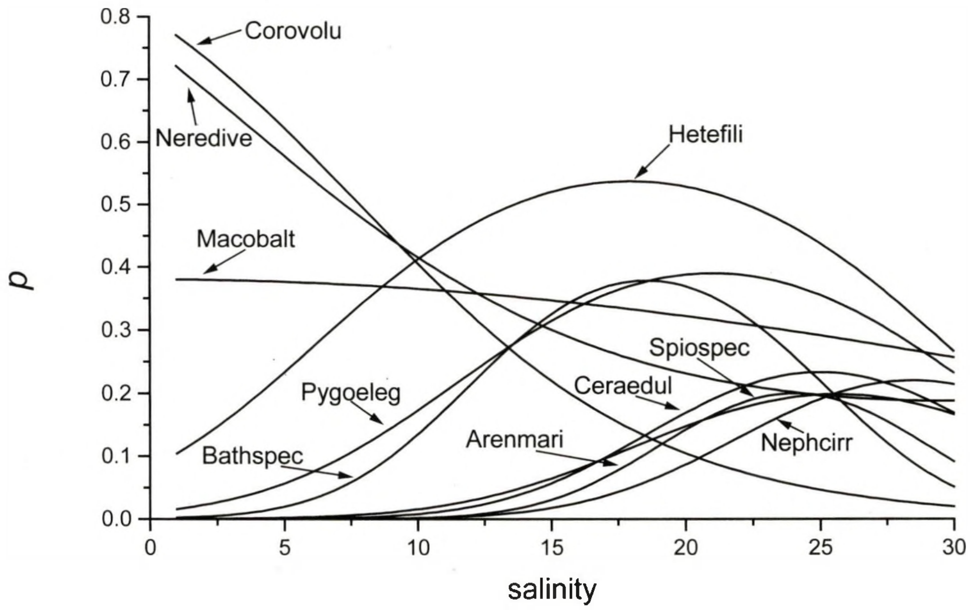
Macrobenthos of the Schelde estuary: predicting macrobenthic species responses in the estuarine environment

a statistical analysis of the Schelde estuary macrobenthos within the ECOFLAT project

Tom Ysebaert & Patrick Meire



Instituut voor Natuurbehoud

MACROBENTHOS OF THE SCHELDE ESTUARY:

PREDICTING MACROBENTHIC SPECIES RESPONSES IN THE ESTUARINE ENVIRONMENT

- a statistical analysis of the Schelde estuary macrobenthos within the ECOFLAT project -

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CONTENTS

PART I : The macrobenthos of the Schelde estuary: a statistical analysis within the Ecoflat project

PART II : Ecoprofiles for 20 macrobenthic species of the Schelde estuary

PART III : External validation of the 'response curve' regression models from the Schelde estuary in another coastal area, the Oosterschelde

PART ONE

The macrobenthos of the Schelde estuary -a statistical analysis within the ECOFLAT project-

INTRODUCTION

THE ECOFLAT PROJECT

The ECOFLAT project (ECO-metabolism of an estuarine tidal FLAT) is a research project funded by the European Commission in the framework of ENVIRONMENT & CLIMATE Programme (contract number ENV4-CT96-0216) and is part of ELOISE (European Land Ocean Interactions Studies). The aim of ECOFLAT is to understand the role of intertidal flats in the ecology of estuaries, and to upscale from process understanding at the small scale to predictions relevant for management at the estuarine scale. The general objectives of the whole project are:

1. A multidisciplinary study of processes important for the carbon and nutrient cycling within a tidal flat ecosystem, and between the tidal flat system and the estuary. Integrated measurements performed at the appropriate scales for the processes of interest.
2. Development of predictive mathematical models describing the processes and relating them to the main forcing factors for the tidal flat system.
3. Bridging the gap between the scales at which the processes operate and are measured, and the ecological target values for environmental management and prediction of the ecological consequences of global change.

Within the last objective, the Institute of Nature conservation is involved in the 'upscaling to the estuarine scale by modelling: derivation of target variables from process knowledge'. Responsible partners are the Institute of Nature Conservation, RIKZ and Delft Hydraulics. The main objectives are:

- ◊ Predict, using the ecosystem model and a hydrodynamical model, the importance of tidal flat processes to the general ecosystem functioning
- ◊ Predict macrobenthic biomass and structure from water quality variables (derived from an ecosystem model and observations) and from a hydrodynamical model on the one hand, and from process knowledge gained in the project on the other hand
- ◊ Predict changes in ecosystem functioning under different scenarios of changed morphological/physical forcing and of changed anthropogenic impact on the estuary
- ◊ Validate predictions against existing data on a different estuary
- ◊ Extension of macrobenthos data base where critical data are missing

The specific tasks of the Institute of Nature Conservation are:

- ◊ create a database on the macrobenthos of the Schelde estuary, based on existing and available data, and coupled with a database on abiotic variables, derived from models (ecosystem model and hydrodynamical models) and observations
- ◊ extend the existing database on the macrobenthos of the Schelde estuary where critical data are missing (especially towards the temporal variability of the benthos)
- ◊ explore the relations between macrobenthic invertebrates and environmental variables in order to couple these data with models of the estuary and predict distributions and biomass of benthos (based on existing data and knowledge)
- ◊ draw up response curves (habitat suitability curves, ecoprofiles) for the dominant macrobenthic species

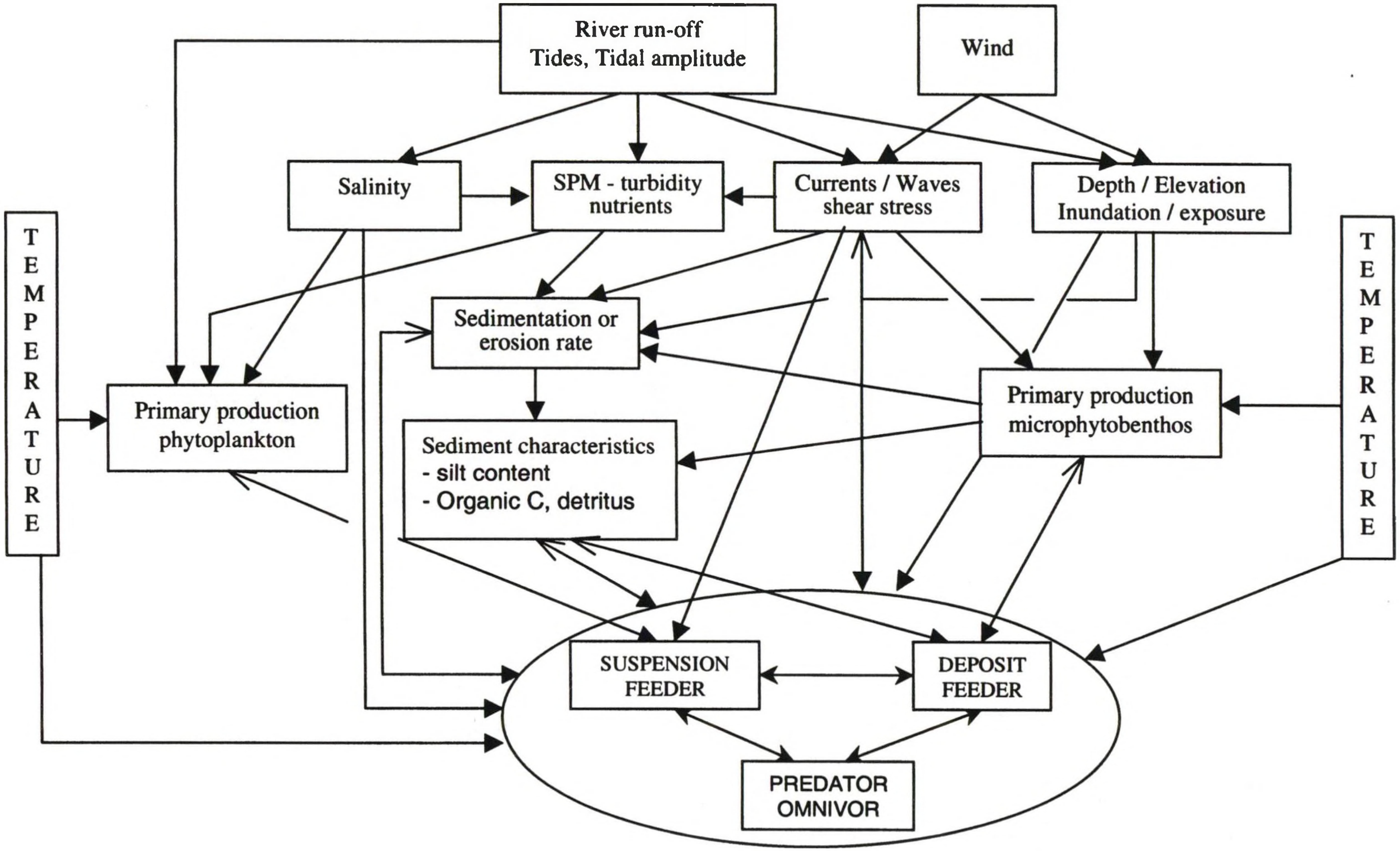

Figure 1.1. A schematic representation of the major environmental variables and their role in structuring macrobenthic communities in the estuarine environment.

BACKGROUND AND OUTLINE OF THE REPORT

Macrobenthos is a central element of estuarine foodwebs. Macrobenthos is an important food resource for crustaceans, fish and birds. Humans also harvest many species of shellfish and crustaceans. Macrobenthos is an important component of estuarine ecosystems and in general plays an important role in the system dynamics (structure and function) of estuaries (HERMAN *et al.*, 1999). Therefore, evaluation of the consequences of human induced changes will likely include the possible responses of the macrobenthos and the analysis of benthic infauna is a key element of many marine and estuarine monitoring programmes.

The starting point is that macrofaunal species distributions reflect the present state of the estuarine ecosystem. Human impact on estuaries will affect the ability of these ecosystems to support macrofaunal occurrence (in terms of diversity, density or biomass).As macrobenthos could be considered as sedentary and relatively long-lived, the benthos will integrate environmental influences at a particular place.

The occurrence and distribution of macrobenthic species and communities in the Schelde estuary has been studied in detail by WOLFF (1973), VERMEULEN & GOVAERE (1983), MEIRE *et al.* (1991), YSEBAERT *et al.* (1993,1998) and CRAEYMEERSCH (1999). Like most other studies on estuarine macrobenthos, these studies mainly evaluated the relationship between multivariate community structure and environmental variables (through different clustering and/or ordination techniques), or described the distribution (in terms of density and biomass) of some indicator species along different spatiotemporal gradients (e.g. salinity). The (statistical) responses of individual species to estuarine gradients, represented by environmental variables that are essential factors for their occurrence (presence/absence, density or biomass), have not been widely studied. Indeed, within coastal marine and estuarine ecosystems little attempts have been made to statistically model the responses of individual macrobenthic species to environmental variables on a large, e.g. estuarine scale and use these models to predict the distribution and occurrence of macrobenthos (CONSTABLE, 1999). However, there are increasing demands for reliable and quantitative predictive tools. On the one hand, these are required to interpret *post-hoc* any changes that have been observed in the benthic community. A quantification of species preferences and tolerances to environmental conditions may help to understand and establish system properties On the other hand, they are needed to predict future species response to anticipated changes in environmental conditions.

In our approach physicochemical factors are used as predictors for the occurrence of macrobenthic species on the estuarine macro-scale. In shallow-water coastal and estuarine systems, environmental factors such as salinity, sediment characteristics and hydrodynamic processes play a definite role in structuring benthic communities. Figure 1 gives a schematic representation of the main (a)biotic variables which are involved in structuring the macrobenthic communities. In this study the following variables, obtained both from field observations and numerical model simulations, were selected for incorporating in the macrobenthic database: salinity, depth/height, sediment characteristics and current velocities.

In estuaries salinity is one of the most deterministic factors for the occurrence of a certain macrobenthic species (SANDERS *et al.*, 1965; CARRIKER, 1967; WOLFF, 1973; BOESCH, 1977; MICHAELIS, 1983; HOLLAND *et al.*, 1987; YSEBAERT *et al.*, 1993,1998).

Depth (or height) in estuaries will clearly influence the occurrence of macrobenthic species, as this abiotic factor is related to the physical environmental stress in estuaries. Of course, one should realise the pronounced difference between the subtidal zone and the intertidal zone. In the subtidal zone the physical conditions, related to the tidal stress which is most pronounced in the channels, will predominate (WILDISH & KRISTMANSON, 1977;

WARWICK & UNCLES, 1980; WARWICK *et al.*, 1991) In the intertidal zone depth (or height) is better being expressed as tidal inundation or exposure time. Here a complex interaction exists between periods of tidal (and wave) currents, a changing tide level (water depth) and periods of exposure to the air, which will influence, besides the hydrodynamic processes themselves (see further), also food availability, predation pressure (e.g. birds), etc.

Sediment grain-size distributions are the result of sorting processes during sedimentation, erosion and transport and are therefore linked to the prevailing currents. Several studies have indicated sediment characteristics (e.g. mud content) as being important factors influencing benthic populations (e.g. GRAY, 1974; BEUKEMA, 1976; DANKERS & BEUKEMA, 1981; MEIRE *et al.*, 1994) and mud content is often used as an indicator of food availability for deposit feeders, supposing a relation between mud content and organic fraction of the sediment, or between mud content and microphytobenthos occurrence on the sediment.

Most macrobenthic studies only dealt with the "static" factors mentioned above. However, several studies clearly showed the importance of hydrodynamical conditions such as current velocity and bed shear stress for the transport of sediment, food and juvenile macrofauna (both larval settlement and post-settlement transport) (GRANT, 1983; BUTMAN, 1987; COMMITO *et al.*, 1995; WILDISH & KRISTMANSON, 1997) Recent studies also showed hydrodynamic factors affecting the stability of the sediment by mobilising bed material, including macrofauna (BELL *et al.*, 1997; GRANT *et al.*, 1997) . Wind waves were not considered in this study. The effect of waves in the intertidal zone of estuaries will be certainly less than in the surf zone along beaches, but during storm periods wave action will certainly episodically influence the macrofaunal distribution (DOLPHIN *et al.*, 1995). However, no data on wind waves were available for the Schelde estuary. Also the direct effect of currents, namely the sediment mobilisation (depth of bed disturbance) and sediment transport was not taken into account in this study, as also for these parameters no data were available at the estuarine scale.

The aim of this study is to statistically model the responses of individual macrobenthic species to the above mentioned environmental variables on a macro-scale, this is estuarine scale. The individualistic response of (indicator) species should be an integral part of any attempt to model the distribution of macrobenthic populations and communities. These models could then be implemented in management strategies. This will only work if the parameters used in the model to describe the spatial occurrence of macrobenthic species are the only deterministic factors. One should indeed keep in mind that some important factors, like food availability (in terms of phytoplankton for the suspension feeders and in terms of particulate organic matter in the sediment for the deposit feeders) are not included in this study. Also biotic interactions are not incorporated.

The objectives of this study were:

(1) to describe the main characteristics of the macrobenthos along estuarine gradients
(2) to model the response of some important macrobenthic species to the abiotic environmental predictors salinity, depth, current velocities and sediment characteristics
(3) to define the realised niches of some estuarine macrobenthic species on an estuarine, thus broad scale.

MATERIAL & METHODS

STUDY AREA

The Schelde estuary measures 160 km from the mouth near Vlissingen (The Netherlands) to Gent (Belgium) (Figure 2) and is one of the longest estuaries in NW-Europe with still a complete estuarine gradient: at the mouth and in the lower reaches a marine (polyhaline) zone, in the middle and inner reaches a brackish (mesohaline) zone and in the upper reaches an oligohaline and freshwater tidal zone. The mean tidal range increases from 3.8 m at Vlissingen to 5.2 m near Antwerpen. At Gent the tidal range is still 2 m. The river discharge varies from 20 m^3s^{-1} during summer to 400 m^3s^{-1} during winter, with a mean yearly average of 105 m^3s^{-1}. The total volume of the estuary ($2.5*10^9$ m^3) is large in comparison with the volume of fresh water that enters each day from the river ($9*10^6$ m^3). The residence time of the water in the estuary is rather high, ranging from one to three months, depending on the river discharge (SOETAERT & HERMAN, 1995).

Between the mouth and the Dutch/Belgian border the estuary is called Westerschelde; between the border and Gent it is called Zeeschelde. The study area is limited to the Westerschelde and a small part of the Zeeschelde near the Dutch-Belgian border (Figure 2), making up the complete polyhaline and mesohaline zone of the estuary. The lower and middle estuary, the Westerschelde (55 km), is a well mixed region characterised by a complex morphology with flood and ebb channels surrounding several large intertidal mud- and sand-flats. The surface of the Westerschelde is 310 km^2, with tidal flats and marshes covering 43 %. The average depth is ± 10 m. Upstream the Dutch/Belgian border, the estuary is characterised by a single channel, and here industrial activities are concentrated (harbour of Antwerpen). The turbidity maximum is situated in this region of the estuary but moves over a quite large distance, depending among other things on the tidal action and river run off (WOLLAST & MARIJNS, 1981; FETTWEIS *et al.*, 1998). Nowadays, dredging activities for shipping and pollution are the major anthropogenic stressors. Yearly, about 8 million m^3 of sediment has to be dredged and because of an ongoing deepening of the channel, dredging activities will further increase (VROON *et al.*, 1997). For a detailed description of the ecological and physicochemical properties of the estuary see several papers in MEIRE & VINCX (1993) and HEIP & HERMAN (1995).

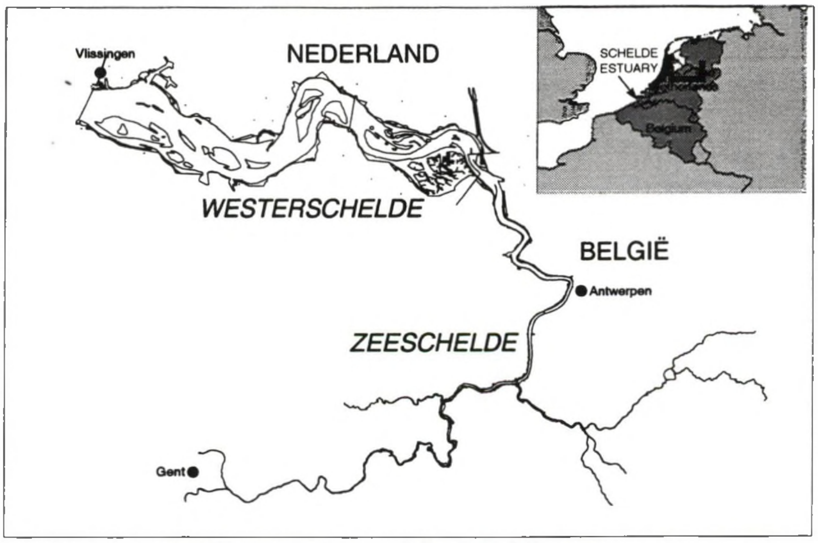

Figure 2. Map of the Schelde estuary

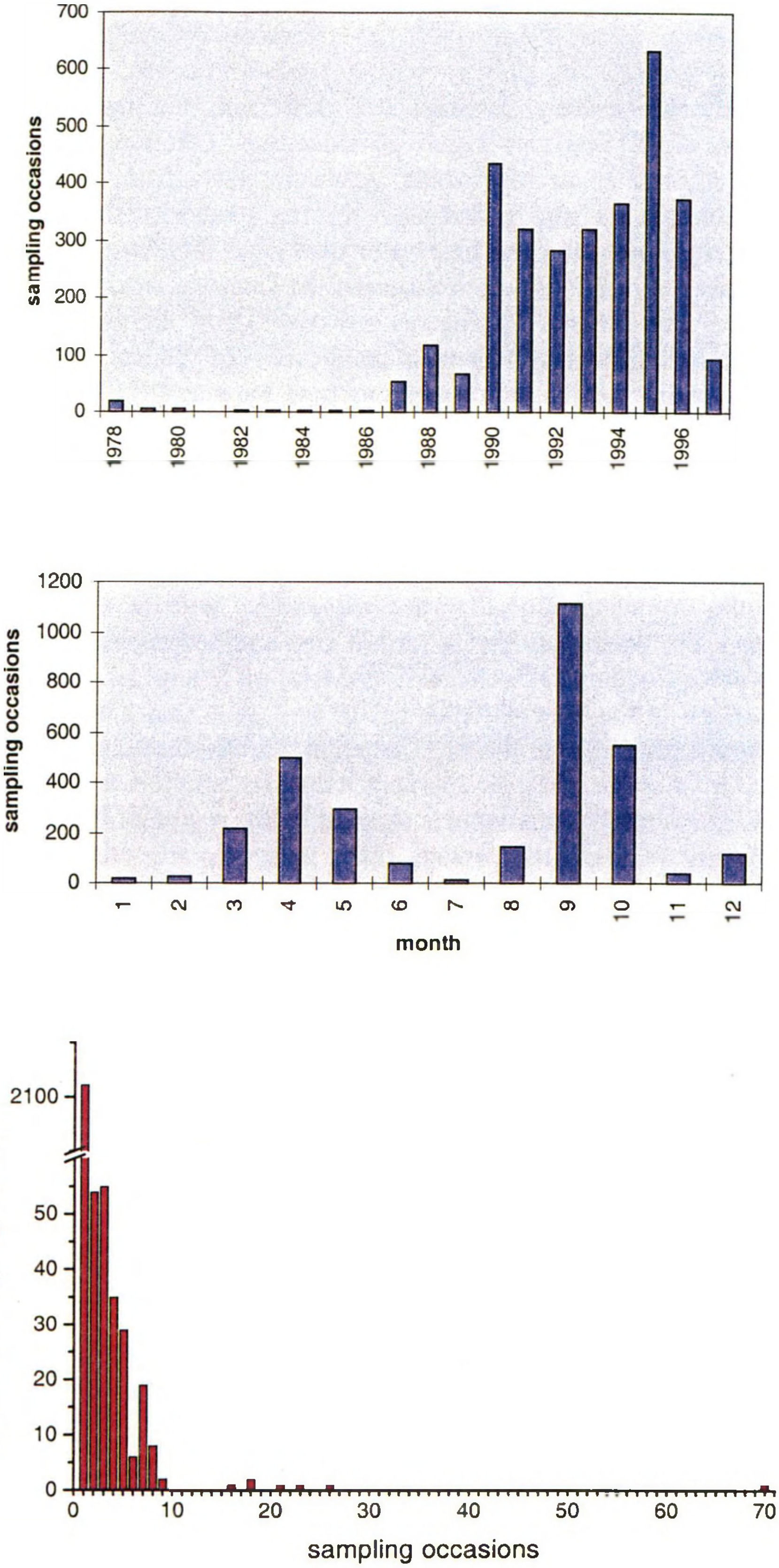

Figure 3. Yearly macrobenthic sampling effort in the Schelde estuary (a), seasonal dispersal of the total sampling effort (b), and the frequency of sampling at the different sampling locations (c).

THE MACROBENTHOS DATABASE

Sampling effort

The macrobenthos database contains all available data collected by different institutes since 1978 (Figure 3a) and which were available in June 1998. A total of 3112 sampling occasions were put in the macrobenthos database and used for further analysis.

In the eighties only relatively few samples were taken. In the nineties the sampling effort increased substantially, mainly by the start-up of a Dutch national monitoring programme (BIOMON) in the Westerschelde and of a Flemish monitoring programme in the mesohaline part of the Zeeschelde. By far most data were collected and analysed by two institutes, namely the Centre for Estuarine and Coastal Ecology (NIOO-CEMO) and the Institute of Nature Conservation (before that at the University of Gent), mainly by order of and in co-operation with the National Institute for Marine and Coastal Management (RWS-RIKZ) at Middelburg.

Most samples were taken in autumn period (September-October), with a smaller peak in spring (March-April-May) (Figure 3b). Most sampling locations (68%) were sampled only once (Figure 3c). However, several sampling locations were sampled two to five times, and a few were sampled more frequently within a long term programme and therefore the term sampling occasion is used rather than the term sampling location. One sampling location on the mudflat Groot Buitenschoor in the mesohaline part of the Zeeschelde was sampled on a monthly basis since 1990 and 70 sampling occasions were included for this location in the database (Figure 3c).

Different collecting methods were used, but in general multiple sediment cores were used for sampling the intertidal zone, and Van Veen grab or Reineck box corer for the subtidal zone. All samples regard the macrobenthos, this is all animals retained on a sieve with mesh size 1 mm. All density data were transformed to ind m^{-2}, and biomass data to g AFDW m^{-2}. For more details on the sampling methods and the design of the monitoring programmes we refer to CRAEYMEERSCH (1999).

The macrobenthos database

A lot of the data was already stored in a relational database structure, which was developed at the Centre for Estuarine and Coastal Ecology (NIOO-CEMO) (see Craeymeersch, 1999). The database was extended with data collected at the Institute of Nature Conservation, mainly dealing with the mesohaline part of the Zeeschelde. A total of 3.112 sampling occasions were put into the macrobenthic database.

The database contains, besides information on the density (ind m^{-2}) and biomass (g AFDW m^{-2}) of individual macrobenthic species, information on each sampling occasion (location, short description of the location, date of sampling, geographical position, depth). A file containing information on the abiotic variables was added to the macrobenthos database (see further).

