(i)*fncockle(time)
                            wprey(i)=fwcockle(time)/fac2*yavg(i)
                            biom(i)=nprey(i)*wprey(i)
                            cumdepl(i)=depl(i)+cumdepl(i)
                            predation(i)=biom(i)+cumdepl(i)
                            tcons=tcons+depl(i)*surface(i)*fac3
        50          CONTINUE
                    END
        C****************************************************************
```

APPENDIX B: CALCULATING MAINTENANCE METABOLISM

To arrive at the energy needs of a bird with a given basal metabolic rate (BMR), **EFFECT1.1** relies heavily on the publication of Wiersma & Piersma (1994). These authors studied the heat loss of heated taxidermic mounts of Knots under a great many environmental conditions and derived regression equations to predict the heat loss of the mount in a particular environment and to convert this predicted heat loss to the heat loss of a live Knot under the same environmental conditions. In an appendix they also indicate how their equations may be modified for a larger bird like the Oystercatcher. They argue that two major adjustments are necessary: (1) the basal metabolism and the conductance will differ between bird species, (2) the wind speed that is experienced will depend on the species specific body height.

First, the expected heat loss of the taxidermic mount must be estimated for the particular environmental conditions:

$$H_{sm}= (0.045+K_u[c.u]^{0.75})(T_m-Y_a)-K_r.R_g$$

In this equation:

H_{sm} = heat loss of the standard taxidermic mount (W)

K_u = conductance paramter related to convective heat loss (W.°C^{-1})

u = wind speed measured at a height of 10 m above the ground (m.s^{-1})

c = dimensionless constant to arrive at the wind speed as it applies to other birds; Wiersma and Piersma estimate c to be 1.15 for the larger andespecially higher Oystercatcher

T_m = temperature of the core of the mount, held at 41 °C to conform as much as possible to the core temperature of live birds

T_a = ambient temperature (°C)

K_r = radiative conductance (W.°C^{-1})

R_g = global solar radiation (W.m^{-2})

The wind speed, the ambient temperature and the global solar radiation are the three environmental variables that must be measured and that are included as forcing functions in **EFFECT1.1**. Bos (1994) took long-term monthly averages for ambient temperature and wind speed from the KNMI, while global radiation was assumed constant at 33 W.m^{-2}.

Once the heat loss of the mount is estimated, it can be used to to predict the standard operative temperature T_{es} (°C), i.e. the ambient temperature in the standard environment (the respirometry unit of Wiersma & Piersma where u = 1 m.s^{-1}) at which the mount would have the same heat loss as measured in the field. This is done as follows:

$$T_{es}=41-H_{sm}/0.055$$

Next, the standard metabolic rate SMR (W) can be estimated. The standard metabolic rate, which is also referred to as the maintenance metabolism, is defined as the energy expenditure of postabsorptive resting live birds under non-radiative forced-convection conditions. If the standard operative temperature T_{es} is above the lower critical temperature T_{lc} (°C) and not lethally high, the standard metabolic rate SMR corresponds to BMR. When T_{es} is less than T_{lc} than SMR is estimated as follows:

$$SMR = K_{es}(T_b - T_{es})$$

where:

K_{es} =overall conductance (W.°C^{-1}) at a wind speed of 1 m.s^{-1}, i.e. the standard environment

T_b =body temperature (°C); assumed to be 41 °C

T_{es} =predicted standard operative temperature, i.e. ambient temperature in the standard environment (the respirometry unit of Wiersma & Piersma where u = 1 m.s^{-1})

For the Oystercatcher, Wiersma & Piersma estimate BMR at 2.9 W, K_{es} at 0.12 W.°C^{-1} and T_{lc} at 16.8 °C for the standard environment. Clearly, the windiness of the standard environment will not affect the level of BMR, but only decrease the range of ambient temperatures at which the birds do not have to pay energy costs for thermoregulation.

APPENDIX C: EMPIRICAL STUDIES OF FOOD INTAKE

This appendix is an excerpt of the review by Zwarts et al. (1996b) on the available empirical studies of the food intake of the Oystercatcher.

The data were taken from several sources, usually already published, but also unpublished theses, reports and data files. Zwarts et al. (1996b) give a full list of all sources. They also describe how these data were combined and how all measurements on prey size, prey weight, intake rate, time spent on the feeding time, and feeding activity were assembled into one data file; the intake rates were averaged per month of Oystercatchers feeding on a certain prey. In addition to these studies, their paper also includes long-term observations on individual birds studied in the Exe estuary (Ens & Goss-Custard et al. 1984, Urfi et al. 1996), and the Dutch Wadden Sea (Blomert et al. 1983, Ens et al. 1996a, 1996b, Kersten 1996).

Nearly all field studies give food consumption of Oystercatchers as AFDM. Hence we also use this as the measure of food intake. Since, as discussed by Zwarts et al. (1996a), the energy content of marine invertebrates usually varies between 22 and 22.5 kJ g^{-1} and Oystercatchers digest 85% of the ingested energy, the factor 19 can be used as a common multiplier to convert gross intake (mg AFDM) into metabolized energy (kJ) if necessary.

To investigate whether a digestive bottleneck forces Oystercatchers to feed during both low-tide periods, we must know how much food the birds need each day. These data are hard to get for free-living birds due to the difficulties in accurately measuring intake rate at night. There are two ways around this problem. First, we can exploit situations where the birds only feed by day. For intertidally-feeding birds, this occurs in the summer when the short night falls over the high water period. Blomert et al. (1983) selected such a day to measure the total consumption of a marked individual over 24 h. Inland birds usually feed only during the daylight period and habitually roost communally at night, and a few studies have been made. Veenstra (1977) measured the feeding rate and feeding activity of inland Oystercatchers in March over the entire daylight feeding period, but since he did not measure prey weight, his data allow only a very crude estimate of the daily consumption to be made. Zwarts & Blomert (1996) observed some breeding pairs from sunrise until sunset in April, in the week before egg-laying, and measured prey fragments in the droppings to reconstruct prey weights. Second, it is possible to estimate nocturnal food consumption in nesting birds from weight changes recorded on an electronic balance placed under the nest (Kersten & Visser 1996b, Ens, Dirksen, Nieuwenhuis & Smit unpubl. and Exo & Scheiffarth unpubl.). The relation between weight change and consumption was calibrated by comparing weight changes to measured food consumption during the day.

Compared to these few field studies, many studies have measured daily consumption in captive birds (Table C1). With daily consumption expressed as AFDM, the variation is large. The average gross consumption is 32.3 g AFDM with a SD of 5.1 g, or 15.8% of the mean. This large variation is not

due to daily variation in consumption, since the data in Table C1 for captive birds all refer to studies that averaged the consumption over longer periods, and in some cases over several individuals. We therefore first investigate to what extent this variation was due to differences in (1) energy content of the prey, (2) digestibility of the prey, (3) costs of thermoregulation, (4) weight changes, (5) body weight, (6) activity costs, (7) age and (8) season. This will then allow us to assess whether a difference in food consumption occurs between captive and free-living birds.

(1) Energy content of the prey The captive Oystercatchers were fed artificial food pellets, Cockles or Mussels. The four field studies refer to breeding birds feeding mainly on Cockles (Ens *et al.* unpubl.) and Leatherjackets (Ens *et al.* unpubl., Zwarts & Blomert 1996) and to a non-breeding bird feeding on *Scrobicularia* (Blomert *et al.* 1983). As different prey types contain different amounts of energy, this diversity of food types makes it likely that the variation in daily consumption would be less if it was expressed as gross energy intake. Hulscher (1974) found that three Oystercatchers alternately offered Cockles and Mussels, consumed, on average, per day 37.4 g AFDM if Cockles were taken, but 33.2 g, or 11% less, if their food was Mussels. The energy content of both prey was not measured, but other studies have found that the energy content of Mussels is 5-10% higher than that of Cockles (Chambers & Milne 1979, Merck 1983, Zwarts & Wanink 1993). The energy content of the food offered has been determined in 8 of the 13 studies and was estimated by us for the remaining ones (Table C1). The daily consumption of Oystercatchers averaged for all studies is 728 kJ (SD 103); SD as percentage of the mean is 14.1% and thus marginally smaller than the variation in the daily AFDM consumption.

(2) Digestibility of the prey A further reduction in the variation may occur were the digestibility of the food to be known so that the daily metabolizable energy could be calculated. Digestibility in Oystercatchers feeding on Mussels was 85% of the energy (Speakman 1987, Kersten & Visser 1996a), whereas it varies between 65% and 89% in various types of food pellet (Kersten & Piersma 1987, Exo & Freimüth unpubl.). Even though a low digestibility might be expected for Leatherjackets because this prey has a thick skin, 83 to 89% of the energy is actually metabolized (Zwarts & Blomert 1996). The metabolized energy consumption, averaged for all studies, amounts to 605 kJ per day on average (SD = 93; relative SD = 15.4%). Thus, in contrast to expectation, the variation in consumption did not decrease when expressed as net, rather than gross, energy.