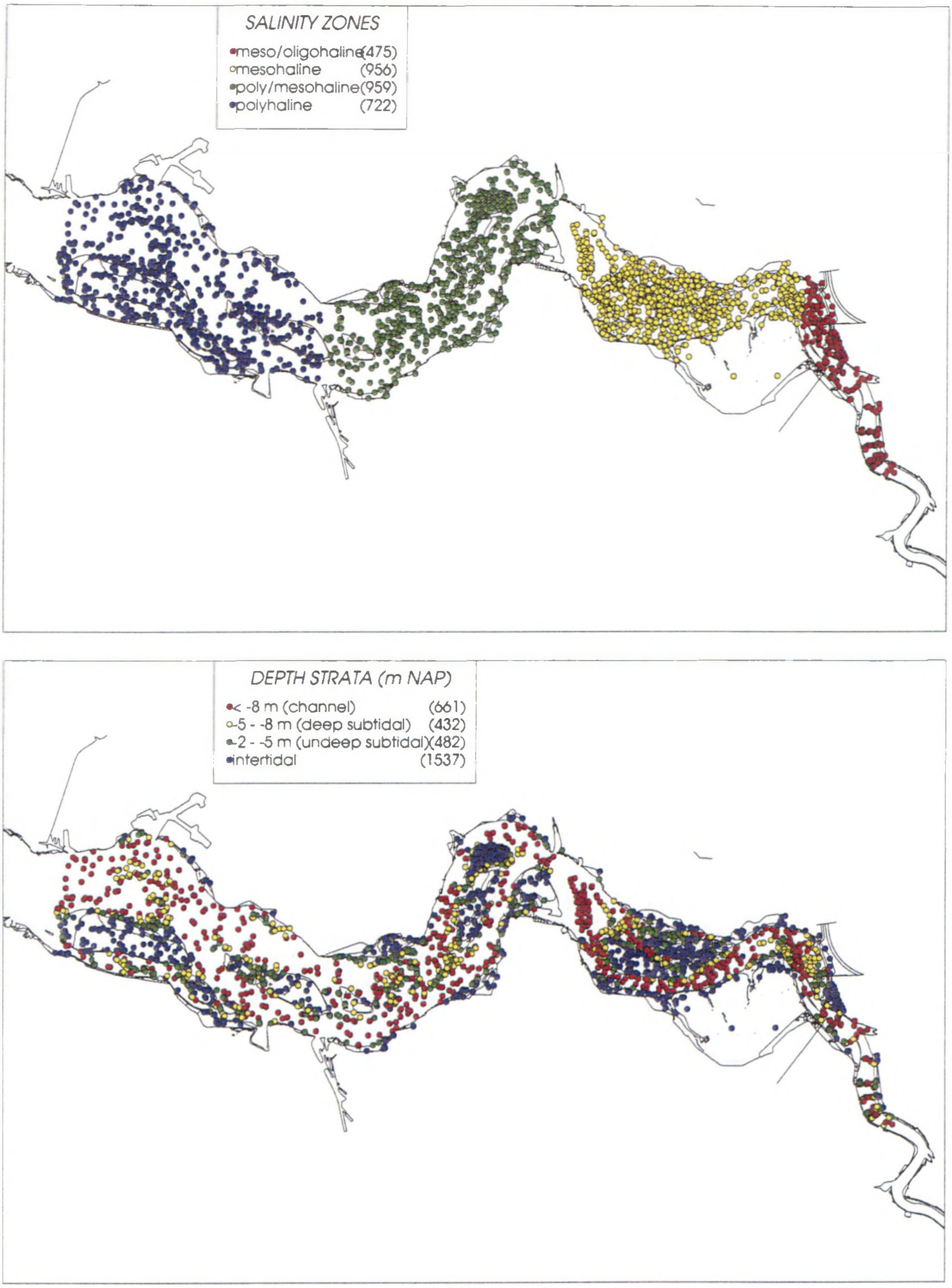

Figure 4.Available macrobenthos data (sampling occasions) along the longitudinal (salinity, top figure) and vertical (depth, bottom figure) gradient of the Schelde estuary.

Abiotic variables

For each sampling occasion the following abiotic environmental variables were added to the macrobenthos database (if available): depth (or height), salinity (model salinity and temporal salinity), current velocities (maximum ebb and maximum flood current velocities), sediment characteristics (median grain size and mud content (fraction $< 63\ \mu m$)).

At all subtidal stations, depth was recorded at the time of sampling. The height of the intertidal stations was for some stations measured directly in the field, but for far the most the height was obtained from a Geographical Information System (GIS), storing all bathymetric data in the area. For 2874 sampling occasions (92 %) a depth value was added in the macrobenthos database. In the database values below NAP had positive signs, whereas values above NAP had negative signs.

Salinity was estimated for each sampling location with the hydrodynamical model SCALDIS400 (VAN DER MEULEN AND SILEON, 1997) with a spatial resolution of 400 meters. Model calculations are based on long term values for an average tide under average, minimum and maximum river discharge conditions, giving an average, maximum and minimum salinity value respectively. A general idea of the available macrobenthos data along the longitudinal (salinity) gradient of the Schelde estuary is given in Figure 4. The advantage of using the SCALDIS model is that a fine spatial scale is obtained but the estimates are not seasonally defined. Therefore also monthly to fortnightly measurements at nine stations along the Westerschelde are used to get an idea of the temporal variation in salinity, but at a much broader spatial resolution as compared to model salinity. For each sampling occasion the temporal salinity was determined as the average salinity of the three months previous to the date of sampling. For all sampling occasions salinity values were added in the macrobenthos database. Estimates obtained from model simulations are called 'model salinities', whereas the values derived from field observations are called 'temporal salinities'.

Current velocity estimates (maximum ebb and flood current velocities in $m.s^{-1}$) for each sampling location were estimated with the SCALDIS100 model, but with a spatial resolution of 100 meters. For 3037 sampling occasions (98 %) current velocity estimates were added to the macrobenthos database.

All hydrodynamical model calculations were performed by RWS-RIKZ (Harm Verbeek).

Several sampling campaigns also collected sediment samples, upon which sediment grainsize analysis was performed by laser diffraction. For 1502 and 1386 sampling occasions (48 % and 45%) median grain size and mud content values were added to the macrobenthos database respectively.

STATISTICAL ANALYSIS

Main characteristics of the macrobenthos along estuarine gradients

All macrobenthos data were averaged per sampling occasion and standardised to numbers per m^2 (ind m^{-2}) and biomass values were expressed as grams Ash Free Dry Weight per m^2 (g $AFDW.m^{-2}$).

Of several groups of species, which have difficult determination keys, the determination was often not performed at species level or was a matter for argument. Therefore, for *Bathyporeia, Ensis, Microphthalmus, Nemertea, Oligochaeta, Ophelia, Polydora, Spio, and Spisula* all individuals were lumped and put under one species name.

All macrobenthos species were classified into five feeding guilds: surface deposit feeders, deposit feeders, suspension feeders, omnivores and predators.

Environmental variables were categorised as followed:

- four salinity regions: lower estuary (Vlissingen-Terneuzen) which is situated in the polyhaline zone ; middle estuary (Terneuzen-Hansweert), also situated in the polyhaline zone; inner estuary (Hansweert-Bath), being the α-mesohaline zone; upper estuary (Bath-Lillo), being the β-mesohaline zone (Figure 4).
- four depth strata: the intertidal or littoral zone and three strata in the subtidal (undeep 2-5 m beneath NAP; deep 5-8 m beneath NAP; channel > 8 m beneath NAP) (Figure 4).
- four sediment types: silt (< 63 μm); very fine sand (63-125 μm); fine sand (125-250 μm); medium sand (250-500 μm).
- six current velocity classes:0-0.2, 0.2-0.4, 0.4-0.6, 0.6-0.8, 0.8-1.0, > 1 $m.s^{-1}$).

Comparisons among these environmental categories were examined with ANOVA on log-transformed data. For the analysis of the relations between environmental variables Spearman rank correlation was used. The general trends in diversity, density and biomass along the longitudinal (model salinity) and vertical (depth) gradients were examined with a Two-way ANOVA on log-transformed data.

Response curves

Relationships between species and quantitative environmental variables are generally non-linear. Therefore, Generalized Linear Models (GLMs) were proposed as a theoretical framework to model (non-linear) species response to several types of environmental data (NELDER & WEDDERBURN, 1972). The theory of GLMs has been well developed (MCCULLAGH & NELDER, 1989) and GLMs have been successfully applied in ecological research. Especially logistic regression, a specialised form of GLM for binary data, has been used in many studies, particularly in vegetation analysis (HUISMAN *et al.*, 1993; LENIHAN, 1993; VAN DE RIJT *et al.*, 1996).

Logistic regression (COX, 1970; HOSMER & LEMESHOW, 1989; MCCULLAGH & NELDER, 1989) was used to model the response of species occurrence to the abiotic environmental predictors. In the logistic regression model, a binary response variable is related to one or more predictor variables through the logistic function. Using the maximum likelihood estimates of the regression parameters, the probabilities of a given state of the response variable can be calculated for different levels of the predictor variables.

The choice of using presence (0) / absence (1) data as a first approach was inspired by the fact that the data could not be considered as homogeneously collected. Different sampling methods, different sampling months (seasonality) and years (long-term fluctuations) certainly affected the observed variation in density and biomass data. To minimise this variation presence/absence data were used. However; as many species were often found in very low densities, often only one individual, it was decided to treat densities < 50 ind m^{-2} and sampling occasions were only one individual was observed, as absences (0) for most species. Only for very large species (*Arenicola marina*) and species typically observed in very low densities (the predators *Nephtys hombergii, Nepthys cirrosa*)

The 'presence-absence response curve' of a species describes the probability p(x) that the species occurs as a function of an environmental variable x.

$$\log \{p(x) / 1-p(x)\} = b_0 + b_1x + b_2x^2 = LP \qquad (1)$$

$$p(x) = \{\exp(LP)\} / \{1 + \exp(LP)\} \qquad (2)$$

The logistic link means that the probability of a species occurring is a logistic, s-shaped function when the linear predictor is a first-order polynomial, but for higher polynomials the predicted probability function will be more complex and for second-order polynomials will approximate a bell-shaped function.

This model has the advantage that the dependent variable is bound between 0 and 1, and that it fits a bell-shaped response curve, which is an ecologically realistic response (TER BRAAK & LOONMAN, 1986). The shape of the response model was in this study limited to a second order linear model, which at the original presence-absence scale corresponds to a unimodal symmetric curve (JONGMAN *et al.*, 1987). Although skewed and more complex response curves can theoretically occur, they could not be fitted with the GLM approach. Generalized additive models (GAMs) were developed for this purpose but were not used in this study (e.g. HASTIE & TIBSHIRANI, 1990; YEE & MITCHELL, 1991; BIO *et al.*, 1998).
In this study, a response surface for 20 macrobenthic species was generated by stepwise logistic regression with the statistical package SAS (SAS Inst. Inc., 1985). In equations (1) and (2), the b_0, b_1, and b_2 are the regression parameters. They were estimated using the maximum likelihood method, assuming binomially distributed errors. Consequently, the global model importance was tested using the –2lnL statistic based on the χ^2-test ($p<0.05$) for the covariates compared with the intercept (α) only model. In the next step, the importance of the included model-variables was tested separately using the χ^2-test ($p<0.05$) on the Wald-statistic. Response curves were obtained for each single abiotic variable separately, and a multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, this analysis was run separately with and without sediment data.

The resulting set of regression equations was validated *internally*. The predictive success of the response surfaces was evaluated by cross tabulating observed and predicted responses (2x2 contingency table). The threshold at which this evaluation was made was determined by choosing that p-level which corresponded with the actually observed ratio between absences and presences. At p-values below that threshold the species was predicted to be absent, whereas at p-values above that threshold the species was predicted to be present. Besides the overall percentage correctly predicted, we examined also the *sensitivity* (the proportion of presences that were predicted to be presences) and *specificity* (the proportion of absences that were predicted to be absences). A Fisher Exact Test was performed on the obtained 2x2 table. The Fisher Exact test calculates an exact probability value for the relationship between two dichotomous variables, as found in the two by two table. It calculates the difference between the data observed and the data expected, considering the given marginals and the assumptions of the model of independence. In other words, how likely is it to obtain cell frequencies as uneven or worse than the ones that were observed?

For some species also a visual, geographical comparison was made between the mapped probability surfaces to the species occurrence maps.

In order to examine the possibilities of validating the observed responses in a more robust way, the macrobenthos dataset on the Schelde estuary was randomly divided in two and as an example, a model was constructed for *Cerastoderma edule* based on one half of the dataset and validated on the other half.

Since this is not sufficient to prove the reliability of the derived set of equations to serve as a predictive model, an *external* validation was conducted, using data on the Oosterschelde. A description of these data and the detailed results on this external validation were put in a separate part of this report (part three) but the main results are discussed in this part.

ECOPROFILES FOR 20 MACROBENTHIC SPECIES OF THE SCHELDE ESTUARY

Based on the macrobenthic database and the above described statistical methods, an ecoprofile for 20 macrobenthic species of the Schelde estuary was constructed. These species represent different types of distribution and are indicator species for the macrobenthic assemblages found in the Schelde estuary, contributing substantially to the total density and biomass observed.

Each profile consists of the following parts:

- INTRODUCTION: short summary of the importance of the species in the Schelde estuary
- AUTO-ECOLOGY: short literature review on the auto-ecology of the species, with focus on habitat preferences, feeding habits and population dynamics. This auto-ecology aimed not at a complete overview of all available literature on the species, but focused on the relevant literature for this study. Information on effects of pollution, ecotoxicology, etc. was not included in the auto-ecology.
- OCCURRENCE IN THE SCHELDE ESTUARY: gives an overview for each species of the occurrence (presence/absence, abbreviated p/a), density and biomass in the Schelde estuary in relation to salinity and depth. Also the seasonal variation, presented as a spring versus autumn comparison, was made for each species. Geographical distribution maps (presence/absence and density/biomass) of each species in the Schelde estuary are also presented.
- RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE: For each species a (stepwise) logistic regression model for binary (presence/absence) data was performed on the following abiotic variables:
  - model salinity and temporal salinity: both were treated together and presented in one table and figure. Salinity was expressed as psu.
  - depth: A positive sign was used to indicate depths below NAP, whereas a negative sign was used to indicate depths above NAP. However, to make all depth values positive (as we worked also with the quadratic term), +2.5 m NAP was added to each value and therefore the data are presented as m NAP + 2.5m. To know the real height +2.5m NAP should be subtracted.
  - maximum ebb (maxeb) and flood (maxfl) current velocity: expressed as $m.s^{-1}$; both were treated together and presented in one table and figure.
  - median grain size and mud content: both were treated together and presented in one table and figure. As mud content was expressed as the volume percentage < 63 μm, the corresponding curve on the accompanying figure only relates to the 0-100 part of the x-axis, whereas median grain size is expressed as μm and the corresponding curve on the figure relates to the complete range of the x-axis.

  For each abiotic variable the regression coefficients (+ standard error) are given, together with the concordance, which gives an indication of the performance of the model based on the association of predicted probabilities and observed responses. Also the fitted response curve is presented in a figure. No legend is added to these standard tables and figures, with the interpretation implied in the accompanying text.
- MULTIPLE STEPWISE LOGISTIC REGRESSION: For each macrobenthic species a multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run separately with and without sediment data. The regression coefficients for both models are presented in a table, together with the concordance (see above). To evaluate the performance of the

model, an internal validation was performed, giving comparative statistics on the predicted and observed occurrence of each species, together with a Fisher exact test (see above).
An ecoprofile was constructed for the following 20 macrobenthic species, presented in alphabetic order:

1. *Arenicola marina*
2. *Bathyporeia spp.*
3. *Capitella capitata*
4. *Cerastoderma edule*
5. *Corophium arenarium*
6. *Corophium volutator*
7. *Eteone longa*
8. *Heteromastus filiformis*
9. *Hydrobia ulvae*
10. *Macoma balthica*
11. *Mya arenaria*
12. *Nephtys cirrosa*
13. *Nephtys hombergii*
14. *Nereis diversicolor*
15. *Nereis succinea*
16. *Polydora spp.*
17. *Pygospio elegans*
18. *Scrobicularia plana*
19. *Spio spp.*
20. *Tharyx marioni*

The detailed ecoprofiles on each species are presented in part two of this report. In part one of the report the main results obtained are summarised, focusing mainly on the modelled response curves and the validation of these models.

Table 1. Average, maximum and minimum salinity (± standard error) of the sampling occasions in each salinity region based on model calculations.

Salinity region	1	2	3	4
average	29.23 ± 1.36	23.96 ± 1.52	16.52 ± 2.04	8.93 ± 1.41
max.	29.84 ± 1.28	24.43 ± 1.09	19.29 ± 1.39	13.89 ± 1.17
min.	29.12 ± 1.43	23.60 ± 1.61	15.59 ± 2.04	7.98 ± 1.49
N	722	959	956	475

Table 2. Mean ± Standard Error for median grain size (µm), mud content (% < 63 µm), maximum ebb and flood current velocities (m/s) for each depth stratum.

	Median grain size	Mud content	Max ebb	Mab flood
Depth stratum				
1 (intertidal)	139.1 ± 69.1 *n=922*	22.9 ± 23.1 *n=888*	0.42 ± 0.19 *n=1481*	0.39 ± 0.23 *n=1481*
2 (undeep subtidal)	192.9 ± 84.8 *n=173*	13.5 ± 21.6 *n=150*	0.74 ± 0.25 *n=471*	0.79 ± 0.27 *n=471*
3 (deep subtidal)	202.7 ± 87.2 *n=143*	14.0 ± 21.9 *n=116*	0.83 ± 0.22 *n=429*	0.88 ± 0.26 *n=429*
4 (channel)	218.2 ± 91.9 *n=264*	10.5 ± 18.4 *n=232*	0.97 ± 0.23 *n=656*	1.00 ± 0.27 *n=656*

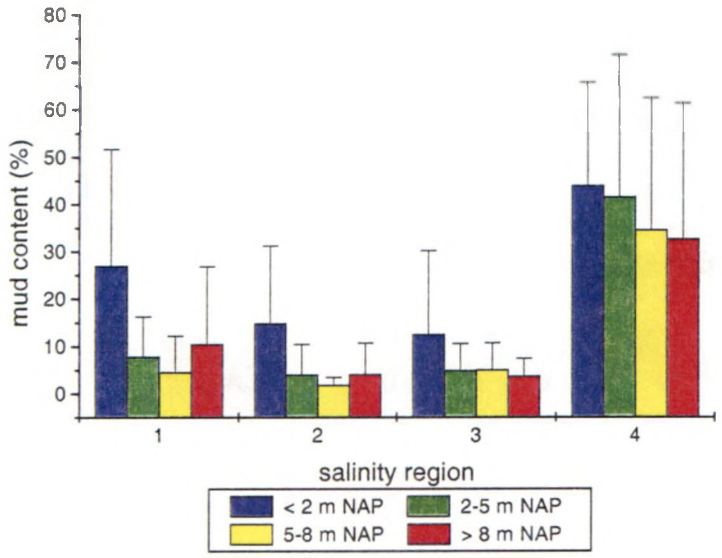

Figure 5. Mean mud content (% ± SD) of the sampling occasions in the different salintity regions and depth strata (salinity regions 1&2: polyhaline zone; salinity regions 3&4: mesohaline zone).

RESULTS

CHARACTERISATION OF THE ABIOTIC ENVIRONMENT

Average model salinity, based on model calculations, varied between 5.7 and 31.6 for the whole study area. Salinity regions 1 and 2 belonged to the polyhaline zone, salinity regions 3 and 4 to the α- and β-mesohaline zone respectively (Table 1, Figure 4). Based on temporal salinity region 2 could be considered as a poly-/mesohaline transition zone, whereas salinity region 4 could be considered as a meso-/oligohaline transition zone.

Although all sediments could be characterised as fine sands within each depth stratum, there is a significant difference between depth strata for median grain size (ANOVA, F=56.72; $p<0.001$) and mud content (ANOVA, F=53.02; $p<0.001$), with a clear trend of coarser sediments with less silt content from the intertidal to the deep subtidal and channel (Table 2), which is also demonstrated by the significant positive correlation between depth and median grain size ($r= .54$; $p<0.01$; $n=1168$) and the significant, but rather weak, negative correlation between depth and mud content ($r= -.41$; $p<0.01$; $n=1058$). This rather weak correlation could be explained by the fact that this trend was not consistent within each salinity region. In the polyhaline zone (salinity regions 1 and 2) and the α-mesohaline zone (salinity region 3) mud content was significantly higher in the intertidal zone as compared to the subtidal zone, but overall means were relatively low. In comparison, in the β-mesohaline zone (salinity region 4), much higher mud contents were observed in all depth strata, but here differences between depth strata were relatively small, with only a weak trend towards coarser sediments with increasing depth.

Significantly higher current velocities, both under ebb and flood conditions, were observed in the subtidal strata as compared to the intertidal zone (ANOVA, F=1165.8 (ebb) and F=1129.9 (flood), $p<0.001$), which was also demonstrated by the highly significant correlation between depth and maximal ebb current velocities ($r=.76$; $p<0.01$; $n=2559$) and maximal flood current velocities ($r=.73$; $p<0.01$; $n=2559$). This pattern is consistent within each salinity region.

Finally a significant, but rather weak, correlation was observed between current velocities and median grain size ($r=.44$; $p<0.01$; $n=1455$) and mud content ($r=-0.38$; $p<0.01$; $n=1340$) respectively, indicating coarser sediments with lower mud contents with higher current velocities.

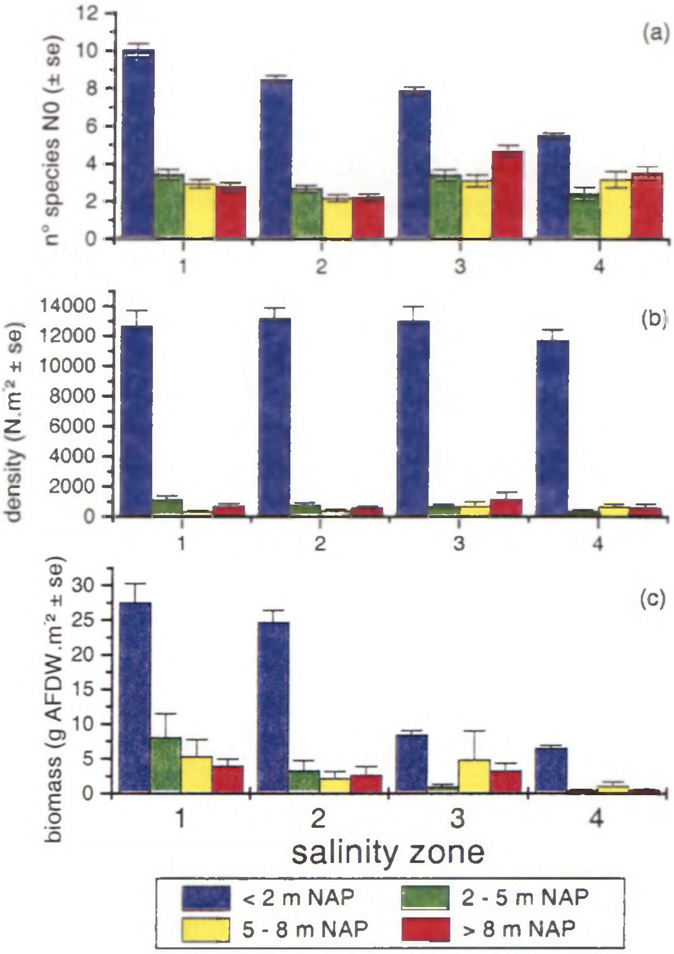

Figure 6. Mean number of species, mean density and mean biomass observed along the longitudinal (salinity regions) and vertical gradient (depth strata) in the Schelde estuary (salinity regions 1&2: polyhaline zone; salinity regions 3&4: mesohaline zone).

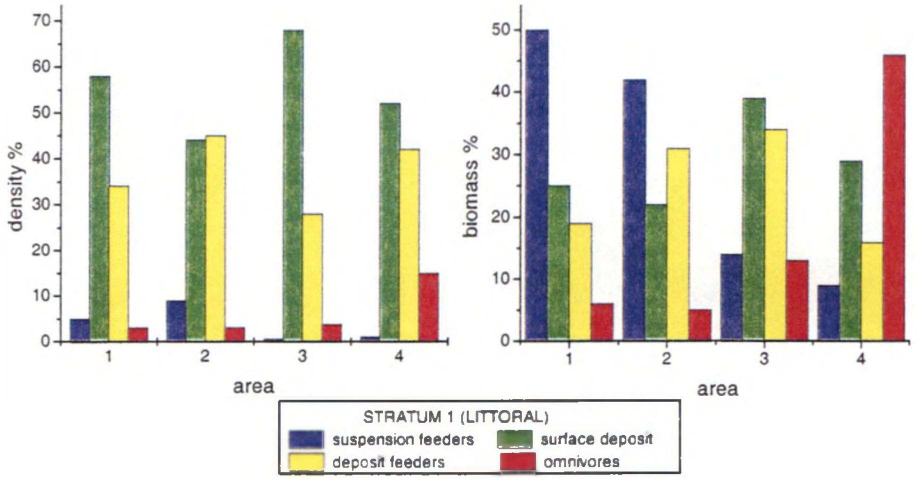

Figure 7. Relative dominance (density and biomass) of the different feeding guilds in the littoral zone of each salinity region (salinity regions 1&2: polyhaline zone; salinity regions 3&4: mesohaline zone).

GENERAL CHARACTERISTICS OF MACROBENTHOS

Macrofauna diversity (number of species, N0) at a single sampling occasion varied between 0 and 25 species. At 202 sampling occasions (6.5 %) no macrobenthic animals were found. Most sampling occasions (51 %) had less then 5 species and at 28 % of the sampling occasions between 5 and 10 species were observed. The most common species was *Heteromastus filiformis*, observed in 58% of the sampling occasions, followed by *Macoma balthica* (41%), *Pygospio elegans* (36%), *Bathyporeia spp.* (30%), *Nereis diversicolor* (26%) and *Hydrobia ulvae* (25%). Other species were observed in less than 20 % of the occasions.

Total density varied between 0 and 225,568 ind m^{-2}. At about half the sampling occasions a density less then 1000 ind m^{-2} was observed and at about one third a density between 1000 and 10,000 ind m^{-2} was observed. The three most abundant macrofauna taxa in the Schelde estuary were Polychaeta, Mollusca and Crustacea.

Total biomass varied between 0 and 466.5 g AFDW m^{-2}. At about half the sampling occasions a biomass less then 1g AFDW m^{-2} was observed and at about one third a biomass between 1 and 10 g AFDW m^{-2} was observed.

GENERAL TRENDS ALONG LONGITUDINAL (SALINITY) AND VERTICAL (DEPTH) GRADIENTS

The average number of species (N0) observed per sampling occasion was significantly different between the salinity regions (Two-way ANOVA, F=15.5; p<0.0001) and the depth strata (Two-way ANOVA, F=499; p<0.0001), with also a significant interaction term salinity*depth (Two-way ANOVA, F=14; p<0.001). A clear decrease in the number of species from the polyhaline zone towards the mesohaline zone was observed and a significantly higher number of species (per sampling occasion) in the intertidal zone as compared to the subtidal zone (ANOVA, F=532; p<0.0001) (Figure 6); in the subtidal zone the average number of species observed per sampling occasion was more or less similar within each salinity region and within each depth stratum. However, the total number of species observed was higher in the subtidal zone as compared to the intertidal zone.

Macrofauna total density was similar between salinity regions, but showed a significant difference with depth (Two-way ANOVA, F=554; p<0.0001), with a higher density for the intertidal zone as compared to the subtidal strata (Figure 6). In the intertidal zone, density of the macrobenthos was in all salinity regions dominated by surface deposit feeders and deposit feeders (Figure 7). Suspension feeders only appeared in low densities in the polyhaline zone and were nearly absent in the mesohaline zone. Omnivore/predator densities were low in the salinity regions 1-3, but their relative importance increased in salinity region 4.

Macrofauna total biomass showed both a significant difference between salinity regions (Two-way ANOVA, F=18.63; p<0.0001) and depth strata (Two-way ANOVA, F=413; p<0.0001), with also a significant interaction term salinity*depth (Two-way ANOVA, F=7; p<0.001). Highest biomass values were observed in the highest salinity regions (polyhaline zone) and the intertidal zone (Figure 6). Within the subtidal strata, no significant difference was observed. In the intertidal zone, clear gradients in biomass dominance of the different feeding guilds was observed. Suspension feeders dominated in the polyhaline zone (salinity regions 1 and 2) and showed a clear decrease with decreasing salinity. Omnivores/predators biomass showed an opposite trend, with an increasing dominance towards the mesohaline zone; in salinity region 4 omnivores/predators were the dominant group. Salinity region 3 acted as an intermediate region with surface deposit and deposit feeders dominating the biomass (Figure 7).

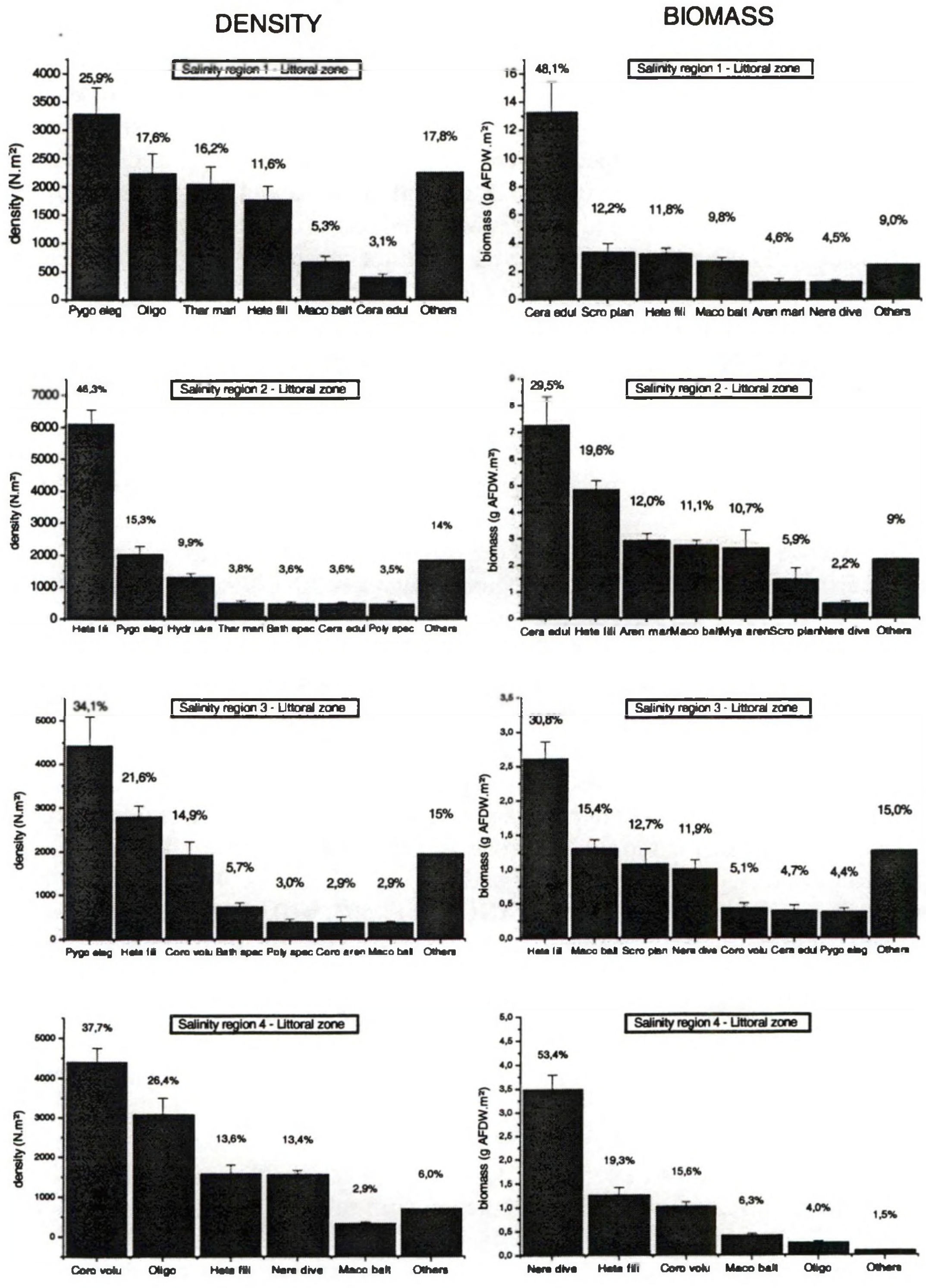

Figure 8. Relative dominance (density and biomass) of the most important macrobenthic species in the littoral zone of each salinity region (salinity regions 1&2: polyhaline zone; salinity regions 3&4: mesohaline zone).

RELATIVE DOMINANCE (DENSITY AND BIOMASS) OF MACROBENTHIC SPECIES IN THE LITTORAL ZONE

The relative dominance (density and biomass) of the most important macrobenthic species in the littoral zone of each salinity region is given in Figure 8. In Appendix 1 the mean density and biomass (± standard deviation), together with the observed minima and maxima for the most common species (58 species) are given for each salinity region separately.

Density

Polychaetes, especially *Pygospio elegans* and *Heteromastus filiformis*, had the largest contribution to the observed density. This was expecially the case in the middle part of the estuary (salinity regions 2 and 3). Only in the β-mesohaline zone (salinity region 4) density was not dominated by polychaetes, but by the amphipod *Corophium volutator* and Oligochaeta. Oligochaeta had also a relatively large contribution to the macrobenthic density in salinity region 1, whereas in the middle of the estuary (salinity regions 2 and 3) Oligochaeta were of no importance. Molluscs (bivalves) had only a very small contribution to the total macrobenthic density in the Schelde estuary.

Biomass

The contribution of bivalves to the overall macrobenthic biomass was much higher, being in the polyhaline zone of the estuary (salinity region 1 and 2) the dominant constituent. Here, especially the filter feeder *Cerastoderma edule*, with 48% and 30% of the total biomass in salinity region 1 and 2 respectively, dominates, but also the deposit feeders *Macoma balthica* and *Scrobicularia plana* had a relatively large contribution to the overall biomass. In the polyhaline zone the most important polychaete was the deposit feeder *Heteromastus filiformis* and to a lesser extent *Arenicola marina*.

In the mesohaline zone of the estuary a clear difference was observed between the α-mesohaline zone (salinity region 3) and the β-mesohaline zone (salinity region 4). In the α-mesohaline zone the deposit feeder *Heteromastus filiformis* dominated the biomass with 31%, followed by the deposit feeding mollusc species *Macoma balthica* and *Scrobicularia plana* and the omnivore polychaete *Nereis diversicolor*. This last species dominated by far the macrobenthic biomass in the β-mesohaline zone with 53%, followed *by Heteromastus filiformis* and the surface deposit feeding amphipod *Corophium volutator*. Except for salinity region 4, crustaceans had only a very small contribution to the total macrobenthic biomass in the Schelde estuary.

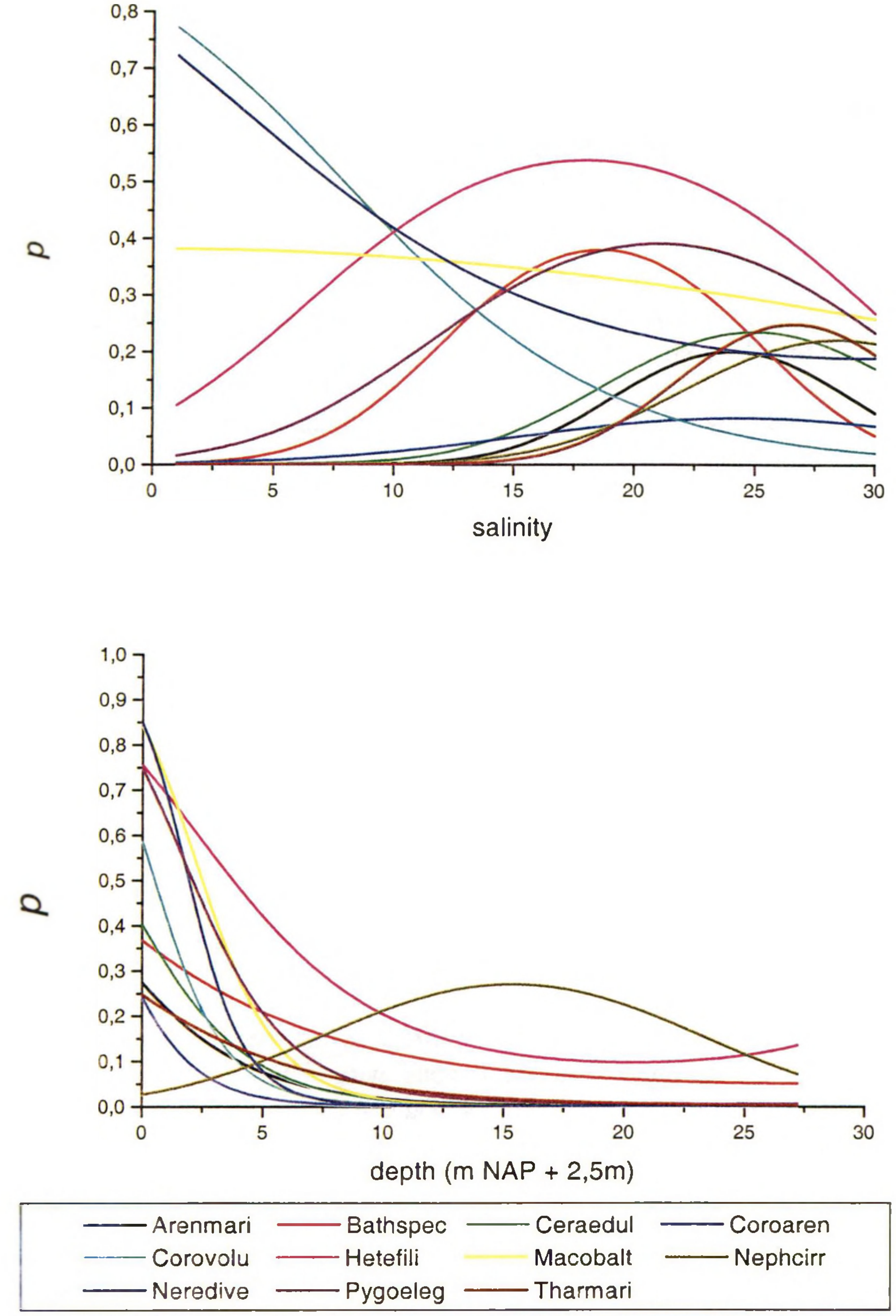

Figure 9. Probability of occurrence of ten macrobenthic species in relation to salinity (temporal salinity) and depth in the Schelde estuary, as fitted with logistic regression (p= species probability of occurrence (p/a)).

ECOPROFILES OF 20 MACROBENTHIC SPECIES

In Part Two of this report a detailed ecoprofile for 20 macrobenthic species of the Schelde estuary is presented. Here a short summary is given on the obtained results, especially towards the modelled response curves and the validation of these models.

Response curves for a single abiotic (explanatory) variable

As an example of the obtained response curves for a single abiotic variable, Figures 9 and 10 show the fitted Gaussian logit curves for ten contrasting macrobenthic species in relation to temporal salinity, depth, maximum ebb current velocity and median grain size.

Temporal salinity

The response curves in relation to temporal salinity clearly showed different responses (Figure 9). Species like *Corophium volutator* and to a lesser extent *also Nereis diversicolor* showed a high probability of occurrence at low salinities. For *Corophium volutator* a steep decrease of the curve was observed with increasing salinities, indicating a very low probability of occurrence at high salinities, whereas for *Nereis diversicolor* the decrease in the curve was much smoother, indicating that also at higher salinities *Nereis diversicolor* could be observed.

Bathyporeia spp. showed a bell-shaped curve with an optimum at intermediate salinities. Both at the lower end as at the upper end of the salinity range the probability of occurrence of this species decreased.

Several species, like e.g. *Cerastoderma edule, Tharyx marioni, Arenicola marina* and *Nephtys cirrosa*, showed a clear optimum towards the higher end of the salinity range, indicating a higher probability of occurrence at high salinities. These species differed in the position of their optimum, and in their tolerance towards the lower end of the salinity range.

Macoma balthica showed an almost horizontal curve, indicating a very broad tolerance for salinity. This coincides with the observed distribution of *M. balthica*, being present along the complete salinity gradient. Another species showing a broad tolerance for salinity was *Heteromastus filiformis*, as could be observed from the very broad bell-shaped curve. Only at very low salinities, and to a lesser extent also at high salinities, the probability of occurrence decreased.

The obtained responses on salinity were in general agreement with the descriptive statistics on the occurrence of the different species along the different salinity regions and with the descriptions in the literature.

In general ‘model salinity’ gave similar results as ‘temporal salinity’. However, for most species with an optimum towards the higher end of the salinity range, the ‘temporal salinity’ model showed a more narrow tolerance with an optimum which shifted towards a higher salinity as compared to the ‘model salinity’ model. The ‘model salinity’ model showed a much broader response curve, extending more into the mesohaline zone. This difference in response was probably the result of the fact that the ‘temporal salinity’ model did take into account the seasonal variation in salinity. The fact that several species were more present in autumn in the mesohaline zone, when in general higher salinities were observed, resulted in this shift in response towards a higher salinity. The fact that much more observations were available for autumn in the β-mesohaline zone as compared to spring, might also have influenced this shift. Therefore it is clear that both salinity measures are useful for the purpose of modelling, the model salinity giving a good idea of spatial variation, the temporal salinity giving a good idea of the temporal (seasonal) variation.

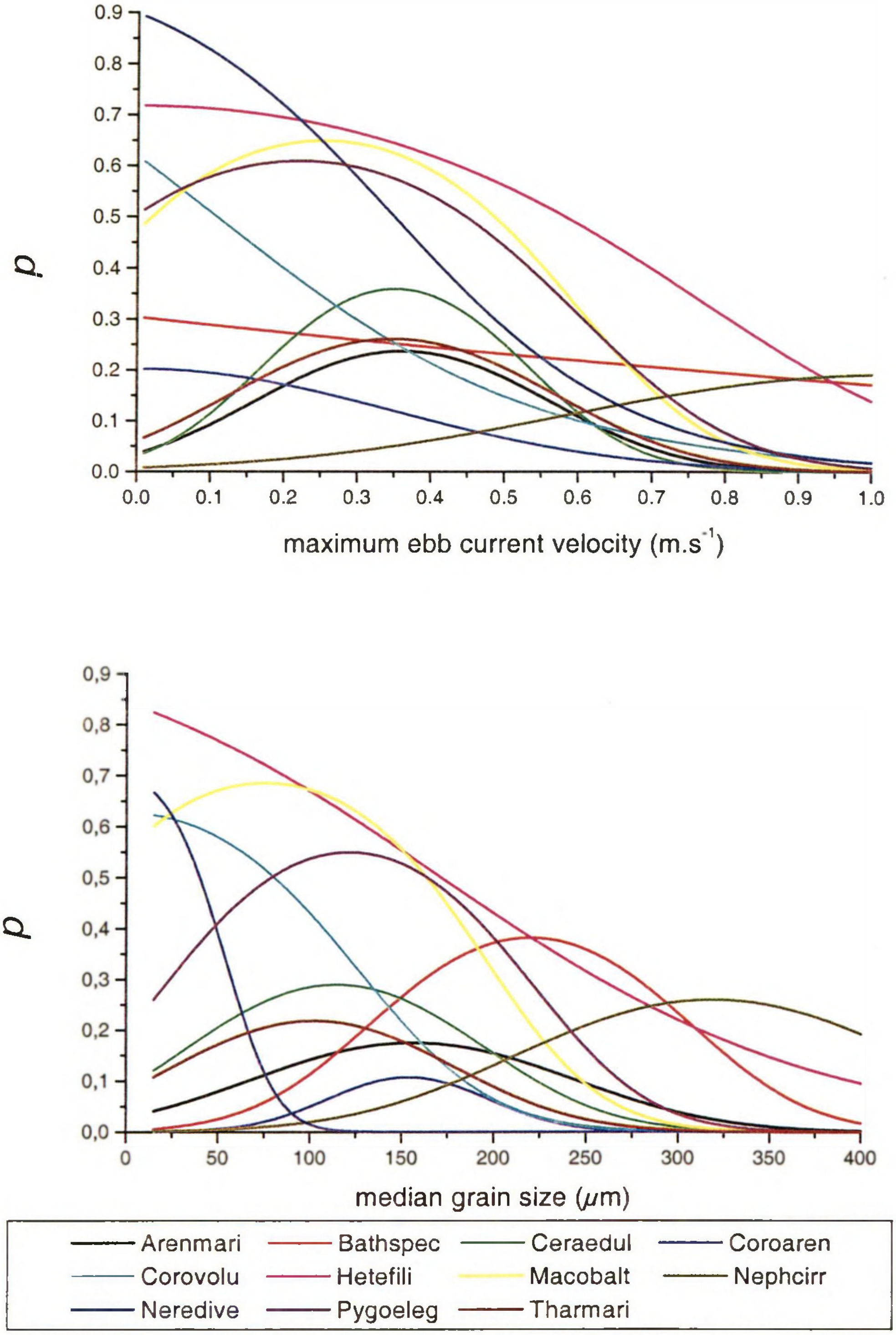

Figure 10. Probability of occurrence of ten macrobenthic species in relation to maximum ebb current velocity and median grain size in the Schelde estuary, as fitted with logistic regression (p= species probability of occurrence (p/a)).

Depth

The response curves in relation to depth showed for most macrobenthic species (e.g. *Nereis diversicolor, Corophium volutator, Cerastoderma edule*) similar curves, with high probabilities of occurrence above NAP (intertidal zone), and decreasing probabilities of occurrence with increasing depth (Figure 9). This coincides with the field observations, with most species having their highest occurrence in the intertidal zone. These species differed in their tolerance towards the deeper end of the depth range. *Heteromastus filiformis*, for instance, showed a relatively high tolerance with still a relatively high probability of occurrence in the subtidal zone.

Bathyporeia spp. showed only a slightly higher probability of occurrence in the intertidal zone, indicating a very broad depth tolerance.

The only species showing an optimum in the subtidal zone of the estuary *was Nephtys cirrosa.*

The obtained responses on salinity were in general agreement with the descriptive statistics on the occurrence of the different species along the different salinity regions and with the descriptions in the literature.

Maximum ebb current velocity

The response curves in relation to maximum ebb current velocity clearly showed different responses (Figure 10). Species like *Corophium volutator* and *Nereis diversicolor* showed the highest probabilities of occurrence at the lowest current velocities, with a more or less linear decrease in probability of occurrence with increasing current velocities.

Other species like *Macoma balthica* and *Pygospio elegans* showed a broad tolerance in the range 0-0,5 m.s^{-1}, after which a steep, linear decline was observed in the probability of occurrence with increasing current velocities. This broad tolerance was even more pronounced for *Heteromastus filiformis*, having only low probabilities of occurrence at the highest current velocities. *Bathyporeia spp.* on the other hand showed an almost horizontal curve, indicating that current velocity is not a good discriminator for this species.

Several species showed a unimodal, bell-shaped curve with a clear optimum (e.g. *Cerastoderma edule, Arenicola marina*).

Nephtys cirrosa was the only species showing an optimum towards the higher end of the current velocity range.

Median grain size

The response curves in relation to median grain size clearly showed different responses for the different macrobenthic species (Figure 10). *Nereis diversicolor* showed a highest probability of occurrence in very muddy sediments with a low median grain size, with a linear and steep decrease in the probability of occurrence with increasing median grain size. The same pattern was observed for *Corophium volutator*, but showing a broader tolerance. This tolerance was even more pronounced for *Macoma balthica* and *Heteromastus filiformis.*

Several species showed a bell-shaped curve with an optimum between 100-150 μm (e.g. *Cerastoderma edule, Arenicola marina, Corophium arenarium*). This optimum shifted even more towards a higher median grain size (± 225 μm) for *Bathyporeia spp.*

Nephtys cirrosa was the only species showing an optimum towards the higher end of the median grain size range, having its highest probability of occurrence in coarse sediments with a high median grain size.

Multiple logistic regression

For each macrobenthic species a multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run separately with and without sediment data.

Table 3 summarizes the number of times an explanatory abiotic variable (both the linear as the quadratic term) was included in the 20 regression models. For the models without sediment characteristics, model salinity and depth (both linear and quadratic term) were most included as explanatory variable, followed by maximum ebb current velocity (both linear and quadratic term). For the models with sediment characteristics temporal salinity, model salinity and depth (both the linear and the quadratic term), together with the linear term of maximum flood current velocity and the linear term of median grain size, were most included as explanatory variable. Mud content was only included a few times as explanatory variable in the models.

Table 3. Number of times an explanatory abiotic variable (both the linear as the quadratic term) was included within a multiple stepwise logistic regression model for 20 macrobenthic species of the Schelde estuary.

Model without sediment characteristics		***Model with sediment characteristics***	
Explanatory variable	# included in the model	Explanatory variable	# included in the model
Temporal salinity	9	Temporal salinity	13
Temporal salinity^2	10	Temporal salinity^2	12
Model salinity	16	Model salinity	12
Model salinity^2	15	Model salinity^2	10
Depth	14	Depth	11
Depth^2	14	Depth^2	11
Maxeb	12	Maxeb	8
Maxeb^2	13	Maxeb^2	7
Maxfl	10	Maxfl	13
Maxfl^2	9	Maxfl^2	6
		Median	12
		Median^2	9
		Mud	6
		Mud^2	4

Validation of the multiple regression models

In order to evaluate the regression models, different validation approaches were applied:

1. The resulting set of regression equations was validated *internally*. The predictive success of the response surfaces was evaluated by cross tabulating observed and predicted responses. As an example, for two species also a visual, geographical comparison was made between the mapped probability surfaces to the species occurrence maps.
2. In order to examine the possibilities of validating the observed responses in a more robust way, the macrobenthos dataset on the Schelde estuary was randomly divided in two and as an example, a model was constructed for *Cerastoderma edule* based on one half of the dataset and validated on the other half.
3. Since this is not sufficient to prove the reliability of the derived set of equations to serve as a predictive model, applicable in other estuarine or coastal areas, an *external* validation on an other area was conducted, using data on the Oosterschelde. A description of these data and the detailed results on this external validation were put in a separate part of this report (part three) but the main results are discussed in this part.

These three different approaches are summarized below.

1. Internal validation

Table 4 summarizes some of the comparative statistics on the predicted and actual observed occurrence of the 20 macrobenthic species. The overall prediction, including both the prediction of the presences and absences, performed for all species very well. But within the framework of predicting macrobenthic occurrence, the interest was of course more towards how well the model predicts presences. When focusing on the % predicted present versus actually observed in the field, a more shaded picture was obtained. For the common species like *Corophium volutator, Heteromastus filiformis, Hydrobia ulvae, Macoma balthica, Nereis diversicolor* and *Pygospio elegans* a very good ratio of predicted presences vs observed presences was obtained. Moderate to good ratios were obtained for *Arenicola marina, Bathyporeia spec, Cerastoderma edule, Nephtys cirrosa, Polydora spp., Scrobicularia plana, Spio spp.* and *Tharyx marioni*. Worst performance was found for *Capitella capitata.*

In general the ratio improved when including sediment characteristics in the models. This was the case for 14 macrobenthic species out of 20. For *Bathyporeia spp., Heteromastus filiformis, Macoma balthica, Nephtys cirrosa, Nereis succinea, Polydora spp., Spio spp.* and *Tharyx marioni* this ratio even improved with more then 10 %.

The visual, geographical comparison between the mapped probability surfaces to the species occurrence maps for both *Corophium volutator* and *Macoma balthica* (probability threshold 0.25) showed a good geographical representation of the predictions. Predicted presences and observed absences, were not put in a random way, but they were mainly situated in the intertidal zone, which corresponded with the habitat preferences of the considered species (Figure 11). It was striking to see that *for Macoma balthica* a lot of the predicted presences, but observed absences, were situated near the edges of the tidal sand and mud flats.