(3) Thermoregulation The air temperature in most studies was above 10 °C, the critical temperature below which the costs of thermoregulation increase (Kersten & Piersma 1987). However, two studies held birds at average temperatures of about 6 °C. The extra amount of energy needed to meet these additional thermoregulation costs is estimated to be 30 kJ for each °C below 10 °C, using the regression equation and conversion factors given by Kersten & Piersma (1987). The thermoregulation costs of waders along the shore are more effected by wind force then by temperature alone (Wiersma & Piersma 1994). The captive birds lived in sheltered cages, however,

whereas the data for free-living birds were collected at air temperatures of >15 °C. Hence there is no need to estimate the extra costs due to wind flow.

(4) Gaining or losing body weight Another source of variation is whether birds were changing body weight. However, body weight remained constant in most of the experiments, the exceptions being indicated in Table C1. We assume that if Oystercatchers gain, or lose, 1 g fresh body weight per day, their net energy intake would be 20 kJ above, or below, the energy consumption required to keep their body weight constant. Oystercatchers are able to keep their body weight constant at a daily gross consumption of 36 g and a net consumption of 670 kJ (see below). They lose 30 g a day if they take no food at all (Kersten & Visser 1996b). Hence, daily food consumption (C, AFDM) is a function of the daily change in body weight (ΔW, g) :

$$C = 36 - 1.2 \Delta W.$$

A slope of 1.2 g AFDM was found indeed in captive Oystercatchers by Kersten & Piersma (1987).
After correction for weight changes (20 kJ for each gram change of body weight) and costs of thermoregulation (30 kJ for each degree below 10 °C), the maintenance metabolism in the birds amounts to, on average, 588 kJ day^{-1} (SD = 85). The coefficient of variation is 14.5%, and thus still quite large.

(5) The effect of body weight Body weight explains a significant part of the variation in daily energy intake. The correlation of the linear regression is +0.59 and +0.61 on a log-log scale (Fig. 2) with an exponent of 1.49 (SE = 0.32). The SD of the residuals from the regression line shown in Fig. 2 is 69, or still 11.7% of the average consumption. The effect of the three remaining variables -activity costs, age and season- has been investigated after removing the effect of body weight by analysing the residuals.

(6) Activity costs The costs of feeding might vary between the studies, being higher for free-living birds (Blomert *et al.* 1983, Ens *et al.* unpubl., Zwarts & Blomert 1996) than for captive birds. Within the captive birds, the feeding costs might differ too, being high if the birds had to feed on an artificial cockle bank (Swennen *et al.* 1989) or a mussel bank (Koene 1978), and low if the birds were offered opened bivalves (Hulscher 1974 & unpubl., Heppleston 1971) or pellets (Kersten & Piersma 1987, Goede 1993, Exo & Freimüth unpubl.). Although the energy expenditure has not been measured, the possible costs of feeding might be derived from an increase in the metabolized energy consumption. However, the daily consumption did not differ among the four categories of studies distinguished (p = 0.81), nor when free-living and captive birds were compared (p = 0.89).

(7) Age All studies dealt with adult birds, but Heppleston (1971) worked with a yearling and Exo & Freimüth (unpubl.) with two subadults three years old. The few data available suggest no reason to assume that the consumption is different for the age classes when birds of similar body weight were compared (p = 0.87).

(8) Season There is also no seasonal variation in the consumption at thermoneutrality (p = 0.31).

In conclusion, the daily consumption of Oystercatchers with constant body weight and living in thermoneutral conditions greatly depends on their body weight but not on whether they live in captivity or in the wild. Oystercatchers in the wild weigh 520 g during most months of the year. Their daily net energy intake can be estimated at 672 kJ, which is equivalent to a gross consumption of 790 kJ or 36 g AFDM.

Table C1. Daily consumption (g AFDM) and body weight (g) of Oystercatchers feeding on Cockles (*Cer*), Mussels (*Myt*), commercial food pellets (pel), *Scrobicularia* (*Scr*) or larvae of *Tipula* (*Tip*). Sources are given in the last column. All birds were adults except one 1-year and four 3-year old birds (see column 'age'). All birds were held in captivity, but studies marked with F in column 'free' were free-living birds. All data were collected in thermoneutral conditions, except four and two birds held at an average air temperature of 6.5 and 6.3 °C (see column '°C'). Body weight was constant in all studies over the periods concerned, but decreased in study 1 (18 g in 8 days), 23 (50 g in 26 days), 28 (19 g in 30 days), and increased in study 26 (38 g in 26 days), 27 (24 g in 28 days), 29 (13 g in 30 days) and 30 (34 g in 34 days); column 'BW$_C$' gives weight change (g day^{-1}). Change in body weight was unknown in field studies 36 and 38, but assumed to be constant. Average body weight (g, column 'BW') and month of observation are indicated. Body weight was not known for the days of observation in field study 36 and 38, but assumed to be equal to the average weight of the birds of the same sex, such as measured in other birds in the same time of the year and the same site. Columns 'g', 'kJ' and 'kJQ' give total daily consumption in terms of gross AFDM (g), gross energy (kJ) and metabolized energy (kJ), respectively. Kersten & Piersma (1987) found in pellets 22.8 kJ g^{-1} fresh weight being equivalent to 25.8 kJ g^{-1} AFDM, Goede (1993) 22.3-25.1 kJ g^{-1} AFDM for different kind of food pellets, Exo & Freimüth (unpubl.) 19.9 kJ in the pellets they used, Heppleston (1971) 22.56 kJ g^{-1} AFDM in Mussels, Merck (1983) 20.7 and 21.9 kJ g^{-1} AFDM in Cockles and Mussels taken by the birds studied by Ens (unpubl.), Blomert & Zwarts (unpubl.) 24.5 kJ in Leatherjackets in the same area where Ens collected his data (same month but later years), Zwarts (unpubl.) 22.2 kJ for *Scrobicularia* taken by the bird studied by Blomert *et al.* (1983), and Zwarts & Blomert (1996) 22.9 kJ for Leatherjackets in April. It is assumed that in the remaining five studies the average energy content of Mussels was 23 kJ and of Cockles 22 kJ g^{-1} AFDM; column 'xkJ' gives the average energy content (kJ g^{-1} AFDM; printed in italics if estimated). Column 'Q' gives the digestibility and 'kJQ$_C$' the metabolized energy consumption (kJQ) corrected for weight change and thermoregulation costs (see text). Each measurement concerns an individual bird, except Kersten & Piersma (1987) and Goede (1993) whose measurements averaged 6 and 12 birds, respectively. Study 32 to 34 concern the same six individuals being weighed each week. After a selection was made of weeks with a temperature > 10 °C and constant body weights, the average consumption was calculated separately for three categories of body weight.

no	prey	month	age	free	°C	BWc	BW	g	xkJ	kJ	Q	kJQ	kJQc	source
1	Cer	6		F		-2.25	518	33.8	20.7	700	0.85	595	640	Ens et al. unpubl.
2	Cer	6					461	36.2	22.0	796	0.85	677	677	Hulscher 1974
3	Cer	6					468	36.2	22.0	796	0.85	677	677	Hulscher 1974
4	Cer	7					474	39.8	22.0	876	0.85	744	744	Hulscher 1974
5	Cer	6					426	24.4	22.0	536	0.85	456	456	Swennen et al. 1989
6	Cer	12			6.3		444	29.6	22.0	652	0.85	554	442	Swennen et al. 1989
7	Cer	12			6.3		450	37.8	22.0	832	0.85	707	595	Swennen et al. 1989
8	Cer	10					467	35.6	22.0	782	0.85	665	665	Swennen et al. 1989
9	Cer	6					469	31.4	22.0	691	0.85	587	587	Swennen et al. 1989
10	Cer	10					490	37.7	22.0	829	0.85	705	705	Swennen et al. 1989
11	Cer	6					495	26.9	22.0	593	0.85	504	504	Swennen et al. 1989
12	Myt	12	1				420	26.2	22.6	591	0.85	502	502	Heppleston 1971
13	Myt	7					442	24.0	23.0	552	0.85	469	469	Hulscher 1974
14	Myt	7					453	25.8	23.0	593	0.85	504	504	Hulscher 1974
15	Myt	7					453	26.8	23.0	616	0.85	524	524	Hulscher 1974
16	Myt	7					456	31.8	23.0	731	0.85	622	622	Hulscher 1974
17	Myt	7					459	33.9	23.0	780	0.85	663	663	Hulscher 1974
18	Myt	7					461	26.9	23.0	619	0.85	526	526	Hulscher 1974
19	Myt	8					467	34.0	23.0	782	0.85	665	665	Hulscher 1974
20	Myt	7					469	26.1	23.0	600	0.85	510	510	Hulscher 1974
21	Myt	7					473	23.5	23.0	541	0.85	459	459	Hulscher 1974
22	Myt	7					522	35.1	23.0	807	0.85	686	686	Hulscher unpubl.
23	Myt	3			6.5	-1.92	466	29.6	23.0	681	0.85	578	511	Koene 1978
24	Myt	3			6.5		512	40.7	23.0	937	0.85	796	690	Koene 1978
25	Myt	3			6.5		519	38.7	23.0	891	0.85	757	652	Koene 1978
26	Myt	3			6.5	1.46	521	39.1	23.0	899	0.85	764	629	Koene 1978
27	pel	8	3			0.86	428	32.4	19.9	644	0.67	432	415	Exo & Freimüth unpubl.
28	pel	7	3			-0.60	428	38.0	19.9	757	0.67	507	519	Exo & Freimüth unpubl.