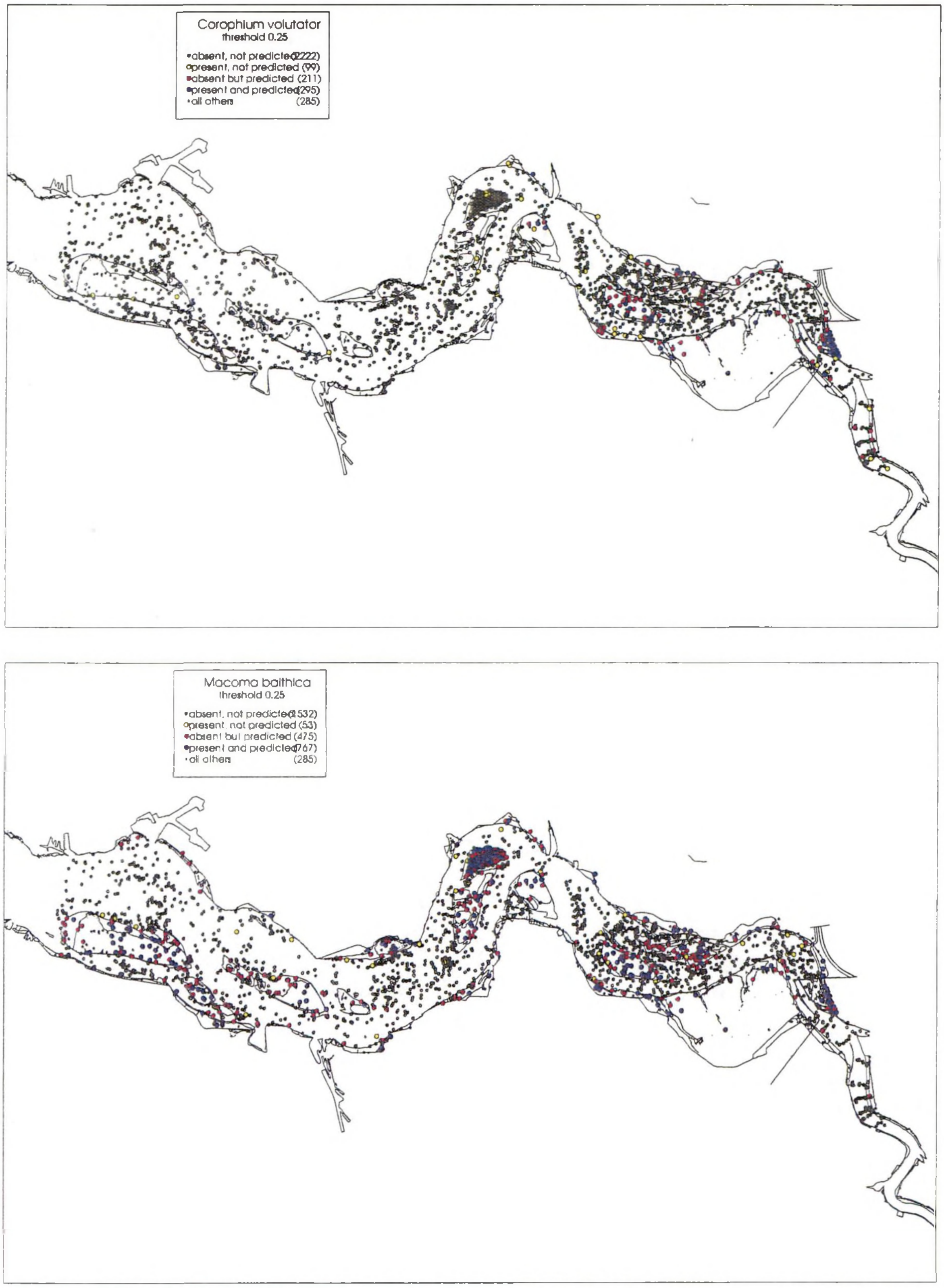

Figure 11. Visual, geographical comparison between the mapped probability surfaces to the species occurrence maps for Corophium volutator and Macoma balthica (probability threshold 0.25).

Table 4. Comparative statistics on the predicted and actual observed occurrence of the 20 macrobenthic species. The predictive success of the response surfaces was evaluated by cross tabulating observed and predicted responses (2x2 contingency table). The threshold at which this evaluation was made was determined by choosing that p-level which corresponded with the actually observed ratio between absences and presences. At p-values below that threshold the species was predicted to be absent, whereas at p-values above that threshold the species was predicted to be present. Besides the overall percentage correctly predicted, also the sensitivity (the proportion of presences that were predicted to be presences) is given.

	Model without sediment characteristics		Model with sediment characteristics	
	% correctly predicted	Sensitivity	% correctly predicted	Sensitivity
Aren mari	89,5	44,6	86,9	50,6
Bath spp.	78,1	46,8	80,8	62,5
Capi capi	80,9	20,1	81,6	29,6
Cera edul	90,0	59,9	87,5	65,1
Coro aren	93,1	33,3	92,8	25,0
Coro volu	90,2	64,7	82,3	56,3
Eteo long	87,5	41,5	82,4	41,1
Hete fili	75,2	69,9	81,4	82,5
Hydr ulva	88,3	67,9	85,6	72,7
Maco balt	85,5	75,0	87,3	85,4
Mya aren	90,7	40,6	84,4	40,1
Neph cirr	84,0	33,3	91,8	48,0
Neph homb	88,5	34,2	92,2	34,5
Nere dive	88,3	75,0	75,9	65,6
Nere succ	88,1	41,7	79,4	60,3
Poly spec	88,3	34,0	88,1	50,3
Pygo eleg	85,6	75,7	79,7	71,1
Scro plan	92,6	44,1	92,0	51,9
Spio spec	83,2	38,9	89,8	60,9
Thar mari	89,5	52,1	91,3	68,0

2. External validation within the Schelde estuary

In order to examine the possibilities of validating the observed responses in a more robust way, the macrobenthos dataset on the Schelde estuary was randomly divided in two equal subsets and as an example, a model was constructed for *Cerastoderma edule* based on one half of the dataset and validated on the other half. Based on the same variables as derived from the logistic model with all data, a full model selection method was performed on the two subsets. The regression coefficients from subset 1 were used to predict the presence/absence in subset 2.

Table 5 summarizes the comparative statistics on the predicted (based on subset 1) and actual observed (based on subset 2) occurrence of *C. edule*. The results were comparable with the internal validation, indicating that reliable predictions can be made within the Schelde estuary.

Table 5. Comparative statistics on the predicted, based on subset 1, and observed, based on subset 2, occurrence of C. edule in the Schelde estuary (regression model without sediment characteristics). (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model).

C. edule

(without sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	*115*	79	194	59,3
Ao	79	*1150*	1229	93,6
Total	194	1229	1423	86,4

3. External validation in an other coastal area (Oosterschelde)

Since this is not sufficient to prove the reliability of the derived set of equations to serve as a predictive model, applicable in other estuarine or coastal areas, an *external* validation on an other area was conducted, using data on the Oosterschelde. A description of these data and the detailed results on this external validation were put in a separate part of this report (part three) but the main results are discussed in this part.

Table 6 summarizes some of the comparative statistics on the predicted (based on Schelde estuary models) and actual observed occurrence of ten macrobenthic species in the Oosterschelde. The overall prediction, including both the prediction of the presences and absences, performed for most species very well and also for the % predicted present versus actually observed in the field, only slightly lower estimates were obtained as for the internal validation (see Table 4). For *Arenicola marina* even a better ratio was obtained in the Oosterschelde. For some species, like e.g. *Heteromastus filiformis*, a rather low ratio was obtained in comparison to the internal validation.

Although the Oosterschelde can be considered as a different system, being more a 'coastal basin' than a 'true estuary', the regression models from the Schelde estuary seem to be applicable in the Oosterschelde.

Table 6. Comparative statistics on the predicted (based on Schelde estuary regression models) and actual observed occurrence of ten macrobenthic species in the Oosterschelde.

	Model without sediment characteristics	
	% Predicted correct	% Predicted correct vs observed
Aren mari	84,0	68,3
Cera edul	77,3	57,1
Eteo long	85,0	43,3
Hete fili	72,0	32,0
Hydr ulva	81,6	55,5
Maco balt	77,1	46,5
Neph homb	57,3	59,3
Nere dive	99,2	95,5
Pygo eleg	76,1	62,4
Thar mari	56,0	41,9

CONCLUSIONS AND SUMMARY

Macrobenthos is a central element of estuarine foodwebs. Therefore, evaluation of the consequences of human induced changes will likely include the possible responses of the macrobenthos and the analysis of benthic infauna is a key element of many marine and estuarine monitoring programmes. The starting point is that macrofaunal species distributions reflect the present state of the estuarine ecosystem. Human impact on estuaries will affect the ability of these ecosystems to support macrofaunal occurrence (in terms of diversity, density or biomass). In order to be able to manage estuaries in a proper way, decision makers should be able to make sound predictions on the effects of human interventions on estuarine ecosystems. Knowledge on the (statistical) responses of individual macrobenthic species to estuarine gradients, represented by environmental variables that are essential factors for their occurrence (presence/absence, density or biomass), is essential for the purpose of predictive modelling. However, large datasets are needed for such an approach. No attempts have been made so far to model the responses of individual macrobenthic species to environmental variables on a large, e.g. estuarine, scale and use these models to predict the distribution and occurrence of macrobenthos. The aim of this study was to construct such a response model for several macrobenthic species, in order to be able to predict the occurrence of macrobenthos in the Schelde estuary and eventually in other estuaries. In our approach physicochemical factors are used as predictors for the occurrence of macrobenthic species on the estuarine macro-scale.

In the Schelde estuary large efforts have been put in research and monitoring on macrobenthos. This probably makes it one of the most extensively studied estuaries in the world. In this study, a compilation of all available macrobenthos data for the period 1979-1997 was made. A large macrobenthos database, containing 3112 records, was constructed and coupled with a database on abiotic variables. Abiotic variables included were salinity (based both on model calculations ('model salinity') as field observations ('temporal salinity')), depth/height of the sampling location, maximum ebb and flood current velocities (based on model calculations), and the sediment characteristics median grain size and mud content (only available for about half the sampling records).

Based on this large dataset, a general description of the macrobenthos of the Schelde estuary was made, focusing on the general distribution patterns of occurrence, density, and biomass of the macrobenthos along the different environmental gradients.

Detailed ecoprofiles for 20 macrobenthic species were constructed. These species represent different types of distribution and are indicator species for the macrobenthic assemblages found in the Schelde estuary, contributing substantially to the total density and biomass observed.

For these 20 macrobenthic species 'response curve' models were constructed by means of logistic regression on binary (presence/absence) data. In the logistic regression model, a binary response variable is related to one or more predictor variables through the logistic function. Both response curves for a single explanatory abiotic variable, as for all abiotic together, were constructed based on multiple, stepwise logistic regression. Since sediment characteristics were only available for a limited set of data, the analysis was run separately with and without sediment data.

The obtained response curves for single explanatory abiotic variables clearly showed different responses for the different species. The obtained responses were in general agreement with the descriptive statistics on the occurrence of the different species along the different environmental gradients in the Schelde estuary and with the descriptions in the literature.

In the regression models with all abiotic variables together, salinity and depth were most included as explanatory variable. Also maximum current velocities and median grain size were often included as explanatory variable into the models. It could therefore be concluded that all abiotic variables (salinity, depth, current velocities and sediment characteristics) contributed to the performance of the model.

In order to evaluate the regression models, different validation approaches were applied. Firstly, the resulting set of regression equations was validated *internally*. The predictive success of the response surfaces was evaluated by cross tabulating observed and predicted responses. The overall prediction, including both the prediction of the presences and absences, performed for all species very well. But within the framework of predicting macrobenthic occurrence, the interest was of course more towards how well the model predicted presences. When focusing on the % predicted present versus actually observed in the field, a more shaded picture was obtained, but with still a good to very good performance for several species. Also the geographical comparison between the mapped probability surfaces to the species occurrence maps, as demonstrated by *Corophium volutator* and *Macoma balthica*, revealed a good performance of the models, not putting predicted presences, but observed absences, in a random way, but rather corresponding to the habitat preference of the species. Secondly, an external validation, based on a regression model, constructed for *Cerastoderma edule* based on one half of the dataset and validated on the other half, revealed similar performances as the internal validation. Finally, since the above mentioned validations were not sufficient to prove the reliability of the derived set of equations to serve as a predictive model, applicable in other estuarine or coastal areas, an *external* validation on an other area was conducted, using data on the Oosterschelde. In general, only slightly lower estimates of predictive success were obtained as for the internal validation, indicating that the regression models for several macrobenthic species from the Schelde estuary were applicable in the Oosterschelde.

It can be concluded that with the presented models the occurrence of several macrobenthic species can be predicted very well, both within the Schelde estuary as in another coastal area (the Oosterschelde).

Despite the relatively good performance of most of the models, still a substantial part was not predicted right. Several drawbacks could be made on our approach. Firstly, there is the problem of accuracy of the selected abiotic variables. Model calculations for salinity and current velocities have the advantage that they cover the whole estuary, making it relatively easy to couple with sampling locations. A disadvantage is the relatively large grid cells with which these models operate. For salinity a grid of 400 m is no problem, but the grid of 100 m used for determining the current velocities could give less reliable results for certain sampling locations where current speeds can change over very short distances. This is especially the case with the edges of the sand and mud flats, where the transition is made towards the subtidal zone. Not surprisingly it was at these edges of sand and mud flats that the model often predicted *Macoma balthica* to be present, whereas it was actually observed as being absent.

Secondly, it was assumed that the included abiotic variables, used in the model to describe the spatial occurrence of macrobenthic species, are the only deterministic factors. This is of course not true. One of the important parameters not included in the model is the food availability for the macrobenthos. Food availability is not only a matter of local concern (e.g. available detritus in the sediment), but for suspension feeders also depends on the overall system primary production of the phytoplankton. Occurrence of e.g. the suspension *feeder Cerastoderma edule* might be hampered because of marginal food conditions (low phytoplankton primary production), even if the 'habitat' was demonstrated as being suitable by the model. It is possible, however, that the effect of these factors shows up in the fitted parameters for other variables. Phytoplankton primary production, e.g., is decreasing from the mouth to the inner estuary (KROMKAMP *et al.*, 1995) and thus could be confounded with salinity.

Also biotic interactions were not taken into account in our approach. However, the presence of a certain species might influence, or even completely hamper, the presence of another species, despite the 'habitat' is suitable for that species. Also for these factors it is possible that the effect (partially) shows up in the fitted parameters for other variables. Predation effects could show up in depth, and interspecific competition, as far as it is mediated through changes in sediment structure (e.g. *Arenicola marina* bioturbation keeping the sediment sandy and mobile, FLACH, 1993) could be hidden in sediment granulometry. As biotic interactions are very well documented for several species in the literature, it might be useful to look for possible effects on the model performance in our study.

Extreme events were also not taken into account in our approach, as there are e.g. severe winters or storms. The role of these episodic events should be studied in more detail, as they can have dramatic influences on the occurrence of macrobenthos, which might work on for a long period after the event itself took place.

Another drawback of our approach is that only presence/absence is dealt with, with no information on density or biomass included. The choice of using presence(0)/absence(1) data as a first approach was inspired by the fact that the data could not be considered as homogeneously collected. Different sampling methods, different sampling months (seasonality) and years (long-term fluctuations) certainly affected the observed variation in density and biomass data. To minimise this variation presence/absence data were used. However, it should be very useful if e.g. predictions could be made based on the same approach of logistic regression, but now for different density or biomass classes. A first attempt *on Macoma balthica* biomass, divided into two classes, gave relatively good prediction estimates for both biomass classes. This approach could further refine the regression models.

The logistic response curves for four benthic species were also applied in the Ecomorphological Module from Delft Hydraulics (work by M. Baptist) to obtain a spatial coverage of the benthic distribution in the Westerschelde. The Ecomorphological Module computes the morphological development of the Westerschelde on a long time scale and subsequently calculates the suitability of the habitats of benthic species. This module can for instance be used for an evaluation and analysis of morphological, hydrodynamic and ecological changes under different dredging scenario's, and this might support decision-makers to optimise the dredging operation with respect to ecological damage. For more details on this we refer to the work performed by M. Baptist at Delft Hydraulics.

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APPENDIX 1

Mean density and biomass (± standard deviation), minimum and maximum, per salinity region (littoral zone only) for the most common macrobenthic species (58 species) observed in the Schelde estuary

SALINITY REGION 1 - LITTORAL ZONE

	Density					Biomass				
	Valid N	Mean	Min.	Max.	Std.Dev.	Valid N	Mean	Min.	Max.	Std.Dev.
ABRAALBA	262	3.79	0	337	27.45	258	0.0074	0	1.2054	0.0808
ABRATENU	262	12,32	0	2067	129,89	258	0,0154	0	1,8323	0,1241
ACTINIAR	262	0	0	0	0	258	0	0	0	0
ANAIMUCO	262	18,17	0	1730	120,57	258	0,0196	0	1,9389	0,1383
ANGUTENU	262	3,00	0	135	15,39	258	0,0084	0	0,4695	0,0517
ARENMARI	262	10,46	0	133	21,18	258	1,2557	0	21,4075	3,1674
BATHSPEC	262	269,87	0	8000	1053,13	258	0,0484	0	1,5377	0,1515
BOCCREDE	262	0	0	0	0	258	0	0	0	0
CAPICAPI	262	71,37	0	1590	212,14	258	0,0103	0	0,4292	0,0352
CARCMAEN	262	14,99	0	741	70,76	258	0,063	0	3,5533	0,3337
CERAEDUL	262	398,47	0	7448	908,30	262	13,24	0	340,1589	35,4113
COROAREN	262	375,88	0	22867	2176,41	258	0,0754	0	3,8133	0,4120
COROINSI	262	0	0	0	0	258	0	0	0	0
COROLACU	262	0	0	0	0	258	0	0	0	0
COROVOLU	262	22,58	0	1273	128,98	258	0,0059	0	0,3925	0,0341
CRANCRAN	262	21,03	0	606	65,06	258	0,0191	0	0,4800	0,0608
CYATCARI	262	0	0	0	0	258	0	0	0	0
ENSISPEC	262	27,79	0	6733	416,27	258	0,0132	0	2,4133	0,1583
ETEOLONG	262	216,94	0	5118	510,86	258	0,2365	0	7,9731	0,8511
EURYPULC	262	13,05	0	1010	88,15	258	0,0038	0	0,4500	0,0319
GAMMSALI	262	0	0	0	0	258	0	0	0	0
GAMMSPEC	262	0,32	0	67	4,23	258	2E-05	0	0,0048	0,0003
GASTSPIN	262	0,77	0	67	7,13	258	0,0006	0	0,1414	0,0088
HARMSPEC	262	0,80	0	67	7,15	258	0,0001	0	0,0246	0,0015
HAUSAREN	262	1,17	0	157	11,32	258	0,0021	0	0,2649	0,0225
HETEFILI	262	1774,91	0	27000	3869,15	258	3,2541	0	43,2793	5,8646
HYDRULVA	262	275,90	0	8700	847,31	258	0,1282	0	3,7000	0,3891
LANICONC	262	19,76	0	1145	113,77	258	0,1257	0	7,6824	0,8089
MACOBALT	262	673,89	0	14680	1639,17	258	2,7054	0	17,2193	3,6707
MAGEPAPI	262	2,03	0	200	14,88	258	0,0022	0	0,2905	0,0197
MANAAEST	262	2,57	0	674	41,64	258	3E-05	0	0,0090	0,0006
MESOSLAB	262	0	0	0	0	258	0	0	0	0
MICRSPEC	262	1,25	0	135	10,75	258	0,0001	0	0,0135	0,0012
MYA_AREN	262	5,41	0	180	20,43	258	0,034	0	3,4818	0,2446
MYSEBIDE	262	20,51	0	733	78,38	258	0,0092	0	0,3719	0,0345
MYSIDACE	262	0,25	0	67	4,12	258	5E-05	0	0,0125	0,0008
MYTIEDUL	262	2,13	0	200	15,21	258	0,0001	0	0,0093	0,0008
NEMERTEA	262	17,30	0	380	54,18	258	0,0208	0	0,8893	0,0898
NEOMINTE	262	0	0	0	0	258	0	0	0	0
NEPHCAEC	262	0,57	0	84	6,60	258	0,0012	0	0,2352	0,0152
NEPHCIRR	262	6,35	0	333	28,62	258	0,0224	0	0,9600	0,1029
NEPHHOMB	262	21,77	0	252	38,32	258	0,2241	0	5,2469	0,5808
NEREDIVE	262	250,24	0	4400	553,84	258	1,2445	0	19,0808	2,4994
NERESUCC	262	14,90	0	1190	92,95	258	0,0324	0	2,3023	0,2010
OLIGOCHA	262	2232,08	0	56949	5720,65	258	0,2005	0	3,1933	0,4575
OPHESPEC	262	3,58	0	204	22,65	258	0,0006	0	0,0613	0,0049
PETRPHOL	262	0,26	0	67	4,16	258	0,0036	0	0,9226	0,0574
PLEUGLAB	262	0	0	0	0	258	0	0	0	0
POLYSPEC	262	176,32	0	13000	924,75	258	0,0178	0	0,8970	0,0783
PYGOELEG	262	3285,15	0	61549	7539,59	258	0,2728	0	3,6094	0,5151
RETUOBTU	262	20,82	0	713	91,41	258	0,0097	0	0,4234	0,0459
SCOLARMI	262	69,71	0	2750	254,21	258	0,1584	0	5,2000	0,5034
SCOLSQUA	262	5,14	0	487	35,51	258	0,0292	0	2,2495	0,2044
SCROPLAN	262	136,40	0	4333	478,13	258	3,3456	0	90,5387	9,4728
SPIOBOMB	262	2,59	0	200	17,04	258	0,0027	0	0,5400	0,0339
SPIOSPEC	262	50,92	0	2333	206,19	258	0,0064	0	0,2267	0,0243
SPISSPEC	262	20,64	0	2492	172,03	258	0,0636	0	16,3636	1,0187
THARMARI	262	2051,81	0	44916	4954,03	258	0,3453	0	6,2166	0,7572
SUM	262	12674,2	0	106117	16631,6	258	27,515	0	349,2736	44,2168

SALINITY REGION 2 - LITTORAL ZONE

	Density					Biomass				
	Valid N	Mean	Min.	Max.	Std.Dev	Valid N	Mean	Min.	Max.	Std.Dev.
ABRAALBA	503	0.44	0	202	9.04	491	3.38E-05	0	0.0166	0.0007
ABRATENU	503	0,21	0	105	4,69	491	6,33E-05	0	0,0311	0,0014
ACTINIAR	503	0,54	0	135	7,34	491	4,11E-05	0	0,0101	0,0006
ANAIMUCO	503	3,87	0	667	35,32	491	0,0064	0	2,3877	0,1094
ANGUTENU	503	0,36	0	105	5,58	491	5,35E-05	0	0,0119	0,0007
ARENMARI	503	36,49	0	316	59,59	491	2,9224	0	44,3273	6,1465
BATHSPEC	503	476,56	0	11717	1290,12	491	0,0914	0	2,1173	0,2377
BOCCREDE	503	0	0	0	0	491	0	0	0	0
CAPICAPI	503	39,93	0	1751	147,21	491	0,0069	0	0,4569	0,0334
CARCMAEN	503	2,72	0	135	13,53	491	0,0510	0	14,9801	0,6891
CERAEDUL	503	469,18	0	7744	1149,27	503	7,2727	0	276,2029	23,1130
COROAREN	503	137,21	0	12400	840,42	491	0,0276	0	1,9807	0,1664
COROINSI	503	0	0	0	0	491	0	0	0	0
COROLACU	503	0	0	0	0	491	0	0	0	0
COROVOLU	503	176,76	0	24733	1475,90	491	0,0390	0	4,6945	0,3073
CRANCRAN	503	16,47	0	832	57,87	491	0,0258	0	2,7843	0,1680
CYATCARI	503	8,89	0	1430	80,05	491	0,0030	0	0,3600	0,0259
ENSISPEC	503	4,46	0	1279	59,06	491	0,4564	0	221,0000	9,9735
ETEOLONG	503	83,26	0	5051	298,52	491	0,0370	0	1,4427	0,1094
EURYPULC	503	22,97	0	1263	109,04	491	0,0077	0	0,4100	0,0373
GAMMSALI	503	0	0	0	0	491	0	0	0	0
GAMMSPEC	503	0,27	0	67	4,22	491	2,07E-05	0	0,0067	0,0003
GASTSPIN	503	2,10	0	400	22,77	491	0,0019	0	0,4823	0,0271
HARMSPEC	503	0,19	0	67	3,28	491	0,0005	0	0,2483	0,0112
HAUSAREN	503	3,52	0	533	33,44	491	0,0047	0	0,7074	0,0464
HETEFILI	503	6104,14	0	66326	10105,3	491	4,8405	0	61,1950	7,3158
HYDRULVA	503	1304,79	0	26533	2838,17	491	0,4563	0	42,9570	2,4146
LANICONC	503	1,27	0	555	24,91	491	0,0009	0	0,4200	0,0190
MACOBALT	503	351,67	0	8700	663,12	491	2,7441	0	24,2524	4,0935
MAGEPAPI	503	0	0	0	0	491	0	0	0	0
MANAAEST	503	1,90	0	867	38,74	491	2,52E-05	0	0,0106	0,0005
MESOSLAB	503	0	0	0	0	491	0	0	0	0
MICRSPEC	503	0	0	0	0	491	0	0	0	0
MYA_AREN	503	185,26	0	5159	536,27	491	2,6478	0	223,2266	14,5840
MYSEBIDE	503	0,34	0	67	4,41	491	8,97E-05	0	0,0202	0,0012
MYSIDACE	503	0,13	0	67	2,97	491	1,55E-05	0	0,0076	0,0003
MYTIEDUL	503	0,24	0	67	3,56	491	0,0002	0	0,0755	0,0034
NEMERTEA	503	17,74	0	832	67,29	491	0,0215	0	1,6462	0,1004
NEOMINTE	503	0	0	0	0	491	0	0	0	0
NEPHCAEC	503	0,34	0	105	5,55	491	0,0017	0	0,4372	0,0272
NEPHCIRR	503	2,46	0	135	15,59	491	0,0069	0	0,5365	0,0482
NEPHHOMB	503	11,81	0	277	38,97	491	0,1132	0	8,4417	0,6215
NEREDIVE	503	102,61	0	3928	346,52	491	0,5497	0	18,3810	1,7317
NERESUCC	503	269,12	0	3425	571,24	491	0,3047	0	5,7065	0,6916
OLIGOCHA	503	200,14	0	18779	1166,02	491	0,0251	0	2,2887	0,1550
OPHESPEC	503	2,77	0	316	26,00	491	0,0083	0	3,4806	0,1576
PETRPHOL	503	3,23	0	600	38,76	491	0,2159	0	59,4955	3,3714
PLEUGLAB	503	0	0	0	0	491	0	0	0	0
POLYSPEC	503	465,19	0	13867	1737,24	491	0,0425	0	4,1525	0,2244
PYGOELEG	503	2021,36	0	58788	5752,97	491	0,1574	0	5,2890	0,4956
RETUOBTU	503	0,43	0	60	4,22	491	2,42E-05	0	0,0119	0,0005
SCOLARMI	503	22,00	0	421	58,04	491	0,1209	0	3,8142	0,4203
SCOLSQUA	503	4,24	0	555	33,45	491	0,0174	0	2,6069	0,1580
SCROPLAN	503	63,60	0	5267	396,60	491	1,4582	0	186,1820	9,3262
SPIOBOMB	503	0,20	0	67	3,17	491	3,93E-05	0	0,0126	0,0006
SPIOSPEC	503	26,41	0	2867	182,25	491	0,0034	0	0,3101	0,0224
SPISSPEC	503	4,30	0	1414	67,70	491	0,0043	0	2,0875	0,0942
THARMARI	503	497,00	0	10317	1380,41	491	0,0713	0	1,9300	0,2048
SUM	503	13183,9	0	89884	15834,5	491	24,6586	0	317,3023	39,4918

SALINITY REGION 3 - LITTORAL ZONE

	Density					Biomass				
	Valid N	Mean	Min.	Max.	Std.Dev.	Valid N	Mean	Min.	Max.	Std.Dev.
ABRAALBA	485	0	0	0	0	473	0	0	0	0
ABRATENU	485	0	0	0	0	473	0	0	0	0
ACTINIAR	485	0	0	0	0	473	0	0	0	0
ANAIMUCO	485	0,09	0	42	1,90	411	5,1E-05	0	0,0210	0,0010
ANGUTENU	485	0	0	0	0	473	0	0	0	0
ARENMARI	485	4,20	0	277	19,38	411	0,2118	0	12,9483	1,0533
BATHSPEC	485	744,61	0	20183	1900,35	411	0,1282	0	5,2564	0,3557
BOCCREDE	485	0	0	0	0	473	0	0	0	0
CAPICAPI	485	7,07	0	335	29,67	473	0,0020	0	0,3098	0,0172
CARCMAEN	485	2,97	0	335	19,51	411	0,0168	0	1,6000	0,1094
CERAEDUL	485	160,71	0	5878	676,28	423	0,3947	0	21,5707	1,6965
COROAREN	485	376,30	0	38910	2707,89	411	0,0462	0	2,4396	0,2314
COROINSI	485	0	0	0	0	473	2,11E-	0	0,0100	0,0005
COROLACU	485	0,16	0	80	3,63	473	0	0	0	0
COROVOLU	485	1933,07	0	57008	6465,64	411	0,4342	0	17,0000	1,4738
CRANCRAN	485	24,77	0	960	85,09	411	0,0237	0	3,3743	0,1742
CYATCARI	485	216,22	0	7671	937,40	411	0,1031	0	2,3893	0,3548
ENSISPEC	485	1,29	0	67	7,58	473	0,0025	0	0,6598	0,0324
ETEOLONG	485	130,55	0	11402	848,62	411	0,0534	0	2,3096	0,1997
EURYPULC	485	30,63	0	1173	123,86	411	0,0174	0	0,8350	0,0765
GAMMSALI	485	0,22	0	67	3,57	473	9,45E-	0	0,0335	0,0016
GAMMSPEC	485	2,73	0	159	15,37	473	9,67E-	0	0,0252	0,0013
GASTSPIN	485	0,13	0	25	1,44	411	7,96E-	0	0,0269	0,0013
HARMSPEC	485	0	0	0	0	473	0	0	0	0
HAUSAREN	485	15,92	0	1089	72,65	411	0,0274	0	1,0228	0,1072
HETEFILI	485	2800,88	0	33911	5436,03	411	2,6080	0	43,4419	5,1236
HYDRULVA	485	289,87	0	9599	957,23	411	0,0802	0	2,8091	0,2646
LANICONC	485	0	0	0	0	473	0	0	0	0
MACOBALT	485	372,31	0	7522	808,33	411	1,3031	0	28,2325	2,6400
MAGEPAPI	485	0,22	0	67	3,53	411	9,28E-	0	0,0341	0,0017
MANAAEST	485	80,94	0	26497	1220,09	473	0,0004	0	0,0740	0,0038
MESOSLAB	485	0,54	0	42	3,88	473	0,0001	0	0,0117	0,0010
MICRSPEC	485	0	0	0	0	473	0	0	0	0
MYA_AREN	485	87,98	0	4352	395,56	411	0,2527	0	13,1735	1,1234
MYSEBIDE	485	0,22	0	67	3,53	473	3,10E-	0	0,0120	0,0006
MYSIDACE	485	0,45	0	67	3,76	411	0,0002	0	0,0140	0,0014
MYTIEDUL	485	0,08	0	26	1,26	411	0,0003	0	0,1167	0,0058
NEMERTEA	485	14,87	0	755	56,78	411	0,0089	0	0,4820	0,0407
NEOMINTE	485	0,16	0	67	3,05	411	7,71E-	0	0,0208	0,0011
NEPHCAEC	485	0,16	0	50	2,54	473	0,0002	0	0,0433	0,0024
NEPHCIRR	485	0,08	0	17	0,93	411	0,0003	0	0,0675	0,0039
NEPHHOMB	485	0,83	0	84	6,89	411	0,0069	0	1,6813	0,0911
NEREDIVE	485	348,54	0	4333	775,96	411	1,0085	0	27,4978	2,4658
NERESUCC	485	88,30	0	3800	310,80	411	0,0998	0	2,8000	0,2947
OLIGOCHA	485	354,55	0	20063	1653,38	411	0,0208	0	2,9887	0,1551
OPHESPEC	485	0,02	0	9	0,41	473	0	0	0	0
PETRPHOL	485	7,41	0	1800	90,58	473	0,0393	0	17,0103	0,7828
PLEUGLAB	485	0	0	0	0	411	0	0	0	0
POLYSPEC	485	390,78	0	17190	1535,32	411	0,0518	0	2,2132	0,1811
PYGOELEG	485	4427,74	0	191478	14521,9	411	0,3737	0	11,0620	1,0055
RETUOBTU	485	0	0	0	0	473	0	0	0	0
SCOLARMI	485	0,37	0	99	5,77	411	9,73E-	0	0,0040	0,0002
SCOLSQUA	485	0,19	0	42	2,71	473	0,0002	0	0,0796	0,0039
SCROPLAN	485	38,08	0	951	138,65	411	1,0759	0	63,5364	4,4074
SPIOBOMB	485	0,37	0	154	7,09	473	9,30E-	0	0,0040	0,0002
SPIOSPEC	485	1,16	0	92	7,53	411	0,0002	0	0,0126	0,0012
SPISSPEC	485	1,13	0	267	14,97	473	1,73E-	0	0,0058	0,0003
THARMARI	485	17,84	0	6101	278,74	411	0,0077	0	2,4522	0,1214
SUM	485	12996,3	0	225567	22012,8	411	8,4655	0	101,5968	12,7020

SALINITY REGION 4 - LITTORAL ZONE

	Density					Biomass				
	Valid N	Mean	Min.	Max.	Std.Dev.	Valid N	Mean	Min.	Max.	Std.Dev.
ABRAALBA	287	0	0	0	0	287	0	0	0	0
ABRATENU	287	0	0	0	0	287	0	0	0	0
ACTINIAR	287	0	0	0	0	287	0	0	0	0
ANAIMUCO	287	0	0	0	0	287	0	0	0	0
ANGUTENU	287	0	0	0	0	287	0	0	0	0
ARENMARI	287	0	0	0	0	287	0	0	0	0
BATHSPEC	287	63,45	0	9138	590,29	287	0,0066	0	0,6791	0,0507
BOCCREDE	287	165,05	0	47368	2796,04	287	0	0	0	0
CAPICAPI	287	0,27	0	42	3,22	287	0,0002	0	0,0503	0,0030
CARCMAEN	287	0	0	0	0	287	0	0	0	0
CERAEDUL	287	0,45	0	45	4,38	287	2,92E-05	0	0,0042	0,0003
COROAREN	287	1,68	0	252	17,73	287	0,0005	0	0,0660	0,0049
COROINSI	287	0	0	0	0	287	0	0	0	0
COROLACU	287	0,15	0	42	2,47	287	3,48E-07	0	0,0001	5,90E-06
COROVOLU	287	4408,46	0	51350	6771,95	287	1,0181	0	8,6813	1,5647
CRANCRAN	287	4,81	0	126	16,90	287	0,0101	0	0,8132	0,0698
CYATCARI	287	0,73	0	84	7,40	287	0,0006	0	0,1132	0,0071
ENSISPEC	287	0	0	0	0	287	0	0	0	0
ETEOLONG	287	3,18	0	133	16,06	287	0,0019	0	0,1190	0,0113
EURYPULC	287	2,26	0	126	13,07	287	0,0010	0	0,0671	0,0063
GAMMSALI	287	0,44	0	84	5,52	287	1,46E-05	0	0,0021	0,0002
GAMMSPEC	287	0,93	0	267	15,74	287	3,75E-05	0	0,0108	0,0006
GASTSPIN	287	0	0	0	0	287	0	0	0	0
HARMSPEC	287	0	0	0	0	287	0	0	0	0
HAUSAREN	287	0	0	0	0	287	0	0	0	0
HETEFILI	287	1592,46	0	25150	3689,12	287	1,2631	0	15,2579	2,6526
HYDRULVA	287	35,21	0	1333	125,43	287	0,0072	0	0,2096	0,0197
LANICONC	287	0,23	0	67	3,97	287	0	0	0	0
MACOBALT	287	337,20	0	4066	530,50	287	0,4123	0	4,8194	0,7035
MAGEPAPI	287	0	0	0	0	287	0	0	0	0
MANAAEST	287	246,80	0	38879	2407,35	287	0,0023	0	0,3982	0,0245
MESOSLAB	287	0,23	0	67	3,94	287	9,92E-06	0	0,0028	0,0002
MICRSPEC	287	0	0	0	0	287	0	0	0	0
MYA_AREN	287	3,34	0	210	20,24	287	0,0020	0	0,3322	0,0205
MYSEBIDE	287	0	0	0	0	287	0	0	0	0
MYSIDACE	287	0	0	0	0	287	0	0	0	0
MYTIEDUL	287	0	0	0	0	287	0	0	0	0
NEMERTEA	287	3,68	0	335	23,88	287	0,0030	0	0,1677	0,0188
NEOMINTE	287	0	0	0	0	287	0	0	0	0
NEPHCAEC	287	0	0	0	0	287	0	0	0	0
NEPHCIRR	287	0	0	0	0	287	0	0	0	0
NEPHHOMB	287	0	0	0	0	287	0	0	0	0
NEREDIVE	287	1573,13	0	6983	1648,00	287	3,4908	0	49,5860	5,1599
NERESUCC	287	7,78	0	667	45,68	287	0,0169	0	1,5006	0,1205
OLIGOCHA	287	3084,94	0	72997	7008,45	287	0,2588	0	5,0804	0,5281
OPHESPEC	287	0	0	0	0	287	0	0	0	0
PETRPHOL	287	0,15	0	42	2,47	287	7,30E-05	0	0,0210	0,0012
PLEUGLAB	287	0	0	0	0	287	0	0	0	0
POLYSPEC	287	15,48	0	606	61,92	287	0,0028	0	0,0808	0,0111
PYGOELEG	287	145,38	0	8740	710,81	287	0,0120	0	0,5942	0,0470
RETUOBTU	287	0	0	0	0	287	0	0	0	0
SCOLARMI	287	0	0	0	0	287	0	0	0	0
SCOLSQUA	287	0	0	0	0	287	0	0	0	0
SCROPLAN	287	1,28	0	84	8,43	287	0,0296	0	2,3306	0,2088
SPIOBOMB	287	0	0	0	0	287	0	0	0	0
SPIOSPEC	287	0	0	0	0	287	2,92E-05	0	0,0084	0,0005
SPISSPEC	287	0	0	0	0	287	0	0	0	0
THARMARI	287	0,23	0	67	3,94	287	2,92E-06	0	0,0008	4,95E-05
SUM	287	11700,6	0	92430	11928,4	287	6,5405	0	52,3739	6,4782

PART TWO

Ecoprofiles for 20 macrobenthic species of the Schelde estuary

INTRODUCTION

In Part Two the detailed ecoprofiles for 20 macrobenthic species of the Schelde estuary is given. Each profile consists of the following parts:

- INTRODUCTION: short summary of the importance of the species in the Schelde estuary
- AUTO-ECOLOGY: short literature review on the auto-ecology of the species, with focus on habitat preferences, feeding habits and population dynamics. This auto-ecology aimed not at a complete overview of all available literature on the species, but focused on the relevant literature for this study. Information on effects of pollution, ecotoxicology, etc. was not included in the auto-ecology. More extended reviews are given for *Cerastoderma edule*, *Corophium volutator*, and *Macoma balthica.*
- OCCURRENCE IN THE SCHELDE ESTUARY: gives an overview for each species of the occurrence (presence/absence, abbreviated p/a), density and biomass in the Schelde estuary in relation to salinity and depth. Also the seasonal variation, presented as a spring versus autumn comparison, was made for each species. Geographical distribution maps (presence/absence and density/biomass) of each species in the Schelde estuary are also presented.
- RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE: For each species a (stepwise) logistic regression model for binary (presence/absence) data was performed on the following abiotic variables separately:
    - model salinity and temporal salinity: both were treated together and presented in one table and figure. Salinity was expressed as psu.
    - depth: A positive sign was used to indicated depths below NAP, whereas a negative sign was used to indicate depths above NAP. However, to make all depth values positive (as we worked also with the quadratic term), +2.5 m NAP was added to each value and therefore the data are presented as m NAP + 2.5m. To know the real height +2.5m NAP should be subtracted.
    - maximum ebb (maxeb) and flood (maxfl) current velocity: expressed as $m.s^{-1}$; both were treated together and presented in one table and figure.
    - median grain size and mud content: both were treated together and presented in one table and figure. As mud content was expressed as the volume percentage < 63 μm, the corresponding curve on the accompanying figure only relates to the 0-100 part of the x-axis, whereas median grain size is expressed as μm and the corresponding curve on the figure relates to the complete range of the x-axis.

  For each abiotic variable the regression coefficients (+ standard error) are given, together with the concordance, which gives an indication of the performance of the model based on the association of predicted probabilities and observed responses. Also the fitted response curve is presented in an accompanying figure. No legend is added to these standard tables and figures, with the interpretation implied in the accompanying text.
- MULTIPLE STEPWISE LOGISTIC REGRESSION: For each macrobenthic species a multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run separately with and without sediment data. The regression coefficients for both models are presented in a table, together with the concordance (see above). To evaluate the performance of the model, an internal validation was performed, giving comparative statistics on the predicted and observed occurrence of each species, together with a Fisher exact test.

For a detailed description of the statistical analysis used, see Material & Methods in Part one of this report.

An ecoprofile was constructed for the following 20 macrobenthic species of the Schelde estuary, presented in alphabetic order:

Figures and tables are numbered per macrobenthic species, e.g. Figure 6.1. is the first figure in the ecoprofile on *Corophium volutator*.

ECOPROFILE OF ARENICOLA MARINA

INTRODUCTION

Arenicola marina is one of the largest macrobenthos species found in the Schelde estuary. Compared to other coastal areas, e.g. Oosterschelde and Wadden Sea, *A. marina* is less common in the Schelde estuary, contributing 4.6 % and 11.9 % to the total intertidal biomass of the polyhaline salinity regions 1 and 2 respectively.

AUTO-ECOLOGY

ARENICOLA MARINA	Annelida, Polychaeta

General

The lugworm *A. marina* is a common species in the intertidal zone of coastal areas and estuaries. It is a large species and reaches relatively high ages (5 to 6 years at least). In the Wadden Sea *A. marina* is by far the most important polychaete species, accounting for no less than 20% of the total macrozoobenthic biomass (BEUKEMA, 1976). The tails of *A. marina* are an important food source for fish (e.g. plaice *Pleuronectes platessa*) (DE VLAS, 1979a,b; BERGMAN *et al*., 1988).

Habitat preferences

Salinity: *A. marina* prefers euryhaline to mesohaline salinity conditions up to 21 psu. The species can occur up to salinities of ± 9 psu. (BRENNING, 1965; KOSLER, 1969; WOLFF, 1973).

Sediment type and tidal elevation: Highest densities of adult *A. marina* are observed where intermediate values of level and silt contents coincide (BEUKEMA & DE VLAS, 1979). Numerical densities as well as biomass values showed a bell-shaped relationship to both silt percentages and heights in the tidal zone (BEUKEMA & DE VLAS, 1979). For juvenile lugworms, the highest densities are found at higher tidal levels.

Feeding

A. marina lives in J-shaped tubes, 20 to 40 cm deep (JAKOBSEN, 1967; DE WILDE & FARKE, 1983). The animal occurs most of its time in the undermost, horizontal part of the tube and inhales water and sediment, leading to the typical funnel-shaped holes at the sediment surface (DE WILDE & FARKE, 1983). *A. marina* is a selective deposit feeder, feeding mainly on benthic microalgae and bacteria (RIJKEN, 1979; DE WILDE & FARKE, 1983). During feeding *A. marina* selects the smaller particles (<300-400μm) (BAUMFALK, 1979), whereas the larger particles are pushed out, forming the typical, so-called 'Hydrobia layer' (VAN STRAATEN, 1956 and SHÄFER, 1962, in CADÉE, 1976) at the sediment surface. *A. marina* is therefore one of the most important bioturbaters and reworkers of the sediment (CADÉE, 1976). As an important bioturbater, A. marina has a large impact on the microbial communities and biochemical activities in the sediment (REISE, 1985; REICHARDT, 1988) and on the remobilization of nutrients (Asmus, 1986). Settlement of macrobenthic larvae and juveniles may be hampered by the activity of sediment reworking invertebrates, such as *Arenicola marina* (FLACH, 1992).

Population dynamics and life history

The time of spawning differs between areas, but mostly occurs in autumn (WOLLF, 1973; DE WILDE & BERGHUIS, 1979; POLLACK, 1979). The adult females lay the eggs in the horizontal part of the tube. The eggs are fertilised by spermatozoids which are inhaleted from the watercolumn into the tube (FARKE & BERGHUIS, 1979a). After a month the larvae leave the tubes and migrate to the lower part of the intertidal zone or even to the subtidal zone (FARKE & BERGHUIS, 1979b). The next summer (first settlement) the juveniles migrate back through passive transport to the higher parts of the intertidal zone (FARKE *et al*., 1979). After this first settlement, a resettllement occurs almost one year later towards lower levels and coarser sediments (BEUKEMA & DE VLAS, 1979).

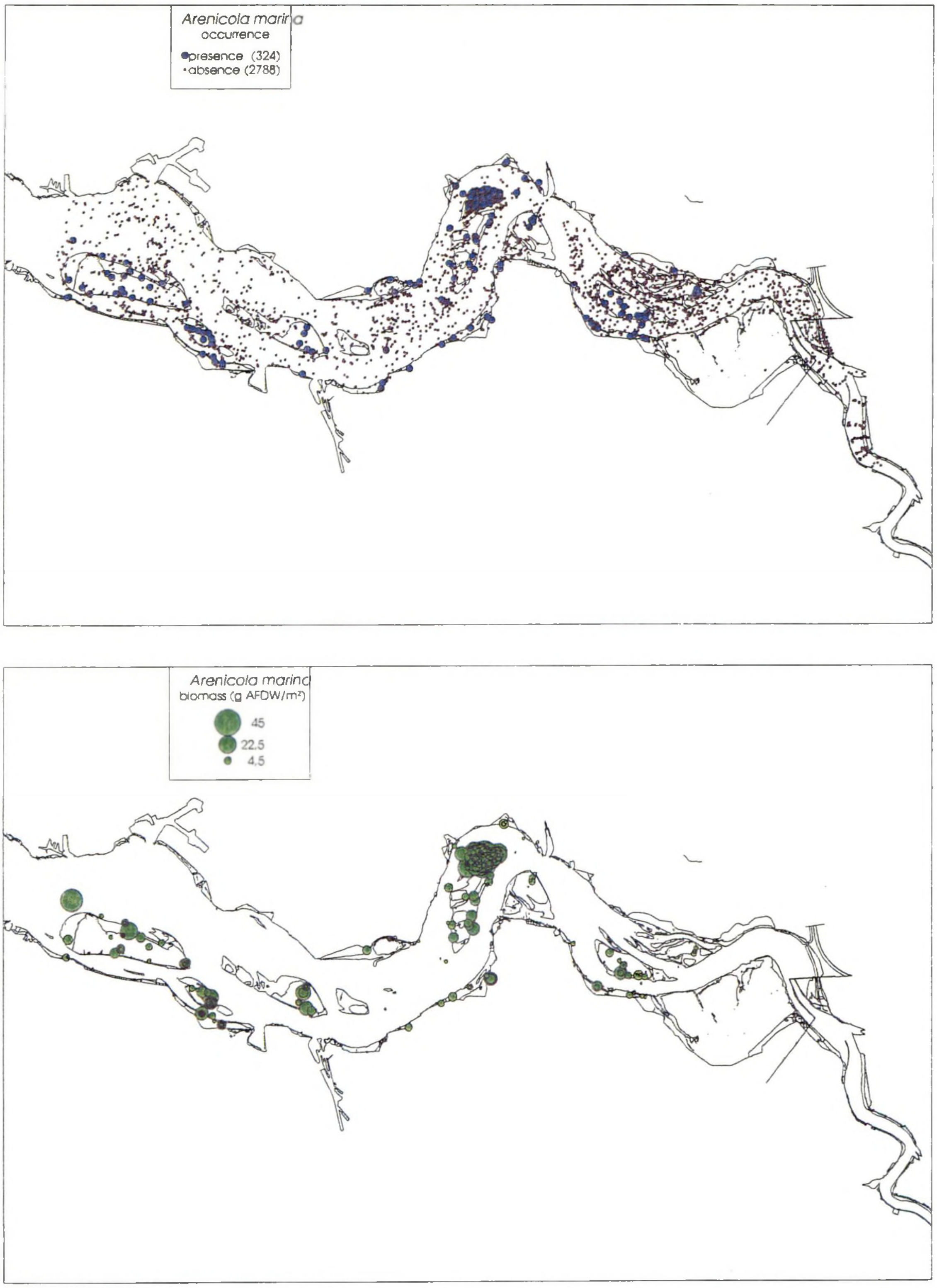


Figure 1.2. Geographical distribution maps of Arenicola marina in the Schelde estuary with presence/absence data (top) and biomass (g AFDW m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

The presence of *A. marina* is mainly restricted to the polyhaline (salinity region 1 and 2), littoral zone (Table 1.1). In the α-mesohaline, intertidal zone (salinity region 3), the species is observed irregularly, and in the β-mesohaline zone (salinity region 4) the species is completely absent. In the subtidal zone *A. marina* was hardly observed.

Both mean biomass and density were highest in salinity region 2 (Figure 1.1). In salinity region 3 biomass and density were very low. *A. marina* contributes 4.6 % and 11.9 % to the total intertidal biomass of the polyhaline salinity regions 1 and 2 respectively.

The geographical distribution of *A. marina* in the Schelde estuary is shown in Fig. 1.2.

Table 1.1. Occurrence (p/a) of A. marina along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
littoral	30,2 % (n=262)	37,0 % (n= 503)	9,1 % (n=485)	0,0 % (n= 287)
undeep subtidal	2,7 % 'n=151)	1,3 % (n=153)	0,8 % (n=127)	0,0 % (n=51)
deep subtidal	0,0 % (n=123)	3,9 % (n=130)	0,0 % (n=112)	0,0 % (n=67)
channel	0,5 % (n=186)	1,2 % (n=173)	0,0 % (n=232)	0,0 % (n=70)

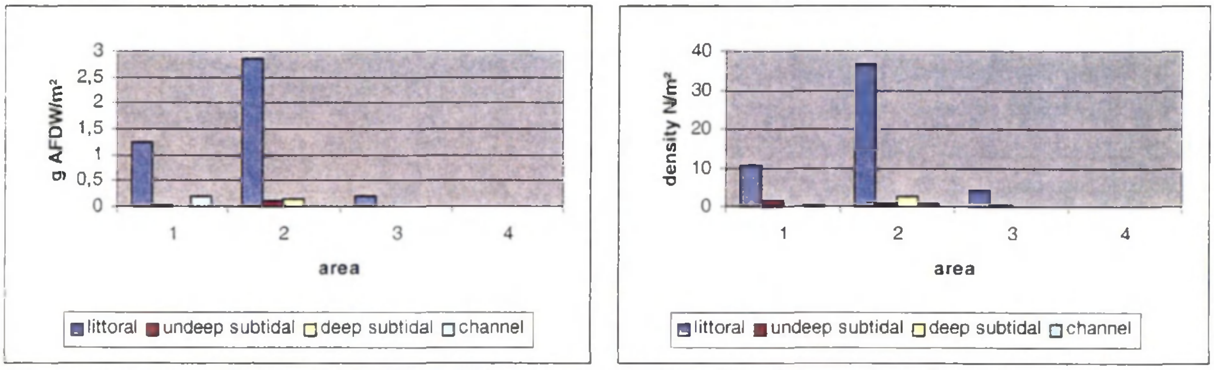


Figure 1.1. Mean density (ind m^{-2}) and biomass (g AFDW m^{-2}) of A. marina along the salinity and depth gradient in the Schelde estuary (area: 1&2: polyhaline zone; 3&4: mesohaline zone).

Seasonal variations: spring versus autumn occurrence

In the polyhaline zone *A. marina* was observed more frequently in spring as compared to autumn, resulting in a higher spring density and biomass (Table 1.2). In the β-mesohaline zone (salinity region 3) the opposite was observed, with a higher occurrence, density and biomass in autumn, which probably is explained by the lower salinities occurring in winter and spring in this salinity region, which caused more unfavourable conditions for this species.

Table 1.2. Spring (March - May) versus autumn (Augustus - October) occurrence (p/a), density (ind m^{-2}) and biomass (g AFDW m^{-2}) of A.marina in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone).