29	pel	7	3			0.40	444	41.8	19.9	833	0.67	558	550	Exo & Freimüth unpubl.
30	pel	8	3			1.21	460	39.1	19.9	778	0.67	521	497	Exo & Freimüth unpubl.
31	pel	7					510	32.9	22.8	750	0.85	638	638	Goede 1993
32	pel	6					465	28.5	25.8	734	0.85	624	624	Kersten & Piersma 1987
33	pel	7					480	29.4	25.8	759	0.85	645	645	Kersten & Piersma 1987
34	pel	5					495	30.1	25.8	775	0.85	659	659	Kersten & Piersma 1987
35	pel	1					515	27.5	25.8	711	0.85	604	604	Kersten & Piersma 1987
36	Scr	7		F			525	33.3	22.2	739	0.85	628	628	Blomert et al. 1983
37	Tip	6		F			470	31.3	24.5	767	0.83	636	636	Ens et al. unpubl.
38	Tip	4		F			500	31.5	22.8	719	0.89	640	640	Zwarts & Blomert 1996

APPENDIX D: EXTENSIONS OF THE SIMPLE PREY CHOICE MODEL

In this appendix, which is taken from Ens *et al.* (1996a), we describe how the prey choice model must be modified when search rate is not a constant, but a decision variable under the control of the animal. We will first provide the minimum number of mathematical equations needed to specify the differences and similarities between the optimal prey choice model and the "search rate" model of Gendron & Staddon (1983). Both models can be traced back to the disc equation of Holling (1959):

$$N = \frac{aDT}{1 + at_h D}$$

where N is the number of prey consumed during time period T (s), D is the prey density (m^{-2}), a is the instantaneous area of discovery (m^2 s^{-1}) and t_h the time (s) needed to handle and ingest one prey item after it has been captured. Since it applies to a single prey species, it must be generalized to a multi-prey "functional response" before it can form the backbone of the optimal prey choice model and the search rate model.

Stephens & Krebs (1986) provide a thorough description of the simple or "classic" prey choice model. Prey of different species and sizes are ranked by their profitability, i.e. the rate of energy gain during handling. From the rate at which prey of a given class are encountered during searching it can then be calculated which classes should or should not be taken to achieve the maximum rate of energy gain during feeding. For i prey types:

$$\frac{E}{T} = \frac{\sum \lambda_i E_i V_i}{1 + \sum \lambda_i h_i V_i}$$

where E is total energy intake (J) during observation time T (s), E_i is energy gain (J) from one item of prey type i, λ_i is the encounter rate (s^{-1}) with prey type i and h_i is the handling time (s) of a prey of type i. Finally, V_i is the decision variable to be optimized and represents the probability that the predator takes a prey item of type i after it is encountered. When prey with a profitability below the critical threshold are encountered, it is more efficient to continue searching than to handle and eat them, i.e. $V_i = 1$ if $< E/T$ E_i/h_i and $V_i = 0$ if $> E/T$ E_i/h_i (Charnov 1976). To find the optimal V_i, i.e. the prey choice that maximizes intake rate of energy, it is necessary to treat the encounter rates λ_i as fixed constants.

However, as Gendron & Staddon make clear, it is very likely that encounter rates are at least partly under the control of the foraging animal since we expect an animal to encounter more prey if it walks faster. Comparing equations (1) and (2) it is tempting to think of each encounter rate λ_i (s^{-1}) as the product of the instantaneous area of discovery a (m^2 s^{-1}) and D_i, the density (m^{-2}) of prey species i. According to Gendron & Staddon (1983) the world is not so simple and they effectively argue that λ_i consists of $a_i D_i$ instead of $a D_i$. In other words, each prey species has it's own area of discovery a_i, which is the product of S, the area searched per unit time (m^2 s^{-1}), and P_{di},

the probability of detecting an encountered prey item of species i. Gendron & Staddon need this subdivision to implement the core assumption of their model that there is a trade-off between search rate S and detection probability P_{di} and that the exact form of that trade-off depends on the crypticity of the prey species. It suffices to show how they model this trade-off for a single prey species:

$$P_d = [1 - (S/M)^K]^{1/K}$$

where M is the maximum search rate ($m^2 s^{-1}$) and K what might be called a "conspicuousness index" providing an operational measure of crypticity. For small K the detection probability P_d drops off steeply with search rate S, while for large K detection probability only declines when S nears the maximum search rate M.

Unlike Getty & Pulliam (1991), who derive the rate at which a predator using pause-travel search detects prey from explicit quantitative assumptions on the process of prey detection and perceptual constraints of the predator, Gendron & Staddon consider equation (3) a qualitative, but heuristically useful speculation. They discuss that a has been broken down into even more components by other authors, but argue that these components can be safely ignored for prey that are familiar, palatable and easy to capture. This last assumption may not apply in our study. Once detected, *Macoma* have no chance to escape. In contrast, *Nereis* can retreat into their burrow and an approaching Oystercatcher will be more successful in capturing a detected *Nereis* if approach is fast. Thus, instead of writing $\lambda_i = SP_{di}D_i$, we may need to write $\lambda_i = SP_{ci}P_{di}D_i$, where P_{ci} is the probability of capturing a detected prey of species i. As should be clear, both P_{ci} and P_{di} are assumed to depend on search rate S. Substituting into equation (2) we see that the "adapted" search rate model would be specified by the following equation:

$$\frac{E}{T} = \frac{\sum SP_{ci}(S)P_{di}(S)D_i E_i V_i}{1 + \sum SP_{ci}(S)P_{di}(S)D_i h_i V_i}$$

where S and V_i represent the decision variables that the bird has to choose such that intake rate is maximized.

APPENDIX E: EMPIRICAL ESTIMATE OF PROFITABILITY, HANDLING TIME AND INTAKE RATE

This appendix provides an excerpt of the methods used by Zwarts et al. (1996a) to review the Oystercatcher literature on handling time, prey profitability and intake rate. It also includes their appendix with the extracted data as Table E1.

Studies The data were taken from 57 articles, 6 student reports, 4 unpublished theses, but also from unpublished data files of Anne-Marie Blomert, Klaus-Michael Exo, Kees Hulsman, Cor Smit and the five authors; all sources are listed in the Table E1. The studies were performed in 19 areas, of which ten are situated in Great Britain and Northern Ireland, six in the Netherlands and one in Denmark, France, Morocco and Mauritania. All studies were done in the field on free-living Oystercatchers, except those indicated as C in column "capt" of Table E1 which refer to caged birds. Captive birds were either taken to the mudflats where they were allowed to feed in temporary cages (Hulscher 1976, 1982, unpubl.) or they were offered food on artificial mudflats (e.g. Swennen et al. 1989). Captive birds thus fed in an almost natural situation, but occasionally the food supply was manipulated either by erasing surface tracks that might reveal the presence of the prey (Hulscher 1982), or by implanting prey at different depths (Wanink & Zwarts 1985, 1996).

Prey size Size classes taken were known because prey remnants could be collected, and/or the prey size was estimated when the birds held the prey in the bill. In the latter case, bill length or the size of the colour ring could be used as a ruler of known size. Calibration experiments showed that observers could estimate prey size this way rather consistently (Ens 1982, Goss-Custard et al. 1987, Boates & Goss-Custard 1989, Ens et al. 1996b). Such estimates were usually accurate. In others, errors could be corrected. For instance, comparison of the size frequency distribution of remnants of fiddler crabs Uca tangeri taken by Oystercatchers (Ens unpubl.) and visual size estimates of Uca as they were being taken (Ens et al. 1993), showed that the visual estimates were systematically 5 mm too low.
Since Oystercatchers only ingest soft flesh, faecal analysis did not reveal information on prey size selection. However, if Oystercatchers swallowed the prey whole, hard prey fragments found in the excreta could be used to predict the prey size taken, as shown by Durell et al. (1996), who measured the jaws of Ragworms, and Zwarts & Blomert (1996) who did the same for jaws and head capsules of Leatherjackets.

Prey weight Although the best measure of prey value would be assimilated energy, we have to rely on gross intake of biomass for two reasons. First, except for a few studies (Speakman 1984, Kersten & Visser 1996 and Zwarts & Blomert 1996), the digestibility of the natural food of Oystercatchers has not yet been measured. However, since the biochemical composition of the flesh of marine bivalves does not vary much (e.g. Beukema & De Bruin 1977,

Dare & Edwards 1975), we assume also that the digestibility of this type of food for Oystercatchers does not vary much either and will remain close to 85%, such as found by Speakman (1984) and Kersten & Visser (1996) for mussel flesh. Second, too few studies have measured the caloric content of the food taken by Oystercatchers. However, the available studies (e.g. Brey *et al*. 1988, Dauvin & Joncourt 1989, Zwarts & Wanink 1993) suggest that the variation is not large, usually between 22 and 23 kJ g^{-1} ash-free dry weight (AFDM). Hence we take the rate of AFDM consumption as a general measure of prey profitability and intake rate.