LITTORAL		1	2	3	4
Presence	Spring	34,0 % (n=97)	46,8 % (n= 169)	5,4 % (n=147)	0,0 % (n= 33)
	Autumn	28,2 % (n=135)	30,3 % (n=218)	10,4 % (n=249)	0,0 % (n= 214)
Density	Spring	13	51	4	0
	Autumn	9	25	5	0
Biomass	Spring	1,71	3,84	0,12	0
	Autumn	0,92	1,89	0,26	0

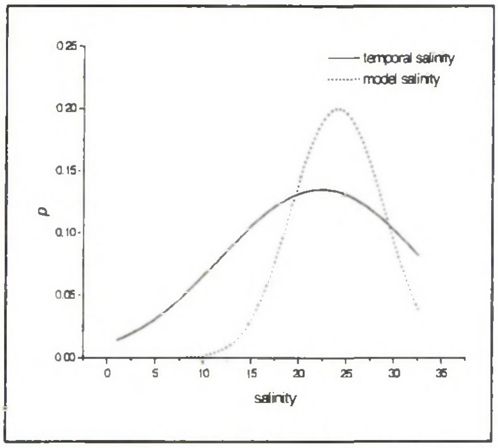
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed.

Model salinity and temporal salinity

Both the linear and quadratic term were included in both salinity models, giving unimodal response curves for both models. An optimum is observed in the polyhaline zone, being around 24 psu and 22 psu for 'model salinity' and 'temporal salinity' respectively. The 'model salinity' model showed a more narrow tolerance with an optimum which shifted towards a higher salinity as compared to the 'temporal salinity' model. The 'temporal salinity' model showed a much broader response curve, extending into the mesohaline zone. This difference was probably the result of the lower salinities occurring in winter and spring in the poly-/mesohaline zone, which were dedected with the 'temporal salinity' model (see Material & Methods), and not with the 'model salinity' model, since this model does not take into account seasonal variations of salinity. It seems that *A. marina* can withstand temporarily lower salinities (the species was frequently observed in spring, see Table 1.2), but the model does not say anything about how long *A. marina* can cope with these lower salinities.

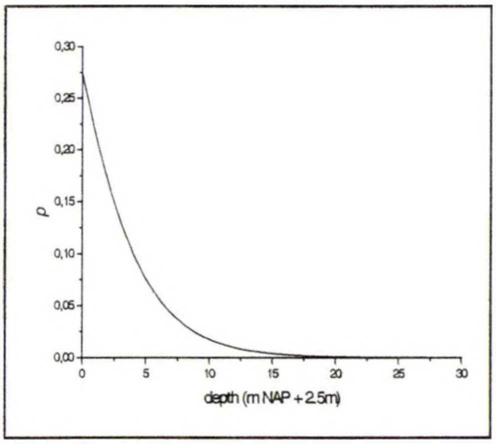
Arenicola marina	*Term*	*Regression coefficient*	*Standard error*
Present: 324			
Absent: 2788			
	intercept	-4,4876	0,4616
	Model salinity	0,2359	0,0502
	Model salinity²	-0,00529	0,00129
	concordance	56,90%	
	intercept	-16,0576	1,5543
	Temporal salinity	1,2208	0,1362
	Temporal salinity²	-0,0254	0,00293
	concordance	71,40%	



Depth

Only the linear term of depth was included in the model, giving a linear logit curve for depth. As *A. marina* was typically observed in the intertidal zone (see Table 1.1), a steep decreasing response was observed with increasing depth.

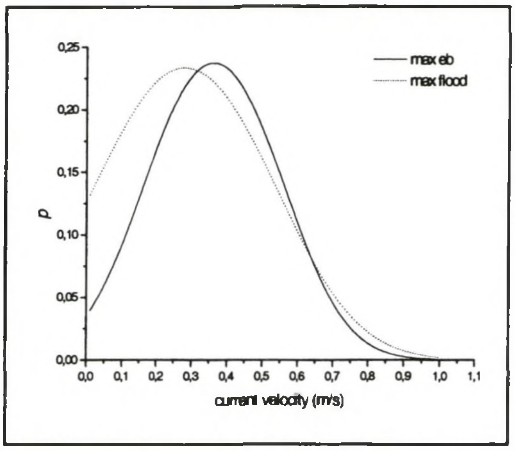
Arenicola marina	*Term*	*Regression coefficient*	*Standard error*
Present: 275			
Absent: 2599			
	intercept	-0,9723	0,0989
	depth	-0,3062	0,0275
	depth²	-	-
	concordance	74,80%	



Maximum ebb and flood current velocities

Both the linear and quadratic terms were included in the maximum ebb and flood current velocity models. This resulted in unimodal response curves for maximum ebb and flood current velocity with an optimum around 0.36 and 0.275 m.s^{-1} respectively.

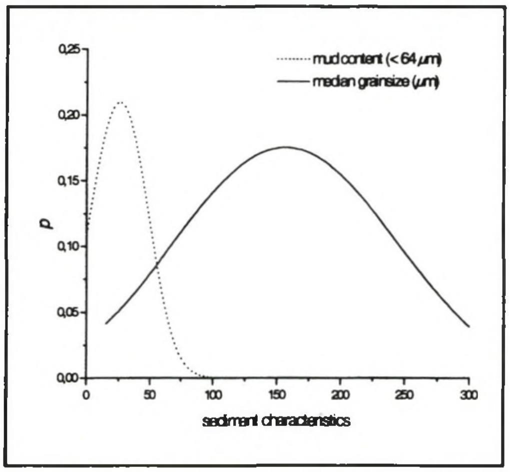
Arenicola marina	*Term*	*Regression coefficient*	*Standard error*
Present: 313 Absent: 2724			
	Intercept	-3,3084	0,3621
	Maxeb	11,8410	1,7419
	Maxeb²	-16,3873	1,9876
	Concordance	78,00%	
	Intercept	-1,9378	0,2319
	Maxfl	5,3515	1,2111
	Maxfl²	-9,5841	1,3902
	Concordance	78,90%	



Sediment characteristics: median grainsize µm) and mud content (%)

Both the linear and quadratic term were included in the median grain size model and the mud content model. *A. marina* clearly prefered fine sandy sediments, showing unimodal response curves for median grain size with an optimum at ± 155 µm and for mud content with an optimum of 25%. However, *A. marina* showed a relatively broad tolerance and only in very coarse or very muddy sediments the chance of observing this species was very small.

Arenicola marina	*Term*	*Regression coefficient*	*Standard error*
Present: 186 absent: 1200			
	intercept	-3,5036	0,4026
	median	0,0250	0,0518
	median²	-0,00008	0,000016
	concordance	62,60%	
present: 172 absent: 1121			
	intercept	-2,0977	0,1333
	mud	0,0600	0,0146
	mud²	-0,00117	0,000257
	concordance	63,90%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, linear and/or quadratic terms of all abiotic variables were included in the model (Table 1.3), with the linear term of maximum flood current velocity (maxfl), the linear and quadratic term of model salinity and the linear term of depth adding most to the change in deviance. The model with sediment characteristics performed slightly better, with the linear term of model salinity, the linear term of maximum flood current velocity (maxfl), the quadratic term of temporal salinity and the linear term of depth adding most to the change of deviance in the model.

Table. 1.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Arenicola marina	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment presence: 269 absence: 2558			with sediment Presence: 172 Absence: 1121		
	intercept	-13,4934	1,7360	Intercept	-9,3460	0,9117
	Temporal salinity^2	-0,00099	0,000497	Temporal salinity^2	-0,00260	0,000701
	Model salinity	1,0284	0,1600	Model salinity	0,2921	0,0361
	Model salinity^2	-0,0194	0,00360	Depth	1,4338	0,3824
	Depth	-0,2633	0,0559	Depth^2	-0,3155	0,0785
	Depth^2	0,00438	0,00155	Maxeb	3,0047	1,0111
	Maxeb	5,4847	1,9563	Maxfl	-3,3583	0,7804
	Maxeb^2	-6,6295	2,0977	Median	0,0208	0,00625
	Maxfl	-1,9627	0,4712	Median^2	-0,00007	0,000018
	concordance	88,8%		Concordance	90,8%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 89,5 % of the responses correctly (Table 1.4). However, only 44,6 % of the modelled (or predicted) presences were also actually observed in the field. When including sediment characteristics in the model, this percentage increased up to 50,6 %.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 1.4. Comparative statistics on the predicted and observed occurrence of A. marina in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model). Fisher exact one-tailed test (observed by model: Po<Ao).

Arenicola marina (p=0,354)
(without sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	120	149	**269**	44,6
Ao	149	2409	**2558**	94,2
Total	**269**	**2558**	**2827**	89,5

Difference between proportions	0,388	
95% CI	-1,000 to 0,438	(normal approximation)
Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)	

Arenicola marina (p=0,364)
(with sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	87	85	**172**	50,6
Ao	85	1036	**1121**	92,4
Total	**172**	**1121**	**1293**	86,9

Difference between proportions	0,430	
95% CI	-1,000 to 0,494	(normal approximation)
Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)	

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ECOPROFILE OF BATHYPOREIA SPP.

INTRODUCTION

The genus *Bathyporeia* is, together with the genus *Corophium*, by far the most frequently observed group of Arthropoda (Amphipoda) in the estuarine sediments of the Schelde estuary. Despite *Bathyporeia spp.* (mainly determined as *B. pilosa*) was a common and widespread species in the Schelde estuary, its density and biomass were in general very low and therefore its contribution to the total system biomass was also very low. Only in the subtidal part of the α-mesohaline *zone Bathyporeia spp.* makes up ± 20% of the total density observed.

AUTO-ECOLOGY

BATHYPOREIA SPP.	Arthropoda, Amphipoda, Haustoriidae

General

As the genus *Bathyporeia* is a difficult group in terms of determination, and as this genus was not always determined at species level, all individuals belonging to the genus *Bathyporeia* were lumped to *Bathyporeia spp.* However, by far most individuals were determined as *Bathyporeia pilosa*. Other species observed *were Bathyporeia sarsi, Bathyoreia pelagica, Bathyporeia elegans*. The auto-ecology given here is therefore mainly based on *Bathyporeia pilosa* literature.

Bathyporeia spp. is a benthic amphipod, widely distributed in the shallow coastal areas of the North Temperate Zone. This euryhaline species lives in the sediment, but does not built permanent tubes. The animals move through the top layer of the sediment but can also been observed crawling at the sediment surface (LINKE, 1939).

Habitat preferences

Salinity: *Bathyporeia pilosa* is a euryhaline species which enters the estuary up to the mesohaline zone (LELOUP & KONIETZKO, 1956; VADER, 1965). *B. pilosa* is very tolerant to low salinities (SEGERSTRALE, 1943), which was also observed in experimental studies of PREECE (1970).

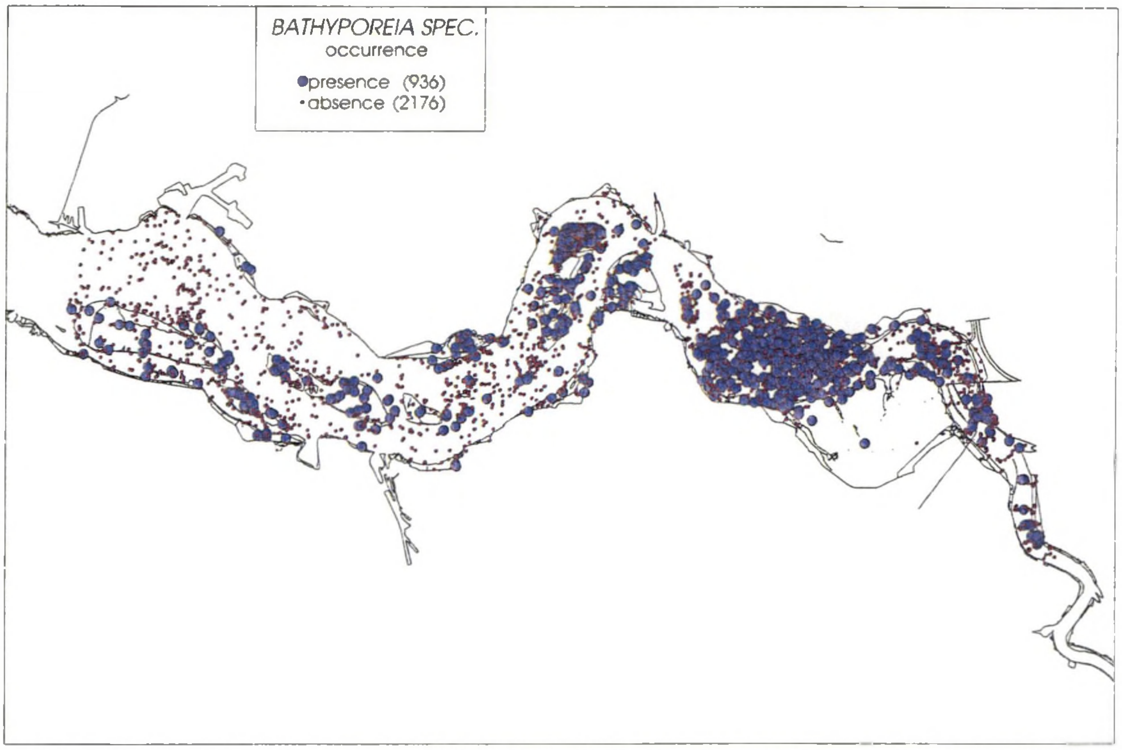
Sediment type: The preferred substratum of *Bathyporeia spp.* are sandy (< 210 μm), well sorted sediments, with a mud content of up to 25% (DAHL, 1952; VADER, 1965; FISH & PREECE, 1970; BOYDEN & LITTLE, 1973; SHACKLEY, 1981). Field investigations performed by KHAYRALLAH & JONES (1980) showed that *B. pilosa* rarely occurs in sediments with a median particle diameter outside the range 150-220 μm or with a silt and clay content greater than 2%. *Haustoriidae*, to which *Bathyporeia* belonges, have developed a body which allow them to survive in unstable sediments (BOUSFIELD, 1970). They are capable of very fast swimming and digging (CROKER, 1967; NICOLAISEN & KANNEWORFF, 1969; SAMEOTO, 1969) and therefore *Bathyporeia spp.* is a typical inhabitant of unstable, sandy sediments (KHAYRALLAH & JONES, 1980) and exposed beaches with a lot of wave action (SHACKLEY, 1981). B. pilosa prefers more sheltered areas as compared to B. sarsi and B. pelagica (VADER, 1965; NICOLAISEN & KANNEWORFF, 1969).

Feeding

The feeding of the genus *Bathyporeia* may be considered as selective deposit feeders. They feed by cleaning sand grains from adhering micro-organisms and detritus (NICOLAISEN & KANNEWORFF, 1969; SÜNDBACK & PERSSON, 1981).

Population dynamics and life history

Bathyporeia pilosa is generally believed to be bivoltine, , with a long-lived overwintering generation, reproducing in spring and a short-lived spring-summer generation, reproducing in summer (FISH & PREECE, 1970; FISH, 1975; POWELL & MOORE, 1991). Reproductive cycles are closely linked with photoperiod, and environmental temperature dependent (SALVAT, 1967; POWELL & MOORE, 1991), and during that period the species is often observed swimming (e.g. PREECE, 1971).



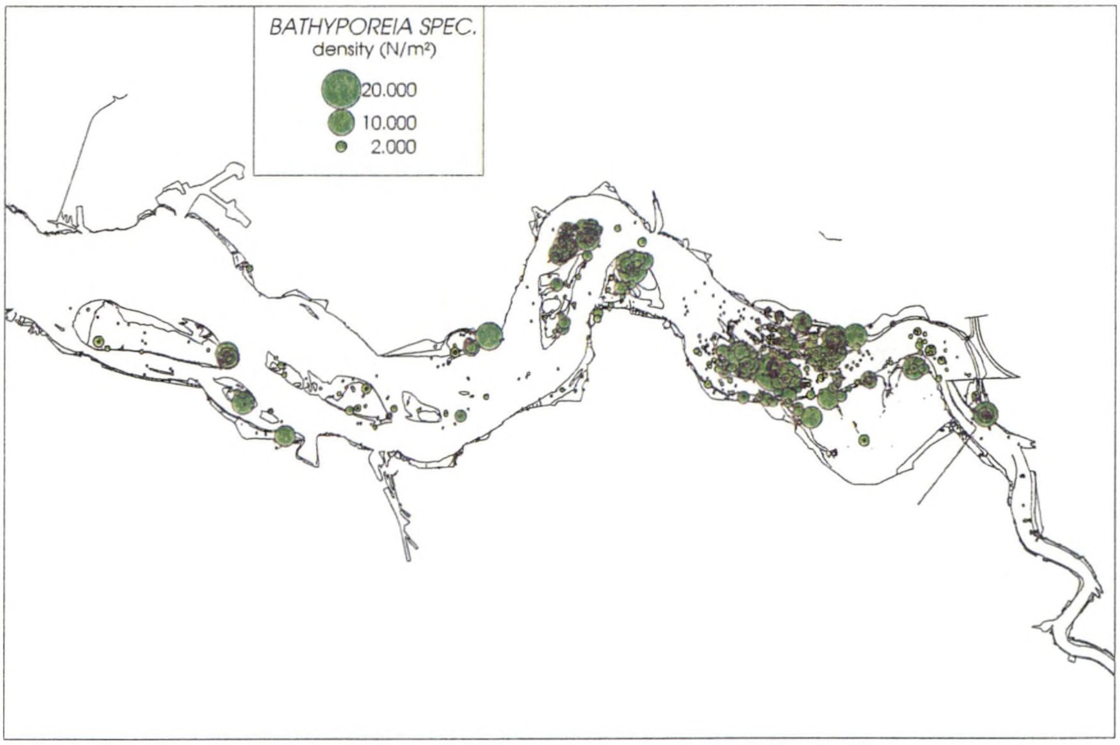


Figure 2.2 Geographical distribution maps of Bathyporeia spp. in the Schelde estuary with presence/absence data (top) and density (ind m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

Bathyporeia spp. occurred along the whole salinity gradient of the Schelde estuary, with a clear optimum in the α-mesohaline zone (salinity region 3) (Table 2.1). In the polyhaline zone *Bathyporeia spp.* clearly preferred the intertidal zone, whereas in the α-mesohaline zone this species was observed frequently in all depth strata. In the β-mesohaline zone *Bathyporeia spp.* showed an opposite trend, with a higher occurrence in the subtidal zone. Both biomass and density showed a same trend, with an increase from salinity region 1 towards salinity region 3 and highest densities in the intertidal zone (Figure 2.1). However, in the subtidal of the α-mesohaline *zone Bathyporeia spp.* makes up ± 20% of the total density observed. In salinity region 4 overall density and biomass was low. The geographical distribution of *Bathyporeia* in the Schelde estuary is shown in Fig. 2.2.

Table 2.1. Occurrence (p/a) of Bathyporeia spp. along the salinity and depth gradients of the Schelde estuary. N=number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	32,8 % (n=262)	46,1 % (n= 503)	57,3 % (n=485)	7,7 % (n= 287)
Undeep subtidal	6,0 % 'n=151)	13,1 % (n=153)	54,3 % (n=127)	17,6 % (n=51)
Deep subtidal	3,3 % (n=123)	7,7 % (n=130)	48,2 % (n=112)	17,9 % (n=67)
Channel	1,1 % (n=186)	6,4 % (n=173)	43,1 % (n=232)	25,7 % (n=70)

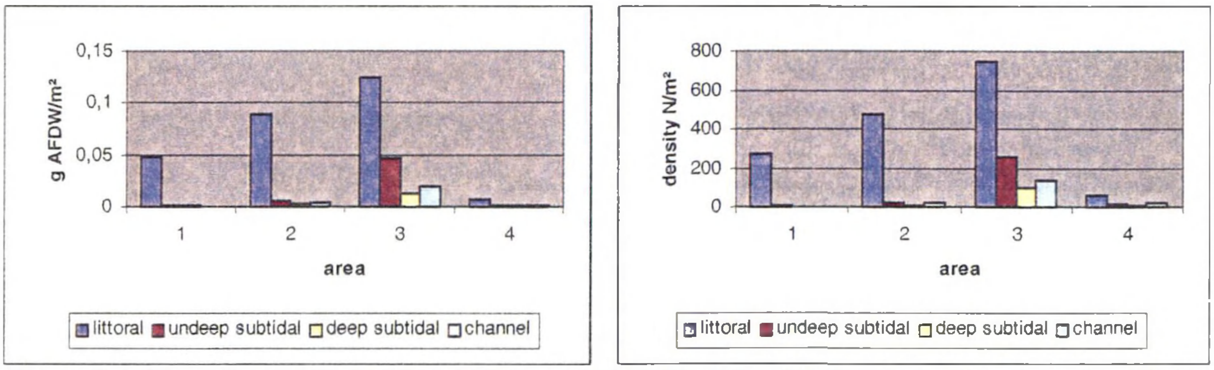


Figure 2.1. Mean density (ind m⁻²) and biomass (g AFDW m⁻²) of Bathyporeia spp. along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

Bathyporeia spp. was more frequently observed in spring as compared to autumn, except in salinity region 4 (Table 2.2). Mean density and biomass were comparable in both seasons.

Table 2.2. Spring (Mar-May) versus autumn (Aug-Oct) occurrence (presence/absence), density (ind m⁻²) and biomass (g AFDW m⁻²) of Bathyporeia spp. in the littoral zone of the Schelde estuary. (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone).

LITTORAL		1	2	3	4
Presence	Spring	40,2 % (n=97)	57,4 % (n= 169)	62,6 % (n=147)	3,0 % (n= 33)
	Autumn	31,1 % (n=135)	32,6 % (n=218)	53,4 % (n=249)	8,9 % (n= 214)
Density	Spring	307	546	628	1,3
	Autumn	294	348	807	85
Biomass	Spring	0,0674	0,1369	0,1259	0,00025
	Autumn	0,0424	0,0481	0,1160	0,0088

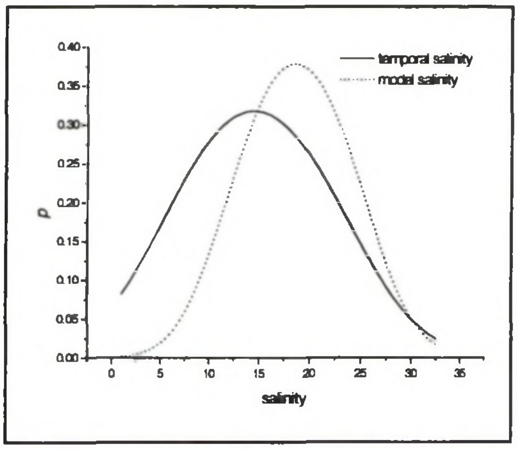
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Both the linear and quadratic term were included in both salinity models, giving unimodal response curves for both models. A clear optimum is observed in the α-mesohaline zone, being around 14 psu and 18 psu for temporal salinity and model salinity respectively. Temporal salinity showed an optimum which shifted towards a lower salinity, which probably was the result of a higher frequency of occurrence of *Bathyporeia spp.* in spring (especially in the littoral zone), when in general lower (termporal) salinities are observed. This was already indicated by Table 2.2., where in the littoral zone *Bathyporeia spp.* was more frequently observed in spring.

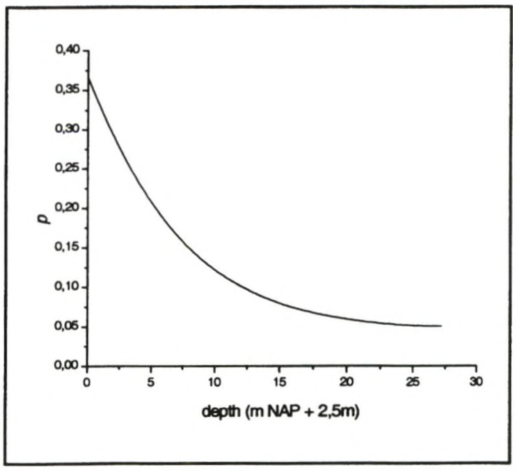
Bathyporeia spp.	*Term*	*Regression coefficient*	*Standard error*
present: 670 absent: 2442			
	Intercept	-2,6619	0,2674
	Temporal salinity	0,2620	0,0334
	Temporal salinity^2	-0,00905	0,000969
	Concordance	64,50%	
	Intercept	-6,9094	0,4742
	Model salinity	0,6907	0,0506
	Model salinity^2	-0,0186	0,00130
	concordance	69,70%	



Depth

Both the linear and quadratic term was included in the model. However, no unimodal response curve was obtained, but it can be concluded that the chance of occurrence of *Bathyporeia spp.* was highest in the intertidal and shallow subtidal zone, but also in the deep subtidal and the channels the species could be observed, although less frequently.

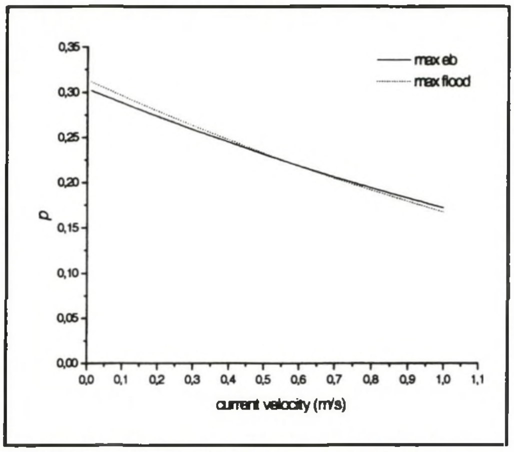
Bathyporeia spp.	*Term*	*Regression coefficient*	*Standard error*
present: 589 absent: 2285			
	intercept	-0,5482	0,0778
	depth	-0,1748	0,0181
	depth^2	0,00139	0,000671
	concordance	66,30%	



Maximum ebb and flood current velocities (m.s^{-1})

Only the linear term was included in both current velocity models. This resulted in a more or less linear curve and *Bathyporeia spp.* seemed to be relatively unaffected by current velocities, with only a slight preference for the lower current velocities.

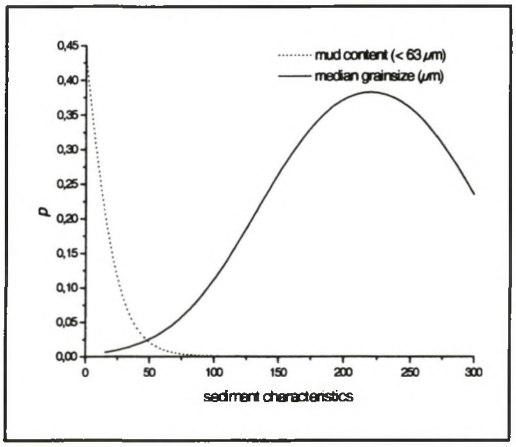
Bathyporeia spp.	*Term*	*Regression coefficient*	*Standard error*
present: 654 absent: 2383			
	Intercept	-0,8305	0,0978
	Maxeb	-0,7429	0,1448
	Maxeb^2	-	-
	Concordance	56,40%	
	Intercept	-0,7845	0,0863
	Maxfl	-0,8207	0,1256
	Maxfl^2	-	-
	Concordance	58,00%	



Sediment characteristics: median grainsize (µm) and mud content (%)

Both the linear and quadratic term were included in the median grain size model, whereas only the linear term was included in the mud content model. This resulted in an unimodal response curve for median grain size; *Bathyporeia spp.* clearly prefered sandy sediments with an optimum for median grain size at ± 220 µm. The response curve for mud content clearly showed a steep, more or less linear decrease with increasing mud content. In very muddy sediments *Bathyporeia spp.* was absent.

Bathyporeia spp.	*Term*	*Regression coefficient*	*Standard error*
Present: 366 Absent: 1136			
	intercept	-5,8042	0,4848
	median	0,0484	0,00501
	median^2	-0,00011	0,000012
	concordance	69,00%	
Present: 347 Absent: 1039			
	intercept	-0,2651	0,0831
	mud	-0,0716	0,00717
	mud^2	-	-
	concordance	71,70%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, both the linear as the quadratic term were included for model and temporal salinity, and depth (Table 2.3). Also the quadratic term for maximum ebb current velocity was included. The linear term of depht, and the linear and quadratic term of temporal salinity added most to the change of deviance in the model. The model with sediment characteristics performed better, with the linear term of mud content and the linear term of depth adding most to the change of deviance in the model.

Table.2.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Bathyporeia* *spp.	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment Presence: 583 absence: 2244			with sediment Presence: 331 Absence: 962		
	Intercept	-7,2309	0,5386	Intercept	-2,6535	0,7288
	Temporal salinity	0,1585	0,0416	Temporal salinity	0,3857	0,0777
	Temporal salinity^2	-0,00626	0,00137	Temporal salinity^2	-0,0125	0,00237
	Model salinity	0,6689	0,0631	Depth	-0,4620	0,0552
	Model salinity^2	-0,0169	0,00174	Depth^2	0,0126	0,00209
	Depth	-0,2882	0,0262	Maxeb	4,1235	1,2321
	Depth^2	0,00571	0,000787	Maxeb^2	-1,7495	0,8251
	Maxeb^2	1,1721	0,1681	Mud	-0,0978	0,0101
	concordance	79,1%		concordance	85,3%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 78,1 % of the responses correctly (Table 2.4). However, only 46,8 % of the modelled (or predicted) presences were also actually observed in the field. When including sediment characteristics in the model, this percentage increased up to 62,5 %. So the model performed better when the sediment characteristics were included in the model.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 2.4. Comparative statistics on the predicted and observed occurrence of Bathyporeia spp. in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model).

Bathyporeia spp. (p=0,38)
(without sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**Correct**
Po	273	310	583	46,8
Ao	310	1934	2244	86,2
Total	583	2244	2827	78,1

Difference between proportions	0,330	
95% CI	-1,000 to 0,366	(normal approximation)
Fisher exact test: 1-tailed p	<0.0001	(exact)

Bathyporeia spp. (p=0,46)
(with sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	207	124	331	62,5
Ao	124	838	962	87,1
Total	331	962	1293	80,8

Difference between proportions	0,496	
95% CI	-1,000 to 0,544	(normal approximation)
Fisher exact test: 1-tailed p	<0.0001	(exact)

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ECOPROFILE OF CAPITELLA CAPITATA

INTRODUCTION

The polychaete *Capitella capitata* was not very common in the Schelde estuary, and both density and biomass were in general very low and therefore therefore its contribution to the total system biomass was also very low. The habitat preferences of *C. capitata* were not very well defined, being e.g. present in all depth strata, in both very muddy as very coarse sediments. Being a very opportunistic species, *C. capitata* probably reacts on local disturbances like e.g. dredging activities.

AUTO-ECOLOGY

CAPITELLA CAPITATA	Annelida, Polychaeta

General

C. capitata is very opportunistic polychaete species, characteristic for estuaries. *C. capitata* makes more or less vertical, non-permament burrows, sometimes edged with mucus (HARTMANN-SCHRÖDER, 1971). Maximum depth in the sediment is 24 cm, but most individuals of *C. capitata* are observed at a depth of 12-18 cm (WARREN, 1976, 1977).

Habitat preferences

Salinity: According to WOLFF (1973) *C. capitata* is rarely seen upstream the isohaline of 10 g Cl^-/l. LELOUP & KONIETZKO (1956) observed the species in the Zeeschelde near the isohaline of 4 g Cl^-/l (just upstream the Dutch/Belgian border) , but according to WOLFF (1973) confusion with *Heteromastus filiformis* could probably explain this observation. Also MUUS (1967) observed the species rarely at salinities lower then 10 g Cl^-/l.

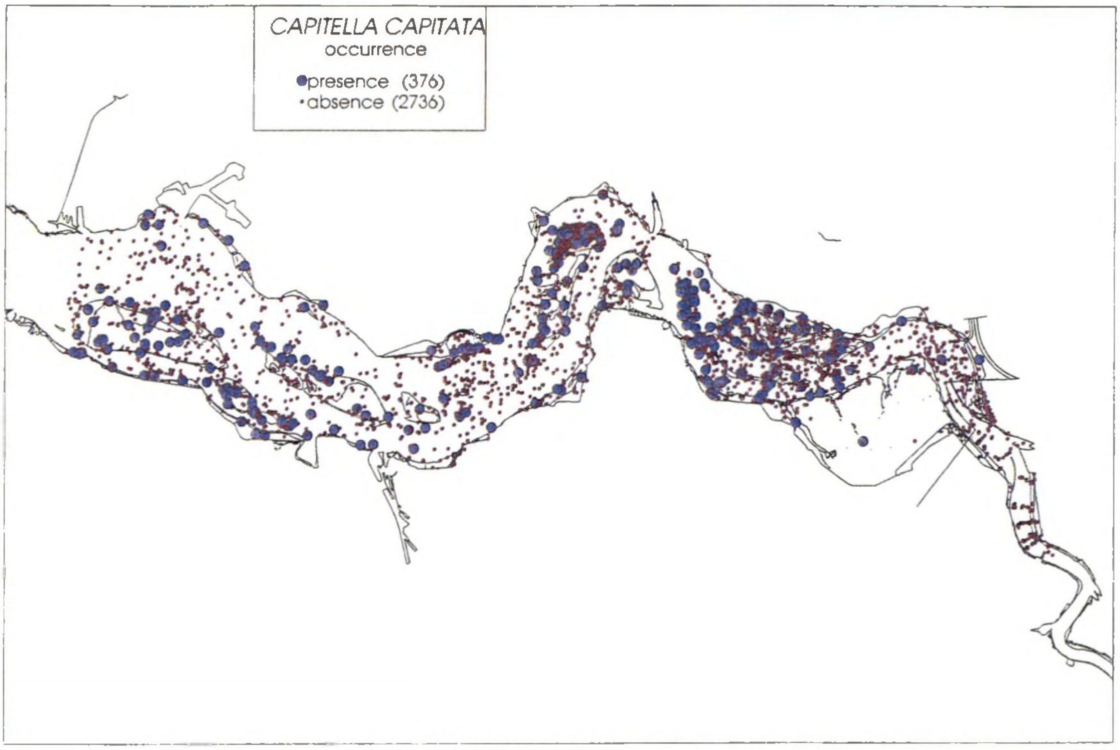
Sediment type: According to HARTMANN-SCHRÖDER (1971) *C. capitata* is found in different substrates. *C. capitata* is most frequently observed in fine to medium sandy sediments which are well sorted (WOLFF, 1973; WARREN, 1977). However, the most important, controlling factor for *C. capitata* seems to be the instability of the sediment: highest densities are observed in instable sediments (GRASSLE & GRASSLE, 1974; JAMES & GIBSON, 1980).

Feeding

C. capitata is a non selective deposit feeders, feeding mainly on micro-organisms (WARREN, 1977), which are living on decaying material (TENORE, 1977; TENORE & HANSON, 1980).

Population dynamics and life history

C. capitata is monotelic and one of the few Polychaeta with sexual dimorfism. Sexually mature females built a brood tube with sand and detritus, in which the fecundated eggs are deposited. After 4 to 5 days the trochophora larvae hatch. The female takes care of the brood (HARTMANN-SCHRÖDER, 1971; TSUTSUMI & KIKUCHI, 1984). After ten days the metatrochophora larvae leave the tube and stay for a week in the pelagic, after which they settle. The settlement is stimulated by sulfur combinations, products of anaerobic processes (CUOMO, 1985).



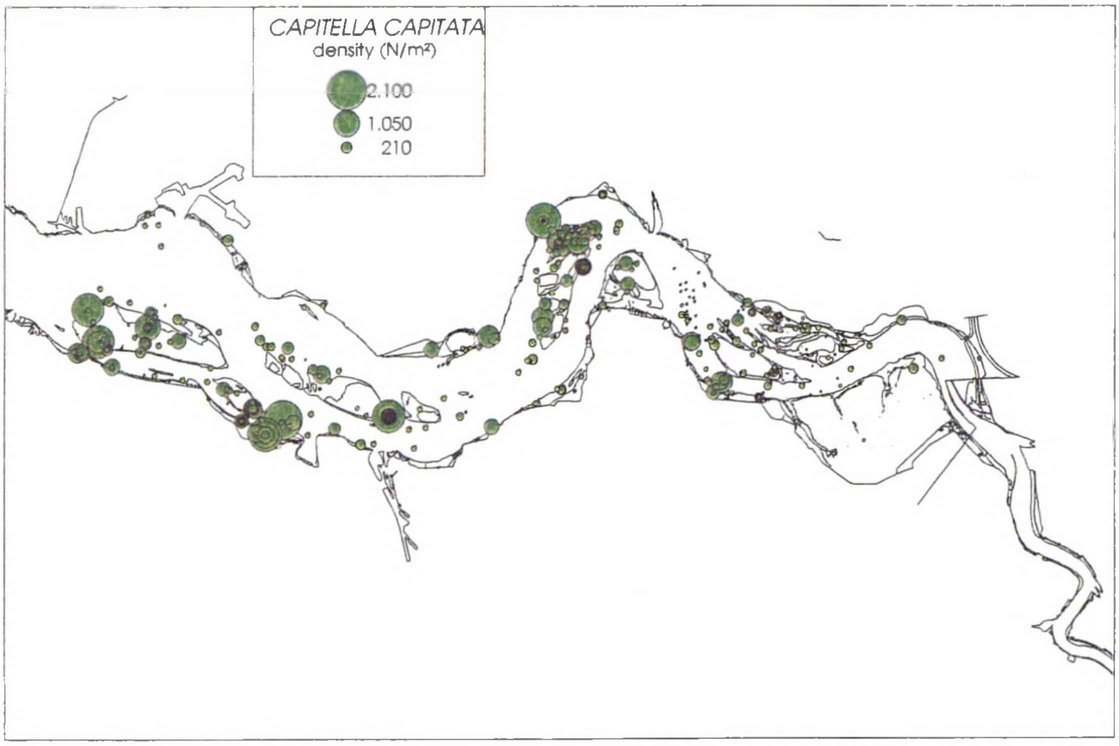


Figure 3.2. Geographical distribution maps of Capitella capitata in the Schelde estuary with presence/absence data (top) and density (ind m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

C. capitata was present in the salinity regions 1 to 3, but was almost completely absent in salinity region 4 (Table 3.1). In the littoral zone and the undeep subtidal zone a decrease in occurrence was observed with decreasing salinity, whereas in the deep subtidal zone and the channel the species was most frequently observed in the salinity region 3.

Both biomass and density were very low (Figure 3.1), and *C. capitata* is of no importance for the overall macrobenthic density or biomass in the Schelde estuary. Densities were in general higher in the littoral and decreased with decreasing salinity, whereas for biomass no clear trend was observed. The geographical distribution of *C. capitata* in the Schelde estuary is shown in Fig. 3.2.

T*able 3.1. Occurrence (p/a) of C. capitata along the salinity and depth gradients of the Schelde estuary. N=number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).*

	1	2	3	4
Littoral	28,6 % (n=262)	18,3 % (n= 503)	10,5 % (n=485)	0,7 % (n= 287)
Undeep subtidal	16,6 % 'n=151)	9,8 % (n=153)	9,4 % (n=127)	0 % (n=51)
deep subtidal	6,5 % (n=123)	7,7 % (n=130)	12,5 % (n=112)	0 % (n=67)
Channel	8,6 % (n=186)	5,2 % (n=173)	20,7 % (n=232)	0 % (n=70)

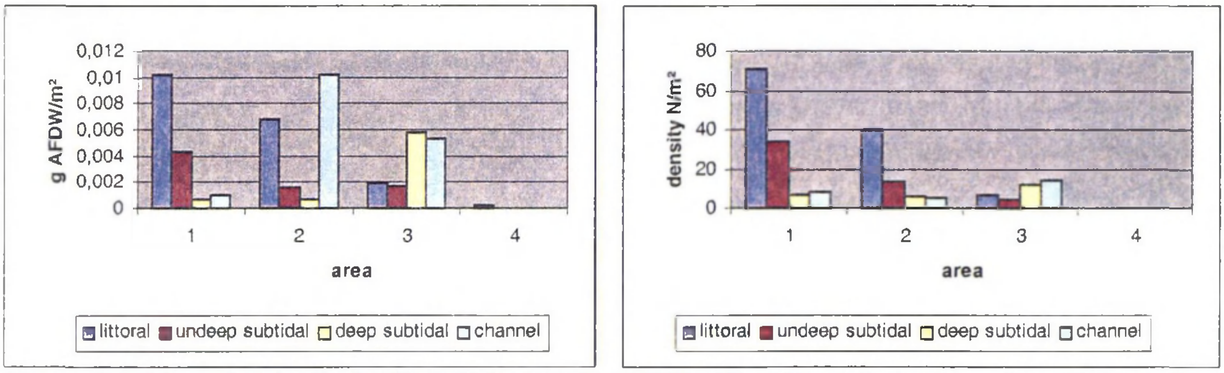


Figure 3.1. Mean density (ind m⁻²) and biomass (g AFDW m⁻²) of C. capitata along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

C. capitata. was slightly more frequently observed in autumn as compared to spring (Table 3.2). In salinity region 1 and 2 mean density was higher in autumn, but for biomass this was only reflected in salinity region 2.

Table 3.2. Spring (Mar-May) versus autumn (Aug-Oct) occurrence (presence/absence), density (ind m⁻²) and biomass (g AFDW m⁻²) of C. capitata in the littoral zone of the Schelde estuary. (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone).

LITTORAL		1	2	3	4
Presence	Spring	23,7 % (n=97)	13,0 % (n= 169)	7,5 % (n=147)	0,0 % (n= 33)
	Autumn	30,4 % (n=135)	22,5 % (n=218)	10,0 % (n=249)	0,9 % (n= 214)
Density	Spring	34	22	6	0
	Autumn	102	59	7	0,4
Biomass	Spring	0,0116	0,0043	0,0025	0
	Autumn	0,0094	0,0080	0,0020	0,0002

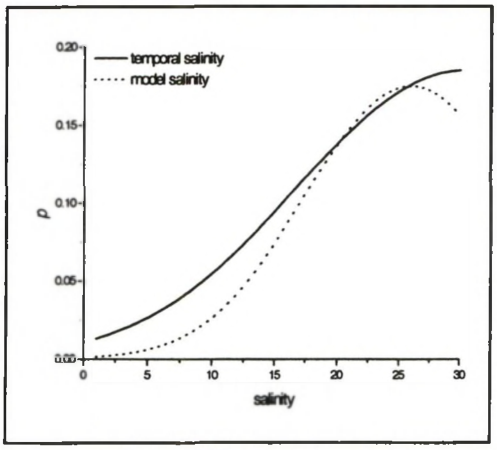
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. *C. capitata* was mainly observed in very low densities. Therefore, at all sampling occassions where the species was observed, the species was also considered being present in the analysis.

Model salinity and temporal salinity

Both the linear and quadratic term of both 'temporal salinity' and 'model salinity' were included in the models. *C. capitata* showed a sigmoidal response for salinity, with a higher chance of occurrence with increasing salinity.

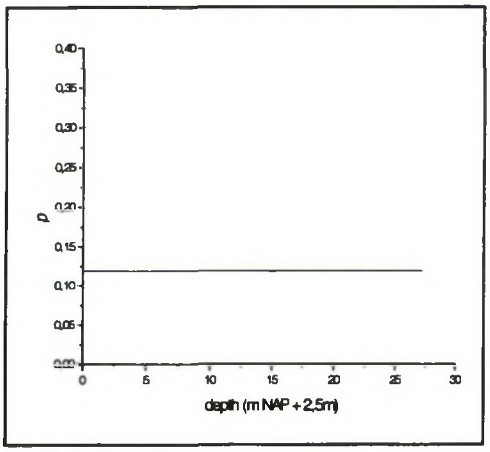
Capitella capitata	*Term*	*Regression coefficient*	*Standard error*
present: 376 absent: 2736			
	Intercept	-4,5302	0,4704
	Temporal salinity	0,2017	0,0492
	Temporal salinity²	-0,00334	0,00122
	Concordance	62,30%	
	Intercept	-7,0033	0,7585
	Model salinity	0,4205	0,0714
	Model salinity²	-0,00811	0,00163
	Concordance	58,10%	



Depth

No term was included in the depth model, indicating no differentiation in the chance of occurrence of *C. capitata* based on depth. This coincides with the observations from Table 3.1, where *C. capitata* was found to be present in all depth strata.

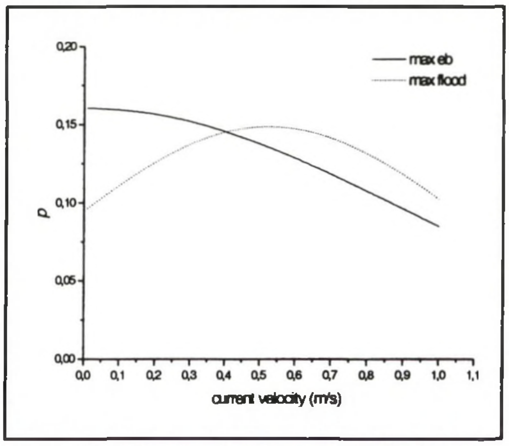
Capitella capitata	*Term*	*Regression coefficient*	*Standard error*
present: 341 absent: 2533			
	Intercept	-2,0053	0,0577
	Depth	-	-
	depth²	-	-
	Concordance	-	



Maximum ebb and flood current velocities (m.s^{-1})

Only the quadratic term was included in the maximum ebb current velocity (maxeb) model, whereas both the linear and quadratic term were included in the maximum flood current velocity (maxfl) model. However, both curves were very broad and *C. capitata* seemed to be relatively unaffected by current velocities, showing a very broad tolerance.

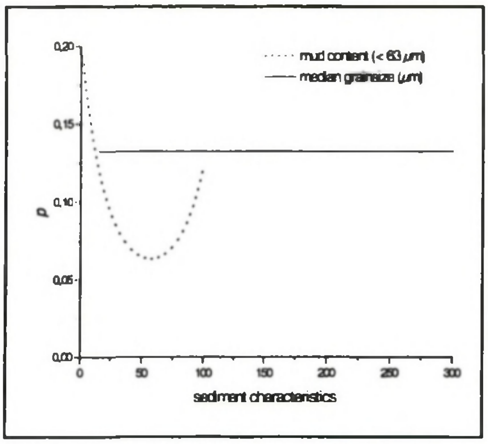
Capitella capitata	*Term*	*Regression coefficient*	*Standard error*
present: 365 absent: 2672			
	Intercept	-1,6555	0,0823
	Maxeb	-	-
	Maxeb²	-0,7265	0,1460
	Concordance	56,60%	
	Intercept	-2,2591	0,1937
	Maxfl	1,9609	0,6711
	Maxfl²	-1,8766	0,5029
	Concordance	55,30%	



Sediment characteristics: median grainsize (μm) and mud content (%)

No term was included in the median grain size model, indicating no differentiation in the chance of occurrence of *C. capitata* based on median grain size. Both the linear and quadratic term were included in the mud model. The resulting response curve for mud showed a relatively high chance of occurrence in very muddy sediments, but also in sediments with a very low mud content a slight increase in chance of occurrence of *C. capitata* was observed.

Capitella capitata	*Term*	*Regression coefficient*	*Standard error*
present: 199 absent: 1303			
	intercept	-1,8791	0,0761
	median	-	-
	median²	-	-
	concordance	-	
present: 191 absent: 1195			
	intercept	-1,3901	0,1138
	mud	-0,0455	0,0138
	mud²	0,000398	0,000202
	concordance	59,50%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, the linear term for temporal salinity, the linear and the quadratic term for model salinity and the quadratic term for maximum ebb current velocity (maxeb) were included in the model (Table 3.3). The linear term of temporal salinity and the quadratic term of maximum ebb current velocity added most to the change of deviance in the model. The model with sediment characteristics performed slightly better, with the linear term of temporal salinity and mud content adding most to the change of deviance in the model.

Table 3.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Capitella capitata	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment			with sediment		
	presence: 338			Presence: 169		
	absence: 2489			Absence: 1124		
	intercept	-7,7042	0,8370	Intercept	-6,3986	1,4484
	Temporal salinity	0,0683	0,0162	Temporal salinity	0,0624	0,0233
	Model salinity	0,4875	0,0778	Model salinity	0,4684	0,1287
	Model salinity^2	-0,0114	0,0018	Model salinity^2	-0,0101	0,00304
	Maxeb^2	-0,8317	0,1577	Depth^2	0,00192	0,000586
				Median	-0,00757	0,00192
				Mud	-0,0403	0,00952
	concordance	67,1%		concordance	72,8%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 80,9 % of the responses correctly (Table 3.4). However, only 20,1 % of the modelled (or predicted) presences were also actually observed in the field, which was the worst prediction of all models. When including sediment characteristics in the model, this percentage increased up to 29,6 %, still being a bad performance.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 3.4. Comparative statistics on the predicted and observed occurrence of Capitella capitata in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model).

***Capitella capitata* (p=0,213)**

(without sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**Correct**
Po	68	270	338	20,1
Ao	270	2219	2489	89,2
Total	338	2489	2827	80,9

Difference between proportions

95% CI (normal approximation)

Fisher exact test: 1-tailed p <0.0001 (exact)

***Capitella capitata* (p=0,236)**

(with sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	50	119	169	29,6
Ao	119	1005	1124	89,4
Total	169	1124	1293	81,6

Difference between proportions

95% CI (normal approximation)

Fisher exact test: 1-tailed p <0.0001 (exact)

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ECOPROFILE OF THE EDIBLE COCKLE *CERASTODERMA EDULE*

INTRODUCTION

The Edible Cockle *Cerastoderma edule* is a common bivalve mollusc species of estuarine and coastal waters. It is the second most common bivalve species in the Schelde estuary, after *Macoma balthica.* It is the most important suspension feeder in the Schelde estuary, and in the polyhaline intertidal zone *C. edule* is the dominant constituent of the total macrobenthic biomass (48% of the intertidal total biomass in salinity region 1 and 30% in salinity region 2).

AUTO-ECOLOGY

CERASTODERMA EDULE	Mollusca, Bivalva

General

The Edible Cockle *Cerastoderma edule* is a common bivalve mollusc species of estuarine and coastal waters. *C. edule* lives always very shallow in the sediment, but there is an increase of depth with size and their burying depth in winter is deeper than in summer (ZWARTS & WANNINK, 1989). *C. edule* is not evenly distributed, but occurs typically aggregated in beds, mainly in the intertidal zone.

The Cockle may play an important role in the estuarine and shallow coastal food webs (HERMAN *et al.*, 1999). When very abundant, this species can filter large amounts of suspended matter (seston) in the water column (SMAAL *et al.*, 1986).

HABITAT PREFERENCES

Salinity: *C. edule* is a euryhaline species which enters the estuary up to the mesohaline zone. The species is absent from the offshore parts of the North Sea and from those parts of the estuaries with an average salinity below about 12 g Cl^-/l at high tide or 10 g Cl^-/l at low tide during normal river discharge (WOLFF, 1973). TEBBLE (1966) and MUUS (1967) also recorded 10-12 g Cl^-/l as the lower limit of occurrence. When *C. edule* is exposed to very low salinities (2-4 g Cl^-/l) due to high river runoffs, massive mortality can occur.

Sediment type: C. edule occurs on a wide range of sediments. According to KRISTENSEN (1957) *C. edule* does not prefer a certain sediment type. WOLFF (1973) gives as range of occurrence a median grain size of 70-250 µm. DANKERS & BEUKEMA (1981) gives as lower limit of occurrence for German and Dutch Wadden Sea cockels a median grain size of 80-110 µm, and an optimum (highest biomass) between 110 and 200 µm. The large range of sediments inhabited by C. edule reflects that it is not influenced so much by the nature of the sediment, but mainly by the hydrodynamical conditions accompanying the sediment (WOLFF, 1973). The currents must not be so fast that the cockles are washed out, but fast enough to provide enough food and to prevent the deposition of a layer of detritus.

Feeding

C. edule is a suspension feeder, ingesting large quantities of seston. Large concentrations of *C. edule* can reduce locally seston concentrations in the water column, and the grazing by benthic suspension feeders might effectively control the phytoplankton in estuaries (e.g. HERMAN & SCHOLTEN, 1990, HERMAN *et al.*, 1999). An extensive literature exists on the feeding and selection mechanisms of suspension-feeding bivalves. The physical resuspension of the bottom sediments has a significant effect on the quantity and quality of the SPM available to suspension-feeders. Suspension-feeders like *C. edule* are able to compensate for reduction in food quality and quantity by means of physiological mechanisms which enhance the energy gain from environments characterised by large fluctuations in the quantity and quality of the seson (e.g. BAYNE & NEWELL, 1983, SHUMWAY *et al.*, 1985, HAWKINS *et al.*, 1996). It has also been demonstrated that filter-feeding bivalves are able to compensate for the dilution of the organic fraction by the inorganic fraction of the seston by preferential ingestion of organic particles from the filtered matter and selective rejection of the inorganic matter within the pseudofaeces, but digestive efficiencies decrease with increasing SPM concentrations (e.g. KIØRBOE & MØHLENBERG, 1981; PRINS *et al.*, 1991; IGLESIAS *et al.*, 1996; NAVARRO & WIDDOWS, 1997). As suspension feeder, C. edule will grow less fast when inundation time is shorter (Kristensen, 1957; Sutherland, 1982).