Dare (1975) found a weight loss of 12.8% if Mussels were stored in formalin. Corrections for weight loss due to formalin have been made in the studies of Meire & Ervynck (1986), Meire (1996b) and Exo *et al*. (unpubl.); these studies are indicated with F in column "lab" of Table E1. The first quantitative studies in the fifties and sixties expressed food consumption not in terms of AFDM, but as volume, wet weight or dry weight. Column "lab" in Table E1 indicates which studies give intake rate as volume (V), wet weight (W) or dry weight (D). Volume (ml) of flesh, determined by emersion in water, is equivalent to 90 - 93% of its wet weight (mg) (Drinnan 1958b, Hulscher 1982). The dry weight of bivalve flesh is 15% to 20% of the wet, or fresh, weight (Hulscher 1974, 1982, Kersten & Visser 1996). The variation in this ratio depends on the laboratory procedures used. The water content varies between 79 and 82% if the flesh is briefly patted dry, but is some percentage points lower if it remains longer on a filter paper and higher if water on the surface of the flesh is not removed (Zwarts unpubl.).

Dry weight includes inorganic material. The ash-free dry weight (AFDM) of the flesh of marine invertebrates varies between 75 and 90% of the dry weight. A part of this variation may be attributed to the season (Zwarts 1991), but the main source of variation is again the laboratory procedure. The ash content of the flesh drops to 10-15% if the animals have been stored in clean sea water, but if their alimentary tract is still full of sediment, the ash-% can be as high as 25 or even 30%. For estuarine prey species, we take a common conversion factor of 0.16 to estimate AFDM if only wet weight is known and 0.17 if only volume has been determined. If the AFDM of prey has not been measured but derived from the volume or wet weight by using these conversion factors, the error of the estimate may be as much as 25% due to variation in the water content of the prey and, especially, the variable amount of ash. The error is still larger in earthworms in which the ash content varies between 25 and 55%.

The relationship between size and weight of the prey has been determined in all studies. If a paper did not give the average prey weight, we calculated it from the frequency distribution of the size classes taken and the size-weight relationship. In a few studies, the frequency distribution was not given. In those cases the weight of the average length class was taken as the average weight. This underestimates, inevitably, the average prey weight, especially if the range of size classes taken was large due to the exponential increase of weight with size.

Some prey were incompletely consumed and additional data have to be collected to know how much flesh remained in the shell (Zwarts & Wanink 1984, Swennen 1990). For instance, Oystercatchers feeding on fiddler crabs (Ens *et al*. 1993), opened the carapace and took the flesh piecemeal but

refused the pincers and legs, hence ignoring half of the biomass of the large specimens (Zwarts & Dirksen 1990). A more difficult error of estimate arose if prey were stolen as they were being eaten, or when Oystercatchers leave behind considerable amounts of flesh in the prey, which were subsequently consumed by other waders. This makes it hard to estimate the fraction of the prey biomass that was actually taken, a problem faced by Swennen (1990) in quantifying the intake rate of birds feeding on Giant Bloody Cockles *Anadara senilis*.

These problems did not arise when the weight of the flesh taken was not derived indirectly from the prey size but instead from direct estimates of the amount of flesh swallowed. The size of pieces of flesh extracted from the prey was estimated and converted to prey weight using calibration experiments with model Oystercatchers in which observers estimated the size of morsels of flesh held near the bill (Blomert *et al.* 1983, Goss-Custard *et al.* 1987, Kersten & Brenninkmeijer 1995, Ens & Alting 1996b). This alternative way of estimating prey weight is the only one that can be used if the size of the individual prey was unknown as, for instance, when the flesh was extracted from prey opened beneath the surface.

Profitability Profitability is defined as mg AFDM per second prey handling. Unless stated to the contrary, this only refers to prey which are actually consumed. Profitability can also be calculated taking into account the time lost on prey that were handled but not taken. The time spent in handling prey taken, and not taken, is known as the 'positive' and 'negative' handling times, respectively. To include negative handling times in the calculation of the profitability, it is necessary to known how often prey of a given size class are not taken and how much time is lost each time. Usually, the inclusion of lost handling times does not matter much, since either the negative handling times are very short, and/or very few prey are rejected, as shown for Ragworms and *Macoma* by Ens *et al.* (1996a). Important exceptions are Mussels being hammered on the dorsal, and especially on the ventral side (Meire & Ervynck 1986, Cayford & Goss-Custard 1990). The feeding method used when eating Mussels is indicated in column "mus" of Table E1.

Intake rate Intake rate is defined as mg AFDM consumed per second of feeding. Feeding time excludes preening and resting pauses, but includes short bouts of aggressive behaviour. Most data are based on observation periods of 5, 10 or 15 minutes. In some cases, however, individual birds were watched continuously for the entire low water period (Blomert *et al.* 1983, Ens & Goss-Custard 1984), or both methods were used (Ens *et al.* 1996b).

Some studies concerned Oystercatchers taking a mixture of prey species. In these cases, observation periods were selected during which at least 80% (and occasionally 100%) of the ingested biomass belonged to one species. This may cause errors of estimation. If an Oystercatcher generally feeds only on a small prey and only incidentally takes a large one, 5 min. periods during which only the large species are taken tend to give untypically high intake rates which birds may seldom attain were they to feed solely on these prey. This was presumably the case in Oystercatchers taking large *Mya* or *Arenicola* while their main prey, *Macoma* and *Nereis*, were smaller (Bunskoeke

1988). According to the same reasoning, estimates of intake rate of small prey taken from feeding bouts with large prey may be spuriously low.

Available feeding period The maximal duration of the feeding period in tidal areas is determined by the exposure time of the feeding area which is usually situated at, and below, mean sea level. The main feeding areas of Oystercatchers, cockle and mussel beds, are available for 5-6 h over an average low water period. The exposure time would overestimate the duration of the feeding time for breeding birds, since they visit the low water feeding areas only in short bouts (e.g. Ens *et al.* 1996b). These measurements are marked with a B in the column "br". The available, sometimes extremely short, feeding periods in captive birds were varied experimentally. Column "time" in Table E1 gives the duration of the feeding period.

Feeding activity The feeding activity was determined in two ways. Counts of feeding and non-feeding birds were conducted at regular intervals over the entire low water period. The alternative was to measure continuously the non-feeding time in individual birds of which the feeding behaviour was registered over long periods. Column "feed" in Table E1 gives the percentage of the time actually spent feeding.

Consumption The product of intake rate, duration of the feeding period and the percentage of time spent feeding estimates the total consumption during the feeding period, given in column "cons" of Table E1. The feeding period refers to the total daylight period in non-tidal habitats and to the low water period by day in tidal habitats.

Analysis We assembled two data files from the literature and our own unpublished data. One contained measurements of the handling time by prey species and by prey size and/or prey weight. The other contained the intake rates of Oystercatchers feeding on a single prey species. If studies spanned several months or years, the data were subdivided by month if intake rates were available for each month and based on sufficient measurements and prey weight and intake rate differed between the months. The same criteria were used to decide whether data would be given separately or lumped for different study plots within the study area or for different individual birds being studied. The intake rates were lumped in the few cases that the intake rates were known per Oystercatcher age class. Since the paper investigates the effect of prey density on intake rate in *Cerastoderma*, the intake rates from four studies have been split up for different subareas where prey size, prey density and intake rate were measured. SPSS (Norušis 1990) was used for all statistical analyses.

Abbreviations in Table E1. Overview of all studies that measured size and weight of prey taken by Oystercatchers, as well as their intake rate and total consumption in different areas. Size is expressed as prey length (mm), weight as mg AFDW and intake rate as mg AFDW s⁻¹ feeding. Column TIME gives the time spent on the feeding area (h), FEED the proportion of the time spent feeding while present on the feeding area, CONS the total consumption (g AFDW) during the time spent feeding. B in column BR indicates whether

the data concern breeding birds. NM^2 gives the prey density (only for Cockles). MUS shows whether mussels were opened by stabbing (S), ventral hammering (V) or dorsal hammering (D). Column CAP shows whether birds were held in captivity (C); all other studies were done on free-living birds. Column LAB shows whether it was necessary to estimate AFDW from prey volume (V), wet weight (W) or dry weight (D); all other studies measured AFDW; F refer to studies using formaline to store the prey, making a weight correction necessary. For further general explanation see methods, but for details the notes in this appendix. The number of the notes corresponds with the digit in first column.

Notes to Table E1:

1: AFDW of *Anadara* taken was 3300 mg, but 56% of the prey could not be eaten completely, due to kleptoparasitism by other bird species. Since Swennen estimated that in these cases, on average, 10% of the flesh was eaten, the weight of the average prey taken was estimated to be 1637 mg.

2-3: Since the birds also took *Macoma* and *Nereis*, a selection was made of 5 min periods during which *Arenicola* was the dominant prey.

4: Cockle height has been converted to length using Table 5 in Zwarts (1991); ash assumed to be 20% (being the average winter level; Zwarts 1991).

5: The intake rate varied between 1.4 and 2.2. mg s^{-1} during six different winter months. The data were pooled since the observation times were limited.

8-15: Since the birds also took *Mytilus*, a selection was made of 5 min periods with *Cerastoderma* as dominant prey.

25: Feeding area was exposed 5 h during daylight in January; this is equivalent to 6.5 h per low water period. Goss-Custard (1977) noted that the avarage prey weight was overestimated since small prey were probably missed and flesh also remained in the shell.

26-29: Ash assumed to be 13% in summer (being the average summer value; Zwarts 1991).

31: The flesh remaining in the shell has been measured (14.8% relative to total AFDW).

33-38: The same data are given separately for individuals by Swennen *et al.* (1989).

52-54: Since the birds also took *Tipula*, a selection was made of 5 min periods during which earthworms were the dominant prey.

55: It is assumed that the birds took the average prey present.

56: It is assumed that the ash content is 40% (data for the same area in later years; Blomert & Zwarts unpubl.).

57-64: Ash of *Littorina* in winter is assumed to be 10% (Chambers & Milne 1979).

65-69: Since the birds also took *Nereis*, a selection was made of 5 min periods during which *Macoma* was the dominant prey.

70: Since the birds also took *Cerastoderma*, a selection was made of 5 min periods during which *Macoma* was the dominant prey.

71-72: The estimation of the consumption per low water feeding period is based upon measurements of the feeding rate in colour-marked non-breeding birds (study 71) and breeding birds (study 72), but the feeding activity and mean prey weight were based on counts and prey collection, respectively, in

which breeding and non-breeding birds could not be distinguished. That is why a calculation of the low tide consumption (41 g AFDW) would be too high for the non-breeding, even if they remained 6 h on the feeding area, since presumably their feeding activity would be lower than for the breeding birds.

74: Intake rate of captive bird averaged for two experimental conditions (erased and non-erased surface).

76-77: A pair of individually marked Oystercatcher visited tidal mudflats adjacent to their nest during short feeding bouts; Study 76 and 77 give the averages for the week before and after eggs were laid, respectively; feeding rate already given by Hulscher (1982: Fig. 29).

81: Since the birds also took Macoma, a selection was made of 5 min periods during which Nereis was the dominant prey.

82: The birds usually only took the siphon. This partial consumption did not cause an overestimation of the consumption, since the flesh taken was estimated from the size of the pieces of flesh extracted from the shell.

83: The birds took small Mya in one jerk, taking the siphon but leaving a part of the body behind in the shell. When this was imitated in the laboratory 22% of the flesh remained behind. This was taken as a correction factor.

85-87: Study 85 and 86 give same data as study 87-93 averaged for all months and split up for stabbers, dorsal and ventral hammerers. Intake rates are given by Boates (1988). Exposure time according to Goss-Custard (unpubl.).

94-112: details in Cayford (1988)

117-126: Summary of the data are published by Ens (1982), Ens & Goss-Custard (1984), Sutherland & Ens (1987).

127-132: Since the birds also took Cerastoderma, a selection was made of 5 min. periods with Mytilus as dominant prey.

134-163: The majority of the data are given in Goss-Custard et al. 1984, Goss-Custard & Durell 1987 & 1988. The intake rates were recalculated, however, from the actual AFDW/mussel length relationships measured on the mussel bed, month and year in question, whereas the original paper gave standardised intakes rates.

164-165: Ash assumed to be 20% in winter. Observations were restricted to 5 h around low water, and give according to Heppleston (1971) an overestimation when extrapolated to the extreme long exposure times in October (study 164), when the birds were less active at the end of the feeding period.

167: Hungry, captive Oystercatchers were offered shelled Mytilus.

182: The flesh remaining in the shell has been measured (7.6% relative to total AFDW).

184-191: The intake rates deviates from those orginally published (Zwarts & Drent 1981), due to recalculation. Exposure time of mussel bed in May was, as in the other months, 6-6.5 h, but the watched adults were breeding birds and visited the musselbed during bouts of 83 min, on average, only.

193-197: AFDW is assumed to be 81% of DW (Zwarts unpubl.). Exposure time according to Goss-Custard (unpubl.).

198-202: Since the birds also took Macoma, a selection was made of 5 min periods during which Nereis was the dominant prey.

203-214: Intake rates of adult and juveniles are pooled.

217: Intake rates pooled over adults and imatures and over three winter periods.

218: AFDW assumed to be 80% of DW.

220-226: AFDW assumed to be 83% of DW (Zwarts 1991). Exposure time according to Goss-Custard (unpubl.).

228-230:Three birds were allowed to take 24 prey each in different sessions with a prey density > 200 prey m^{-2}.

231-232: Intake rate averaged for the experimental sessions with prey density ≥ 100 m^{-2}.

237-241: Since birds took also earthworms, a selection was made of 5 min. intervals during which Leatherjackets were the dominant prey.

242-247: The diet consited not solely of *Tipula*, since sometimes large earthworms were also taken, especially in April and July. The ash content of Leatherjackets and earthworms assumed to be 21% and 40%, respectively (data of the same area in later years; Blomert & Zwarts unpubl.). The feeding activity and consumption refer to the day-light period.

248: AFDW assumed to be 79% of DW (Blomert & Zwarts unpubl.).

249: Birds fed from sunrise to sunset. The feeding activity according to the activity counts was 59.1% (but the observed birds fed 83.5% of the time). Weight of the Leatherjackets taken was not measured, but assumed to be 15 mg AFDW, being the average weight of prey collected in the same area and the same month in later years (Blomert & Zwarts unpubl.).

253: Ens *et al.* (1993) give feeding rate and size selection. Collection of prey remnants showed, however, that prey size was underestimated (Ens unpubl.). Intake rate was calculated on the basis of corrected size selection. The birds opened the carapace to remove the flesh from it; by not eating the pincers and legs, they ignored 50% of the flesh (Zwarts & Blomert 1990, Zwarts & Dirksen 1990). Not all flesh was eaten from the carapace, since other wader species took flesh from it after Oystercatchers had finished. Whimbrels *Numenius phaeopus* opening *Uca* of similar size left behind 100 mg in the carapace (Zwarts & Dirksen 1990); it is assumed this was the same for Oystercatchers.

flo	species	mm	mg	mgs-1	month	year	time	feed	cons	br	nm2	mus	cap	lab	sources	area
1	Anadara	73	1637	1.85	2	86	7.30	39.4	19.16						Swennen 1990	Banc d'Arguin, Mauritania
2	Arenicola		309	4.12	5/7	86/7				B					Bunskoeke 1988	Schiermonnikoog, NL
3	Arenicola		124	1.80	8	86									Bunskoeke 1988	Schiermonnikoog, NL
4	Cerastoderma	22	49	1.13	2	73	8.50	58.6	20.33					D	Brown & O'Connor 1974	Strangford Lough
5	Cerastoderma	21	102	1.86	11/3	61/5	8.50	55.0	31.30					W	Davidson 1967	Burry Inlet, UK
6	Cerastoderma	22	154	2.31	1	54	7.50	42.0	26.20		349			V	Drinnan 1957	Morecambe Bay, UK
7	Cerastoderma	30	291	2.45	10	54	7.50	50.0	33.06		115			V	Drinnan 1957	Morecambe Bay, UK
8	Cerastoderma	12	12	0.61	2	84					1000				Ens et al. 1996b	Texel, NL
9	Cerastoderma	38	316	2.42	2	84									Ens et al. 1996b	Texel, NL
10	Cerastoderma	36	313	1.88	2	84									Ens et al. 1996b	Texel, NL
11	Cerastoderma	12	14	0.93	3	84									Ens et al. 1996b	Texel, NL
12	Cerastoderma	13	33	2.87	4	84									Ens et al. 1996b	Texel, NL
13	Cerastoderma	15	62	3.75	5	84				B					Ens et al. 1996b	Texel, NL
14	Cerastoderma	18	92	2.38	6	84				B					Ens et al. 1996b	Texel, NL
15	Cerastoderma	19	92	2.38	7	84									Ens et al. 1996b	Texel, NL
16	Cerastoderma	34	411	1.91	9	83					4				Ens et al. 1996c	Texel, NL
17	Cerastoderma	36	504	2.05	9	83					10				Ens et al. 1996c	Texel, NL
18	Cerastoderma	39	606	4.19	9	83					23				Ens et al. 1996c	Texel, NL
19	Cerastoderma	31	338	3.09	9	83					49				Ens et al. 1996c	Texel, NL
20	Cerastoderma	39	616	3.54	9	83					64				Ens et al. 1996c	Texel, NL
21	Cerastoderma	31	328	2.57	9	83					79				Ens et al. 1996c	Texel, NL
22	Cerastoderma	32	365	4.45	9	83					107				Ens et al. 1996c	Texel, NL
23	Cerastoderma	11	14	0.57	9	83					3000				Ens et al. 1996c	Texel, NL
24	Cerastoderma	33	274	2.08	1	95	5.00	41.4	15.50		250			F	Exo, Smit, Zwarts unpubl.	Bay of Dakhla, S. Morocco
25	Cerastoderma	28	317	3.94	1	74	5.00	80.3	56.95						Goss-Custard 1977	Wash Bay, UK
26	Cerastoderma	31	313	0.60	7	66					13	C		D	Hulscher 1976	Schiermonnikoog, NL
27	Cerastoderma	31	313	1.21	7	66					40	C		D	Hulscher 1976	Schiermonnikoog, NL
28	Cerastoderma	31	313	1.95	7	66					150	C		D	Hulscher 1976	Schiermonnikoog, NL
29	Cerastoderma	31	313	2.23	7	66	4.00	54.4	17.47		450	C		D	Hulscher 1976	Schiermonnikoog, NL
30	Cerastoderma	19	76	1.40	8	61	4.76	66.0	15.83		680			V	Hulscher unpubl.	Vlieland, NL
31	Cerastoderma	25	117	2.10	10	80	4.50	67.0	22.79		600				Hulscher unpubl.	Frisian coast Paesens, NL
32	Cerastoderma	23	148	1.49	8	76	5.10	63.2	17.29		147				Hulsman unpubl.	Frisian coast Paesens, NL
33	Cerastoderma	33	365	3.05	10	84	2.00				500	C			Leopold et al. 1989	Texel, NL
34	Cerastoderma	33	365	2.97	10	84	3.00				500	C			Leopold et al. 1989	Texel, NL
35	Cerastoderma	33	365	2.19	10	84	5.00				500	C			Leopold et al. 1989	Texel, NL
36	Cerastoderma	29	185	2.74	10	84	2.00				500	C			Leopold et al. 1989	Texel, NL
37	Cerastoderma	29	185	1.64	10	84	3.00				500			C	Leopold et al. 1989	Texel, NL
38	Cerastoderma	29	185	1.77	10	84	5.00				500			C	Leopold et al. 1989	Texel, NL
39	Cerastoderma	8	3.3	0.52	10	87					7600			F	Meire 1996b	Oosterschelde estuary, NL
40	Cerastoderma	34	337	1.28	2	79					10				Sutherland 1982a, b	Traeth Melynog, UK
41	Cerastoderma	30	314	2.37	2	79					25				Sutherland 1982a, b	Traeth Melynog, UK
42	Cerastoderma	31	336	2.55	2	79					33				Sutherland 1982a, b	Traeth Melynog, UK
43	Cerastoderma	35	403	3.88	2	79					49				Sutherland 1982a, b	Traeth Melynog, UK
44	Cerastoderma	30	209	2.25	2	79					145				Sutherland 1982a, b	Traeth Melynog, UK
45	Cerastoderma	24	95	1.57	2	79					287				Sutherland 1982a, b	Traeth Melynog, UK
46	Cerastoderma	29	162	1.87	2	79					442				Sutherland 1982a, b	Traeth Melynog, UK
47	Cerastoderma	29	146	1.80	2	79					450				Sutherland 1982a, b	Traeth Melynog, UK
48	Cerastoderma	26	114	1.50	2	79					542				Sutherland 1982a, b	Traeth Melynog, UK
49	Cerastoderma	29	143	2.00	2	79					582				Sutherland 1982a, b	Traeth Melynog, UK
50	Cerastoderma	28	124	1.97	2	79					598				Sutherland 1982a, b	Traeth Melynog, UK
51	Cerastoderma	26	120	1.77	2	79					609				Sutherland 1982a, b	Traeth Melynog, UK
52	Earthworms		38	1.62	5	84				B					Ens unpubl.	Texel, NL
53	Earthworms		27	0.49	6	83				B					Ens unpubl.	Texel, NL
54	Earthworms		44	1.00	6	84				B					Ens unpubl.	Texel, NL
55	Earthworms		50	0.98	12	66									Heppleston 1971	Ythan estuary, UK
56	Earthworms		197	1.80	4	77	15.00	33.1	32.17					D	Hosper 1978	Friesland, NL
57	Littorina	18	147	1.29	9/3	81/2	6.00	91.8	25.58					D	Boates & Goss-Custard 1992	Exe estuary, UK
58	Littorina	18	128	1.31	1	81								D	Boates & Goss-Custard 1992	Exe estuary, UK
59	Littorina	18	127	1.13	2	81								D	Boates & Goss-Custard 1992	Exe estuary, UK
60	Littorina	18	89	0.85	3	81								D	Boates & Goss-Custard 1992	Exe estuary, UK
61	Littorina	18	166	1.16	9	81								D	Boates & Goss-Custard 1992	Exe estuary, UK
62	Littorina	18	150	1.03	10	81								D	Boates & Goss-Custard 1992	Exe estuary, UK
63	Littorina	18	145	1.40	11	81								D	Boates & Goss-Custard 1992	Exe estuary, UK
64	Littorina	18	154	1.76	12	81								D	Boates & Goss-Custard 1992	Exe estuary, UK
65	Macoma		54	2.70	4	86									Bunskoeke et al 1996	Schiermonnikoog, NL
66	Macoma		59	3.20	5	86				B					Bunskoeke et al 1996	Schiermonnikoog, NL
67	Macoma	16	54	2.90	6	86				B					Bunskoeke et al 1996	Schiermonnikoog, NL
68	Macoma	18	79	3.00	7	86									Bunskoeke et al 1996	Schiermonnikoog, NL
69	Macoma	18	45	2.00	8	86									Bunskoeke et al 1996	Schiermonnikoog, NL
70	Macoma		110	1.73	5	84				B					Ens et al. 1996b	Texel, NL
71	Macoma	17	83.1	2.09	5	79	6.07	90.9							Hulscher 1982	Frisian coast Paesens, NL
72	Macoma	17	83.1	2.67	5	79				B					Hulscher 1982	Frisian coast Paesens, NL
73	Macoma	18	74	2.21	6	66	5.50	85.0	37.19	B				D	Hulscher 1982	Schiermonnikoog, NL
74	Macoma	20	92	2.32	6	66	0.17	100.0	1.42			C		D	Hulscher 1982	Schiermonnikoog, NL
75	Macoma	18	60	1.47	8	63	4.58	76.5	18.54					V	Hulscher 1982	Vlieland, NL
76	Macoma	16	49	2.58	5	81	1.02	76.0	7.20						Hulscher 1982, unpubl.	Frisian coast Paesens, NL
77	Macoma	16	49	3.68	5	81	0.30	75.0	2.98	B					Hulscher 1982, unpubl.	Frisian coast Paesens, NL
78	Macoma	16	64	2.67	6	86	0.50	100.0	4.81					C	Hulscher et al. 1996, unpubl.	Schiermonnikoog, NL
79	Macoma	16	64	3.31	6	86	0.50	100.0	5.96					C	Hulscher et al. 1996, unpubl.	Schiermonnikoog, NL
80	Macoma	15	47	1.51	5	85									Hulscher unpubl.	Schiermonnikoog, NL
81	Mya		154	3.87	4/8	86/8				B					Bunskoeke 1988	Schiermonnikoog, NL

No	species	mm	mg	mgs-1	month	year	time	feed	cons	br	nm2	mus	cap	lab	sources	area
82	Mya	40	135	2.91	5	85				B					Hulscher unpubl.	Schiermonnikoog, NL
83	Mya	36	350	3.00	7	81	0.40	100.0	4.32					C	Wanink & Zwarts 1996	Frisian coast Paesens, NL
84	Mya	28	51	2.65	10	80	5.00	88.0	41.98						Zwarts & Wanink 1984	Frisian coast Paesens, NL
85	Mytilus	39	332	1.27	9/2	81/2	5.25	93.6	22.47			S		D	Boates & Goss-Custard 1992	Exe estuary, UK
86	Mytilus	39	328	1.27	9/2	81/2	5.25	91.3	21.91			D		D	Boates & Goss-Custard 1992	Exe estuary, UK
87	Mytilus	36	249	0.89	9/2	81/2	5.25	93.0	15.64			V		D	Boates & Goss-Custard 1992	Exe estuary, UK
88	Mytilus	40	320	1.12	1	82								D	Boates & Goss-Custard 1992	Exe estuary, UK
89	Mytilus	39	288	1.13	2	82								D	Boates & Goss-Custard 1992	Exe estuary, UK
90	Mytilus	35	342	1.20	9	81								D	Boates & Goss-Custard 1992	Exe estuary, UK
91	Mytilus	34	261	1.09	10	81								D	Boates & Goss-Custard 1992	Exe estuary, UK
92	Mytilus	39	315	0.95	11	81								D	Boates & Goss-Custard 1992	Exe estuary, UK
93	Mytilus	38	234	1.03	12	81								D	Boates & Goss-Custard 1992	Exe estuary, UK
94	Mytilus	43	400	1.89	1	84						D			Cayford & Goss-Custard 1990	Exe estuary, UK
95	Mytilus	44	379	1.67	1	84						V			Cayford & Goss-Custard 1990	Exe estuary, UK
96	Mytilus	50	540	2.03	2	84						D			Cayford & Goss-Custard 1990	Exe estuary, UK
97	Mytilus	50	571	2.37	2	84						V			Cayford & Goss-Custard 1990	Exe estuary, UK
98	Mytilus	52	461	1.98	3	84						D			Cayford & Goss-Custard 1990	Exe estuary, UK
99	Mytilus	47	332	1.31	3	84						V			Cayford & Goss-Custard 1990	Exe estuary, UK
100	Mytilus	37	149	0.85	4	84						V			Cayford & Goss-Custard 1990	Exe estuary, UK
101	Mytilus	28	83	0.48	4	84						D			Cayford & Goss-Custard 1990	Exe estuary, UK
102	Mytilus	27	73	0.42	5	84						D			Cayford & Goss-Custard 1990	Exe estuary, UK
103	Mytilus	32	118	0.77	5	84						V			Cayford & Goss-Custard 1990	Exe estuary, UK
104	Mytilus	32	156	0.84	6	84						D			Cayford & Goss-Custard 1990	Exe estuary, UK
105	Mytilus	44	692	3.30	8	84						V			Cayford & Goss-Custard 1990	Exe estuary, UK
106	Mytilus	42	610	2.94	8	84						D			Cayford & Goss-Custard 1990	Exe estuary, UK
107	Mytilus	44	773	3.53	9	84						V			Cayford & Goss-Custard 1990	Exe estuary, UK
108	Mytilus	45	873	3.90	9	84						D			Cayford & Goss-Custard 1990	Exe estuary, UK
109	Mytilus	45	931	4.29	10	84						D			Cayford & Goss-Custard 1990	Exe estuary, UK
110	Mytilus	43	903	4.20	10	84						V			Cayford & Goss-Custard 1990	Exe estuary, UK
111	Mytilus	44	853	3.93	11	84						V			Cayford & Goss-Custard 1990	Exe estuary, UK
112	Mytilus	44	872	3.90	11	84						D			Cayford & Goss-Custard 1990	Exe estuary, UK
113	Mytilus	38	216	1.76	3	56	9.00	75.0	42.77			V	V		Drinnan 1958a	Conway River, UK
114	Mytilus	26	56	1.58	12	55	7.00	85.6	34.08			V	V		Drinnan 1958a	Conway River, UK
115	Mytilus	45	697	2.41	10	80	3.60	66.5	22.44			D			Ens & Goss-Custard 1984	Exe estuary, UK
116	Mytilus	42	606	2.59	10	80	3.60	89.5	30.04			S			Ens & Goss-Custard 1984	Exe estuary, UK
117	Mytilus	38	498	2.25	10	80	4.44	54.2	19.49			S			Ens & Goss-Custard 1984	Exe estuary, UK
118	Mytilus	41	570	2.91	10	80	3.89	81.0	33.01			D			Ens & Goss-Custard 1984	Exe estuary, UK
119	Mytilus	39	522	1.80	10	80	3.61	87.2	20.40			V			Ens & Goss-Custard 1984	Exe estuary, UK
120	Mytilus	40	533	1.58	10	80	4.00	91.2	20.75			S			Ens & Goss-Custard 1984	Exe estuary, UK
121	Mytilus	39	505	1.55	10	80	4.00	90.9	20.29			D			Ens & Goss-Custard 1984	Exe estuary, UK
122	Mytilus	41	551	1.73	10	80	4.03	90.6	22.74			S			Ens & Goss-Custard 1984	Exe estuary, UK
123	Mytilus	47	749	2.67	10	80	4.33	56.4	23.47			D			Ens & Goss-Custard 1984	Exe estuary, UK
124	Mytilus	41	551	1.98	10	80	4.00	94.0	26.80			S			Ens & Goss-Custard 1984	Exe estuary, UK
125	Mytilus	38	271	2.64	7	83						S			Ens et al. 1996a	Schiermonnikoog, NL
126	Mytilus	45	520	3.22	7	83						V			Ens et al. 1996a	Schiermonnikoog, NL
127	Mytilus	35	390	2.30	2	84						S			Ens et al. 1996b	Texel, NL
128	Mytilus	34	351	2.31	3	84						S			Ens et al. 1996b	Texel, NL
129	Mytilus	27	191	3.28	4	84						S			Ens et al. 1996b	Texel, NL
130	Mytilus	29	224	2.84	5	84				B		S			Ens et al. 1996b	Texel, NL
131	Mytilus	23	134	2.33	6	84				B		S			Ens et al. 1996b	Texel, NL
132	Mytilus	27	217	2.30	7	84						S			Ens et al. 1996b	Texel, NL
133	Mytilus	37	518	2.68	7	83						S			Ens et al. 1996c	Texel, NL
134	Mytilus	44	380	1.69	1	82						D			Goss-Custard unpubl.	Exe estuary, UK
135	Mytilus	40	300	1.33	1	82						S			Goss-Custard unpubl.	Exe estuary, UK
136	Mytilus	47	509	1.91	1	83	4.68	89.4	28.77			D			Goss-Custard unpubl.	Exe estuary, UK
137	Mytilus	49	469	1.58	1	94						V			Goss-Custard unpubl.	Exe estuary, UK
138	Mytilus	43	404	1.72	2	83	4.68	90.0	26.08			D			Goss-Custard unpubl.	Exe estuary, UK
139	Mytilus	44	425	1.73	2	83	4.68	100.0	29.15			S			Goss-Custard unpubl.	Exe estuary, UK
140	Mytilus	50	502	1.71	2	94						V			Goss-Custard unpubl.	Exe estuary, UK
141	Mytilus	39	285	1.38	3	82						S			Goss-Custard unpubl.	Exe estuary, UK
142	Mytilus	44	379	1.99	3	82						D			Goss-Custard unpubl.	Exe estuary, UK
143	Mytilus	43	350	1.29	3	83						S			Goss-Custard unpubl.	Exe estuary, UK
144	Mytilus	46	408	1.62	3	83						D			Goss-Custard unpubl.	Exe estuary, UK
145	Mytilus	42	444	1.55	9	83	4.68	99.0	25.85			S			Goss-Custard unpubl.	Exe estuary, UK
146	Mytilus	44	538	2.31	9	83	4.68	85.7	33.35			S			Goss-Custard unpubl.	Exe estuary, UK
147	Mytilus	43	481	1.70	9	83	4.68	94.2	26.98			S			Goss-Custard unpubl.	Exe estuary, UK
148	Mytilus		480	1.36	9/10	81						D			Goss-Custard unpubl.	Exe estuary, UK
149	Mytilus		400	1.50	9/10	81						S			Goss-Custard unpubl.	Exe estuary, UK
150	Mytilus	45	504	1.45	10	82	4.68	91.3	22.30			S			Goss-Custard unpubl.	Exe estuary, UK
151	Mytilus	46	559	2.06	10	82	4.68	81.3	28.49			D			Goss-Custard unpubl.	Exe estuary, UK
152	Mytilus	48	748	1.81	11	81	4.95	92.5	29.84			S			Goss-Custard unpubl.	Exe estuary, UK
153	Mytilus	41	424	2.12	11	81						S			Goss-Custard unpubl.	Exe estuary, UK
154	Mytilus	50	779	2.27	11	81	4.95	82.5	33.37			D			Goss-Custard unpubl.	Exe estuary, UK
155	Mytilus	44	461	2.10	11	81						D			Goss-Custard unpubl.	Exe estuary, UK
156	Mytilus	47	530	2.19	11	82	4.68	80.6	29.74			D			Goss-Custard unpubl.	Exe estuary, UK
157	Mytilus	46	503	1.54	11	82	4.68	91.6	23.77			S			Goss-Custard unpubl.	Exe estuary, UK
158	Mytilus	39	340	1.67	12	81						S			Goss-Custard unpubl.	Exe estuary, UK
159	Mytilus	43	394	1.93	12	82	4.68	94.6	30.76			S			Goss-Custard unpubl.	Exe estuary, UK
160	Mytilus	45	513	2.10	12	83	4.68	84.6	29.93			D			Goss-Custard unpubl.	Exe estuary, UK
161	*Mytilus*	42	404	1.17	12	83	4.68	94.6	18.65			S			Goss-Custard unpubl.	Exe estuary, UK
162	*Mytilus*	45	647	2.11	12	84	4.68	84.6	30.07			V			Goss-Custard unpubl.	Exe estuary, UK

no	species	mm	mg	mgs-1	month	year	time	feed	cons	br	nm2	mus	cap	lab	sources	area
163	*Mytilus*	45	591	2.12	12	84	4.68	84.6	30.22			D			Goss-Custard unpubl.	Exe estuary, UK
164	*Mytilus*	30	132	1.66	10	66	11.20	80.9	54.15			V		D	Heppleston 1971	Ythan estuary, UK
165	Mytilus	30	136	1.18	12	66	8.90	94.5	35.73			V		D	Heppleston 1971	Ythan estuary, UK
166	Mytilus	34	220	2.07	10	80	6.00	66.4	29.69			S			Hulscher unpubl .	Frisian coast Paesens, NL
167	Mytilus			16.00			0.22	100.0	12.48				C		Hulscher unpubl .	Schiermonnikoog, NL
168	Mytilus	46	580	1.52	3	77	4.70	65.5	16.85			S			Koene 1978	Texel, NL
169	Mytilus	46	740	1.94	10	76	4.68	65.5	21.41			S			Koene 1978	Texel, NL
170	Mytilus	46	251	1.92	3	92	5.00	78.8	27.23			S			Maagaard & Jensen 1994	Skallingen, DK
171	Mytilus	45	448	2.35	9	92	4.00	83.6	28.29			S			Maagaard & Jensen 1994	Skallingen, DK
172	Mytilus			1.60	10	86	4.08	74.0	17.39			V		F	Meire 1996b	Oosterschelde estuary, NL
173	Mytilus			1.67	10	86	4.12	92.0	22.79			V		F	Meire 1996b	Oosterschelde estuary, NL
174	Mytilus	39	270	1.50	10	86						S		F	Meire 1996b	Oosterschelde estuary, NL
175	Mytilus			1.94	10	86	4.57	52.0	16.60			V		F	Meire 1996b	Oosterschelde estuary, NL
176	Mytilus	41	450	2.10	10	86						S		F	Meire 1996b	Oosterschelde estuary, NL
177	Mytilus	35	172	1.24	10	86						S		F	Meire 1996b	Oosterschelde estuary, NL
178	Mytilus	40	296	1.84	10	86						V		F	Meire 1996b	Oosterschelde estuary, NL
179	Mytilus	41	270	1.77	10	86						V		F	Meire 1996b	Oosterschelde estuary, NL
180	Mytilus	42	297	1.95	10	86						V		F	Meire 1996b	Oosterschelde estuary, NL
181	Mytilus	40	524	2.82	9	82						V		F	Meire & Ervynck 1986	Oosterschelde estuary, NL
182	Mytilus	50	230	1.95	9/4	81						S			Speakman 1984	Forth estuary, UK
183	Mytilus	51	765	4.02	9	73	5.90	76.3	65.15			S			Zwarts & Drent 1981	Schiermonnikoog, NL
184	Mytilus	53	604	3.30	5	74	1.38	88.0	14.43	B		S			Zwarts & Drent 1981	Schiermonnikoog, NL
185	Mytilus	50	545	3.27	5	75	1.38	90.2	14.65	B		S			Zwarts & Drent 1981	Schiermonnikoog, NL
186	Mytilus	50	492	3.53	5	76	1.38	87.4	15.33	B		S			Zwarts & Drent 1981	Schiermonnikoog, NL
187	Mytilus	49	487	3.27	5	77	1.38	85.3	13.86	B		S			Zwarts & Drent 1981	Schiermonnikoog, NL
188	Mytilus	26	186	1.65	5	78	1.38	88.9	7.29	B		S			Zwarts & Drent 1981	Schiermonnikoog, NL
189	Mytilus	38	614	2.19	5	78	5.00	76.4	30.12			S	C		Zwarts & Drent 1981	Schiermonnikoog, NL
190	Mytilus	32	299	1.56	5	78	5.00	76.4	21.45			S	C		Zwarts & Drent 1981	Schiermonnikoog, NL
191	Mytilus	34	264	1.52	9	78	6.00	79.0	25.94			S			Zwarts & Drent 1981	Schiermonnikoog, NL
192	Mytilus	28	137	0.86	3	79	6.00	84.1	15.62			S			Zwarts unpubl.	Frisian coast Paesens, NL
193	Nereis		17	0.56	8/11	81	7.00	96.1	13.56						Boates & Goss-Custard 1989	Exe estuary, UK
194	Nereis		35	1.17	8	81									Boates & Goss-Custard 1989	Exe estuary, UK
195	Nereis		19	0.63	9	81									Boates & Goss-Custard 1989	Exe estuary, UK
196	Nereis		9	(0.13)	10	81									Boates & Goss-Custard 1989	Exe estuary, UK
197	Nereis		5	(0.19)	11	81									Boates & Goss-Custard 1989	Exe estuary, UK
198	Nereis		93	2.30	4	86									Bunskoeke et al 1996	Schiermonnikoog, NL
199	Nereis		84	3.10	5	86				B					Bunskoeke et al 1996	Schiermonnikoog, NL
200	Nereis		94	3.30	6	86				B					Bunskoeke et al 1996	Schiermonnikoog, NL
201	Nereis		82	3.00	7	86									Bunskoeke et al 1996	Schiermonnikoog, NL
202	Nereis		69	2.00	8	86									Bunskoeke et al 1996	Schiermonnikoog, NL
203	Nereis		81	1.63	8	84	6.83	100.0	40.08						Durell et al. 1996, unpubl.	Exe estuary, UK
204	Nereis		80	2.25	8	84	6.25	92.8	46.98						Durell et al. 1996, unpubl.	Exe estuary, UK
205	Nereis		58	1.82	9	82									Durell et al. 1996, unpubl.	Exe estuary, UK
206	Nereis		71	2.56	9	82									Durell et al. 1996, unpubl.	Exe estuary, UK
207	Nereis		80	3.46	9	83	6.25	93.4	72.71						Durell et al. 1996, unpubl.	Exe estuary, UK
208	Nereis		87	3.18	9	83	6.83	100.0	78.19						Durell et al. 1996, unpubl.	Exe estuary, UK
209	Nereis		82	2.71	9	84	6.83	99.4	66.23						Durell et al. 1996, unpubl.	Exe estuary, UK
210	Nereis		53	2.44	10	82									Durell et al. 1996, unpubl.	Exe estuary, UK
211	Nereis		60	2.21	10	82									Durell et al. 1996, unpubl.	Exe estuary, UK
212	Nereis		71	2.27	10	83	6.25	100.0	51.08						Durell et al. 1996, unpubl.	Exe estuary, UK
213	Nereis		82	2.27	10	83	6.83	100.0	55.81						Durell et al. 1996, unpubl.	Exe estuary, UK
214	Nereis		85	2.00	10	84	6.25	96.3	43.34						Durell et al. 1996, unpubl.	Exe estuary, UK
215	Nereis		129	3.82	7	83									Ens et al. 1996b	Texel, NL
216	Nereis		65	1.38	5	85				B					Hulscher unpubl.	Schiermonnikoog, NL
217	Nereis		74	1.53	12	84									Triplet 1989	Baie de Somme, France
218	Patella		96	2.35	5/7	65/6								D	Safriel 1976	Skokholm, UK
219	Scrobicularia	32	310	2.20	7	79	4.58	70.0	25.39						Blomert et al 1983	Frisian coast Paesens, NL
220	Scrobicularia	30	132	1.22	10/3	81/2	7.00	96.4	30.25						Boates & Goss-Custard 1989	Exe estuary, UK
221	Scrobicularia	31	121	1.42	1	82								D	Boates & Goss-Custard 1989	Exe estuary, UK
222	Scrobicularia	34	149	2.17	2	82								D	Boates & Goss-Custard 1989	Exe estuary, UK
223	Scrobicularia	30	110	2.27	3	82								D	Boates & Goss-Custard 1989	Exe estuary, UK
224	Scrobicularia	25	101	1.18	10	81								D	Boates & Goss-Custard 1989	Exe estuary, UK
225	Scrobicularia	27	89	1.51	11	81								D	Boates & Goss-Custard 1989	Exe estuary, UK
226	Scrobicularia	24	68	1.32	12	81								D	Boates & Goss-Custard 1989	Exe estuary, UK
227	Scrobicularia	21	25	0.98	3	84	7.00	80.0	19.76						Habekotte 1987	Schiermonnikoog, NL
228	Scrobicularia	39	303	4.43	10	81	0.46	100.0	7.34				C		Hulscher et al. unpubl.	Frisian coast Paesens, NL
229	Scrobicularia	39	303	8.06	10	81	0.25	100.0	7.25				C		Hulscher et al. unpubl.	Frisian coast Paesens, NL
230	Scrobicularia	39	303	9.99	10	81	0.20	100.0	7.19				C		Hulscher et al. unpubl.	Frisian coast Paesens, NL
231	Scrobicularia	35	300	3.00	7	81	0.40	100.0	4.32				C		Wanink & Zwarts 1996	Frisian coast Paesens, NL
232	Scrobicularia	36	274	3.40	8	81	0.40	100.0	4.90				C		Wanink & Zwarts 1985	Frisian coast Paesens, NL
233	Scrobicularia	28	94	1.29	4	79	5.50	89.1	22.76						Zwarts unpubl.	Frisian coast Paesens, NL
234	Scrobicularia	29	169	3.55	5	79									Zwarts unpubl.	Frisian coast Paesens, NL
235	Tipula		50	1.47	7	91									Blomert & Zwarts unpubl.	Friesland, NL
236	Tipula		49	1.37	8	93									Blomert & Zwarts unpubl.	Friesland, NL
237	Tipula		60	1.24	4	84									Ens unpubl.	Texel, NL
238	Tipula	60	1.92	5		84				B					Ens unpubl.	Texel, NL
239	Tipula	75	1.14	6		83				B					Ens unpubl.	Texel, NL
240	Tipula	60	1.04	6		84				B					Ens unpubl.	Texel, NL
241	Tipula	60	0.72	7		84									Ens unpubl.	Texel, NL
242	Tipula		76	1.80	4	78	14.00	35.7	32.39					D	Hosper 1978	Friesland, NL
243	Tipula		62	1.89	5	77				B				D	Hosper 1978	Friesland, NL

no	species	mm	mg	mgs-1	month	year	time	feed	cons	br	nm2	mus	cap	lab	sources	area
244	Tipula		47	1.84	5	78	17.00	22.0	24.77	B				D	Hosper 1978	Friesland, NL
245	Tipula		42	1.05	6	77				B				D	Hosper 1978	Friesland, NL
246	Tipula		61	1.15	6	78				B				D	Hosper 1978	Friesland, NL
247	Tipula		85	1.95	7	78								D	Hosper 1978	Friesland, NL
248	Tipula		42	1.40	5/7	65/6								D	Safriel 1976	Skokholm, UK
249	Tipula		15	0.34	3	77	13.00	59.1	9.40						Veenstra 1978	Friesland, NL
250	Tipula		20	1.04	4	95	14.70	57.3	31.54						Zwarts & Blomert 1996	Friesland, NL
251	Tipula		35	1.45	5	91		39.9		B					Zwarts & Blomert 1996	Friesland, NL
252	Tipula		52	1.28	5	91									Zwarts & Blomert 1996	Texel, NL
253	Uca		786	2.23	9	88									Ens et al. 1993	Banc d'Arguin, Mauritania

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