Population dynamics and life history

One (HANCOCK & FRANKLIN, 1972) or two (SEED & BROWN, 1978) to six year old, *C. edule* spawns in late spring and summer. *C. edule* has a free spawning and external fertilization occurs in the water (Giese & Kanatani, 1987). After a pelagic life of ± 1 month, larvae settle passively on the tidal flats, mainly driven by the local hydrodynamic factors. Juvenile *C. edule,* just like *Macoma balthica*, might actively migrate by crawling and floating. Juvenile *C. edule* has a floating mechansim with one byssus thread (YANKSON, 1986).

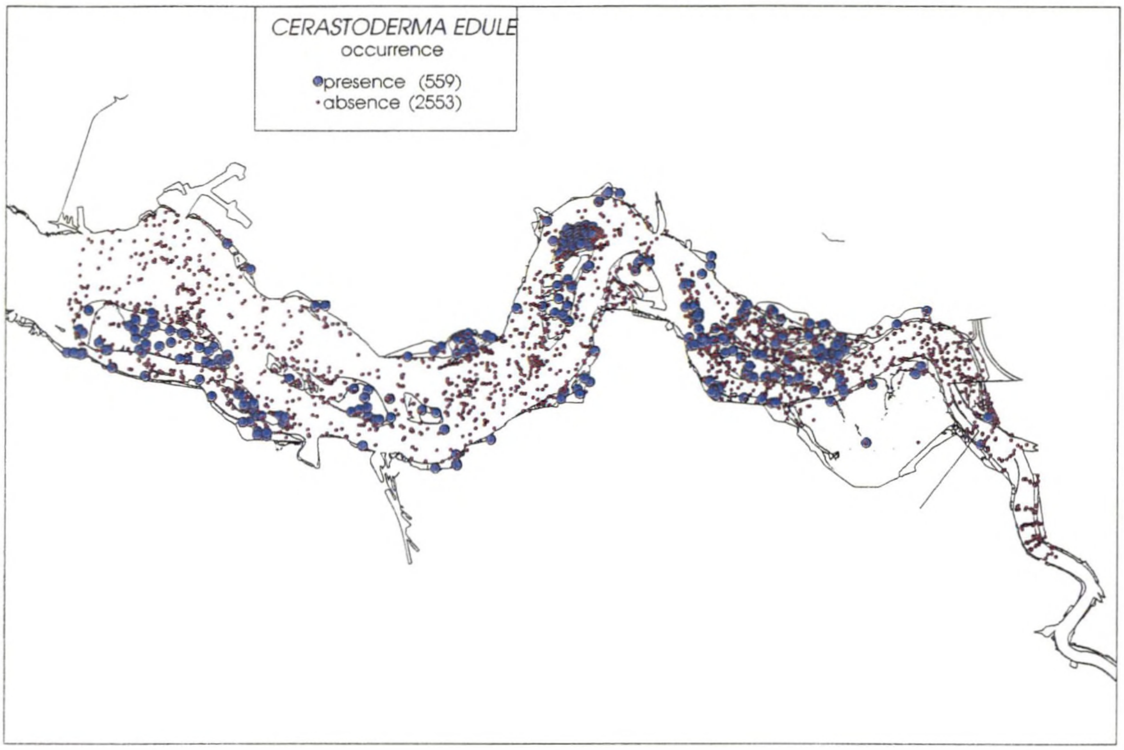
C. edule, just like *M. arenaria,* often have a good spatfall after severe winters (e.g. 1939, 1947, 1979, 1987) (BEUKEMA, 1979, 1982; DÖRJES *et al.*, 1986). This might be a consequence of reduced predation by juvenile crabs (*Carcinus maenas*) and shrimps (*Crangon crangon*), which appear later in the season and with a lowered biomass after a severe winter (VERWEIJ, 1981; BEUKEMA, 1991, 1992a; DIJKEMA, 1992). Also the lowered predation by other benthic invertebrates, togehter with more 'space' after a severe winter, makes conditions more profitable for *C. edule* spatfall to settle and to grow. After mild winters the spatfall is negligible (BEUKEMA, 1992b).

The presence of adult benthic suspension feeders, like *C. edule* and *Mya arenaria*, when present in high densities, might significantly reduce settlement success of bivalve larvae, and hence may limit recruitment of new individuals (HANCOCK, 1973; MÖLLER, 1986; BACHELET *et al.*, 1991; ANDRÉ & ROSENBERG, 1991; ANDRÉ *et al.*, 1993). The mechanism proposed is that adults filter settling larvae out of the water column (WOODIN, 1976) or that the adults through bioturbation hampers the settlement and enhance resuspension of the larvae. GUILLOU & TARTU (1994) mentions two critical periods in the development of the cockle juveniles: one period with a high post-larval mortality until autumn and a second period of high mortality in the winter until spring, probably caused by predation by crabs. Also parasite infestation by trematodes may cause substantial mortality in juvenile cockles (JONSSON & ANDRÉ, 1992).

Biotic interactions

C. edule is an important part of the estuarine food chain. As a suspension feeder it might act as an important controller of the phytoplankton in estuaries (e.g. HERMAN *et al.*, 1999). Shrimps and crabs predate on the small, juvenile cockles (VERWEY, 1981). Shrimps prefer cockles < 2 mm (PIHL & ROSENBERG, 1982); whereas crabs might consume large quantities of cockles up to 10-12 mm (JENSEN & JENSEN, 1985; GUILLOU & TARTU, 1994).

Large adult C. edule, present in high densities, might negatively affect the occurrence of small macrobenthic species living in tubes near the surface of the sediments, such as *Corophium volutator and C. arenarium* (JENSEN, 1985; FLACH, 1994).



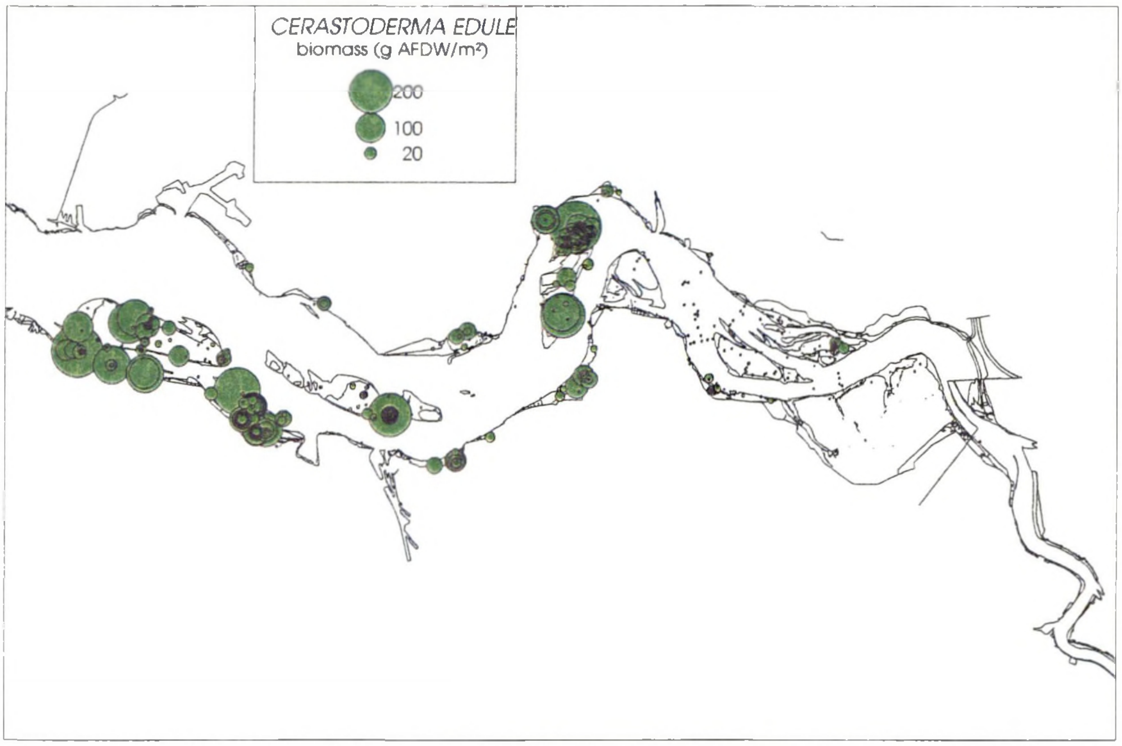


Figure 4.2. Geographical distribution maps of Cerastoderma edule in the Schelde estuary with presence/absence data (top) and biomass (g AFDW m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

C. edule is a typical species of the polyhaline and polyhaline/mesohaline transition zone of the Schelde estuary (salinity regions 1 and 2) (Table 4.1). In the β-mesohaline zone (salinity region 4) the species is absent. *C. edule* was only frequently observed in the littoral zone.

Mean density and biomass was highest in the littoral zone (Figure 4.1). The proportion biomass: density clearly indicated larger individual biomasses in salinity region 1 and very small individuals in salinity region 3. In the undeep subtidal much lower densities and biomasses are observed, and in the deep subtidal and the channel the species is nearly absent.

The geographical distribution of *C. edule* in the Schelde estuary is shown in Figure 4.2.

Table 4.1. Occurrence (p/a) of C. edule along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	54,6 % (n=262)	46,1 % (n= 503)	24,3 % (n=485)	1 % (n= 287)
Undeep subtidal	6,0 % (n=151)	2,0 % (n=153)	8,7 % (n=127)	2,0 % (n=51)
Deep subtidal	4,1 % (n=123)	1,5 % (n=130)	4,5 % (n=112)	0 % (n=67)
Channel	0,5 % (n=186)	1,2 % (n=173)	10,3 % (n=232)	0 % (n=70)

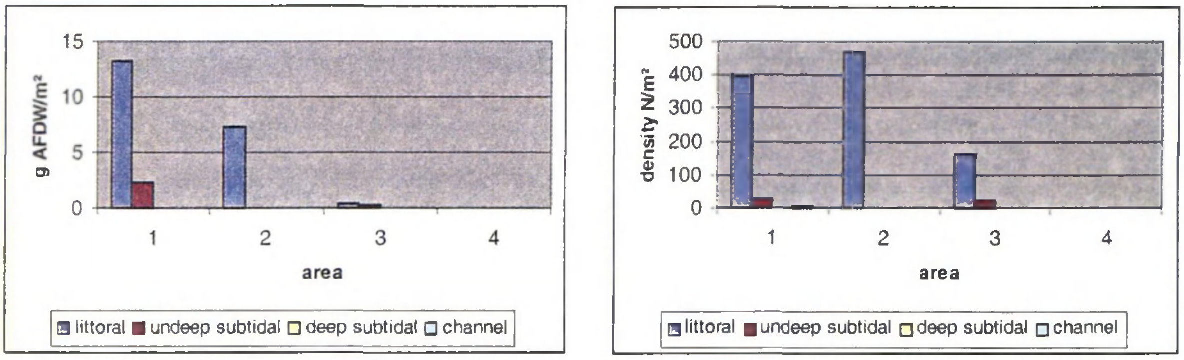


Figure 4.1. Mean density (ind m^{-2}) and biomass (g AFDW m^{-2}) of C. edule along the salinity and depth gradient in the Schelde estuary (area: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

In all salinity regions *C. edule* was more frequently observed in autumn as compared to spring (Table 4.2). This was most pronounced in the α-mesohaline zone (salinity region 3). In salinity region 4 *C. edule* was in both seasons nearly completely absent. Both density and biomass were much higher in autumn as compared to spring.

Table 4.2. Spring (March - May) versus autumn (Augustus - October) occurrence (presence/absence), density (ind m^{-2}) and biomass (g AFDW m^{-2}) of C. edule in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone).

LITTORAL		1	2	3	4
Presence	Spring	39,2 % (n=97)	37,9 % (n= 169)	4,1 % (n=147)	0,0 % (n= 33)
	Autumn	65,9 % (n=135)	53,2 % (n=218)	35,9 % (n=249)	1,4 % (n= 214)
Density	Spring	60	136	2	0
	Autumn	652	843	270	1
Biomass	Spring	3,6	5,9	0,06	0
	Autumn	18,8	11,1	0,57	0,0004

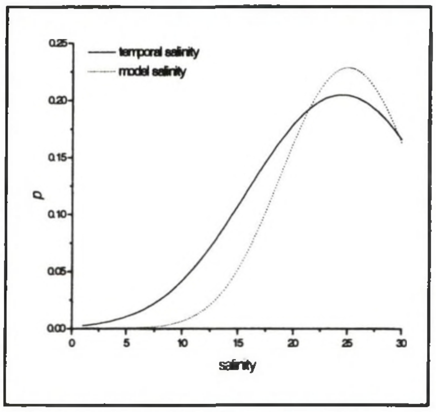
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Both the linear and quadratic term were included in both salinity models. *C. edule* showed a clear optimum in the polyhaline zone at a salinity of 25. Below a salinity of 20 psu there was a steep decline in chance of occurrence, and from a salinity of ± 10 psu the species became nearly absent. The model based on temporal salinity showed a somewhat higher probability of occurrence in the lower salinity region.

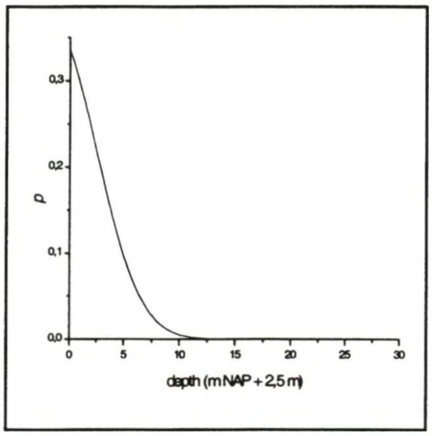
C. Edule	*Term*	*Regression coefficient*	*Standard error*
present: 416 absent: 2696			
	intercept	-6,4215	0,5781
	Temporal salinity	0,4145	0,0581
	Temporal salinity²	-0,00848	0,00140
	Concordance	63,50%	
	Intercept	-11,7787	1,1360
	Model salinity	0,8450	0,1008
	Model salinity²	-0,0169	0,00218
	Concordance	66,20%	



Depth

Only the quadratic term was included in the depth model for *C. edule*. *C. edule* was a typical species of the intertidal zone, resulting in a steep decline in response towards the subtidal zone.

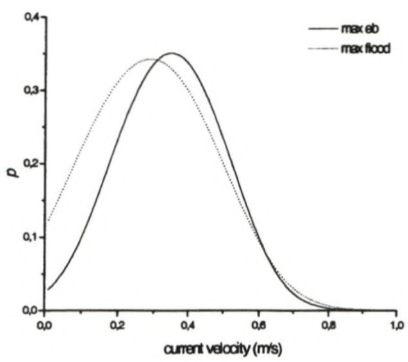
C. Edule	*Term*	*Regression coefficient*	*Standard error*
present: 361 absent: 2513			
	Intercept	-0,8972	0,0722
	Depth	-	-
	Depth²	-0,0494	0,00462
	Concordance	78,30%	



Maximum ebb and flood current velocities

Both the linear and quadratic terms were included in both current velocity models, resulting in a relatively narrow unimodal response curve with an optimum around 0,30-0,35 m.s^{-1}. Both low and high current velocities seemed not to be preferred by *C. edule*.

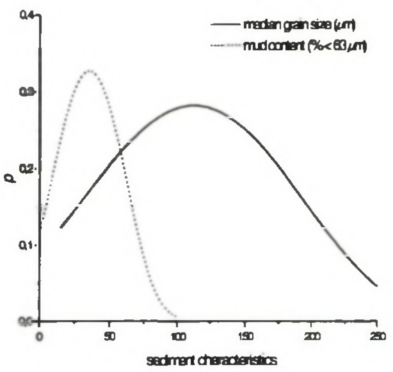
C. edule	*Term*	*Regression coefficient*	*Standard error*
present: 401 absent: 2636			
	Intercept	-3,7158	0,3832
	maxeb	17,7640	2,0178
	maxeb²	-25,4578	2,5168
	Concordance	81,80%	
	intercept	-2,0575	0,2407
	maxfl	9,7087	1,3833
	maxfl²	-16,7715	1,8012
	concordance	83,60%	



Sediment characteristics: median grainsize and mud content

Both the linear and quadratic terms were included in both the median grain size as the mud content models, resulting in a unimodal response curve with an optimum around 110 μm and 35% for median grain size and mud content respectively. However, the response curve was rather broad and *C. edule* seemed rather tolerant concerning median grain size and mud content. Only at very muddy and very coarse sediments, the chance of occurrence of *C. edule* is very low.

C. edule	*Term*	*Regression coefficient*	*Standard error*
present: 264 absent: 1238			
	intercept	-2,3111	0,3181
	median	0,0246	0,00496
	median²	-0,00011	0,000018
	concordance	68,50%	
present: 259 absent: 1127			
	intercept	-2,0283	0,1225
	mud	0,0744	0,0114
	mud²	-0,00106	0,000178
	concordance	66,6%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data. The overall model is significant at the .05 level according to the Model chi-square statistic.

In the regression model without sediment characteristics, both the linear as the quadratic term were included for all abiotic explanatory variables, except the linear term of maximum flood current velocity (Table 4.3). The linear term of maximum flood current velocity (but removed), model salinity and depht added most to the change of deviance in the model. The model with sediment characteristics had a similar performance, as indicated by the concordance, with the quadratic term of median grain size included in the model. The linear term of maximum flood current velocity and model salinity, and the quadratic term of median grain size added most to the change of deviance in this model.

Table 4.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

C. edule	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment			with sediment		
	presence: 352			Presence: 232		
	absence: 2475			Absence: 1061		
	intercept	-13,2667	1,3940	Intercept	-11,5229	1,5962
	Temporal salinity	0,2972	0,0866	Temporal salinity	0,4338	0,1417
	Temporal salinity^2	-0,00503	0,00241	Temporal salinity^2	-0,0103	0,00422
	Model salinity	0,6427	0,1435	Model salinity	0,6943	0,1907
	Model salinity^2	-0,0129	0,00339	Model salinity^2	-0,0114	0,00493
	Depth	-0,3871	0,0637	Depth	-0,1868	0,0652
	Depth^2	0,00696	0,00146	Maxfl	-4,0737	0,6589
	Maxeb	14,7480	2,7711	Median^2	-0,00004	5,64E-6
	Maxeb^2	-18,4287	3,3607			
	Maxfl^2	-4,0479	0,5995			
	concordance	93,0%		concordance	92.0%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 90,0 % of the responses correctly (Table 4.4). 59,9 % of the modelled (or predicted) presences were also actually observed in the field. When including sediment characteristics in the model, this percentage increased up to 65,1 %. So the model performed better when the sediment characteristics were included in the model.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 4.4. Comparative statistics on the predicted and observed occurrence of C. edule in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model).

***Cerastoderma edule* (p=0,42)**
(without sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	*211*	141	352	59,9
Ao	141	*2334*	2475	94,3
Total	352	2475	2827	90,0

Difference between proportions	0,542	
95% CI	-1,000 to 0,586	(normal approximation)
Fisher exact test: 1-tailed p	<0.0001 (exact)	
(observed by model: Po<Ao)		

***Cerastoderma edule* (p=0,42)**
(with sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	151	81	232	65,1
Ao	81	980	1061	92,4
Total	232	1061	1293	87,5

Difference between proportions	0,575	
95% CI	-1,000 to 0,628	(normal approximation)
Fisher exact test: 1-tailed p	<0.0001 (exact)	
(observed by model: Po<Ao)		

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ECOPROFILE OF COROPHIUM ARENARIUM

INTRODUCTION

Corophium arenarium was the second most common Corophiidae in the Schelde estuary, but is much less common as *C. volutator*. The geographical distribution was different from *C. volutator*, with *C. arenarium* occurring at higher salinities (the intertidal polyhaline and α-mesohaline zone). Density and biomass were in general very low and therefore its contribution to the total system biomass was very low.

AUTO-ECOLOGY

COROPHIUM ARENARIUM	Arthropoda, Amphipoda, Corophiidae
General *see Corophium volutator*	
Habitat preferences *Salinity*: C. arenarium has a larger tolerance for higher salinities as compared to C. volutator (Mills & Fish, 1980). Juveniles of *C. arenarium* are less tolerant for long exposure to lower salinities then juveniles of *C. volutator*. Therefore the upstream colonisation (brackish zone) by *C. arenarium* is hampered. *Sediment type*: In comparison to *C. voluator, C. arenarium* prefers more sandy sediments with less mud in it (Meadows, 1964a,b,c ; Meadows & Reid, 1966; Gamble, 1970).	
Feeding *C. arenarium* is a surface deposit feeder (see *C. volutator*).	
Population dynamics and life history *see Corophim volutator*	

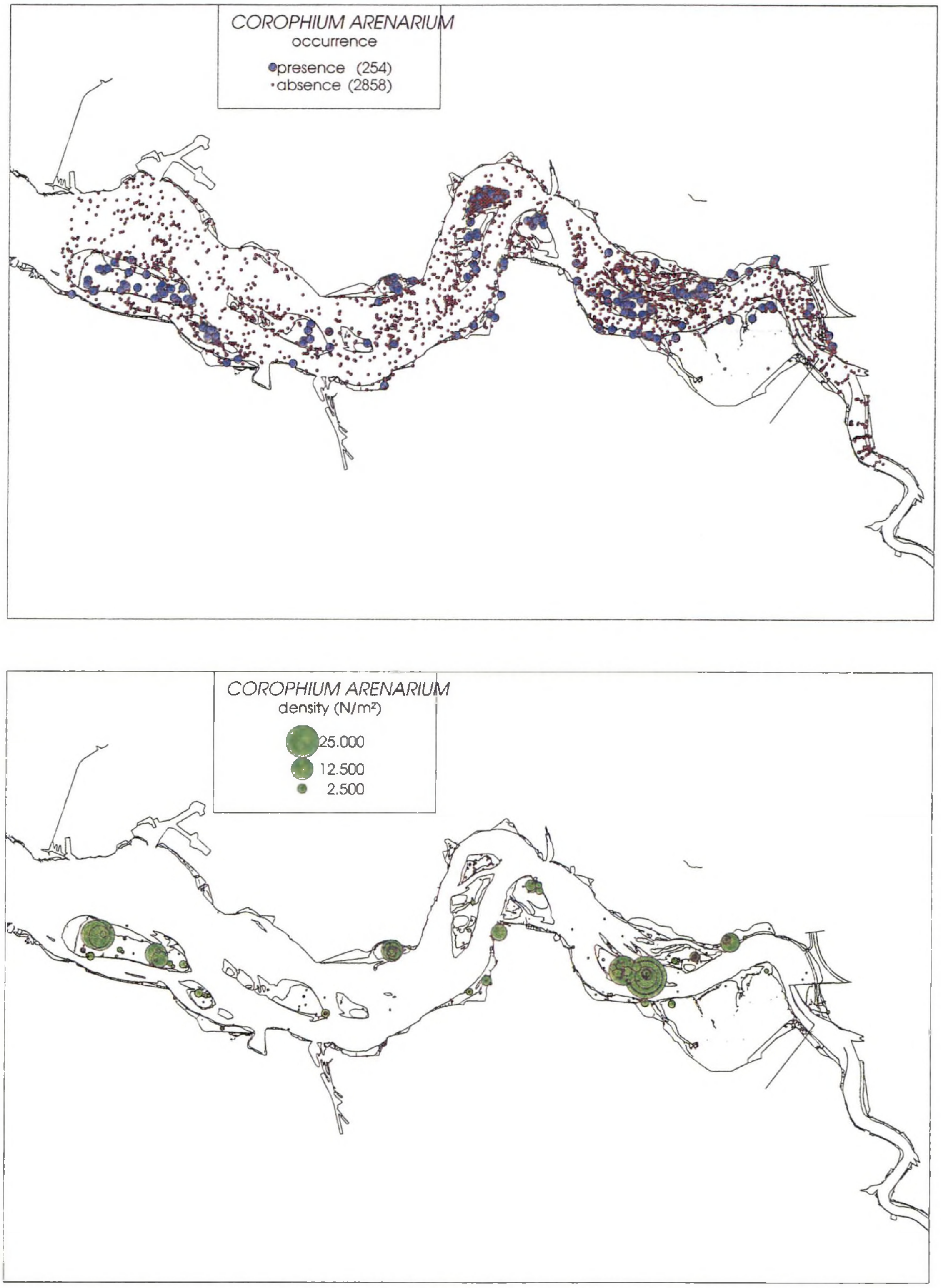


Figure 5.2. Geographical distribution maps of Corophium arenarium in the Schelde estuary with presence/absence data (top) and density (ind m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

C. arenarium was equally present in the salinity regions 1 to 3, but was almost completely absent in salinity region 4 (Table 5.1). It was a typical species of the littoral zone, being almost completely absent in the subtidal zone.

Mean biomass and density was highest in the littoral zone (Figure 5.1). However, both mean density as mean biomass were very low, and the contribution of *C. arenarium* to total macrobenthic biomass and density was therefore very low. The geographical distribution of *C. arenarium* in the Schelde estuary is shown in Figure 5.2.

Table 5.1. Occurrence (presence/absence) of C. arenarium along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	24,0 % (n=262)	16,3 % (n= 503)	19,4 % (n=485)	1,4 % (n= 287)
Undeep subtidal	0,7 % 'n=151)	2,0 % (n=153)	0,8 % (n=127)	2,0 % (n=51)
Deep subtidal	0,0 % (n=123)	0,0 % (n=130)	0,9 % (n=112)	1,5 % (n=67)
Channel	0,0 % (n=186)	0,0 % (n=173)	1,3 % (n=232)	0,0 % (n=70)

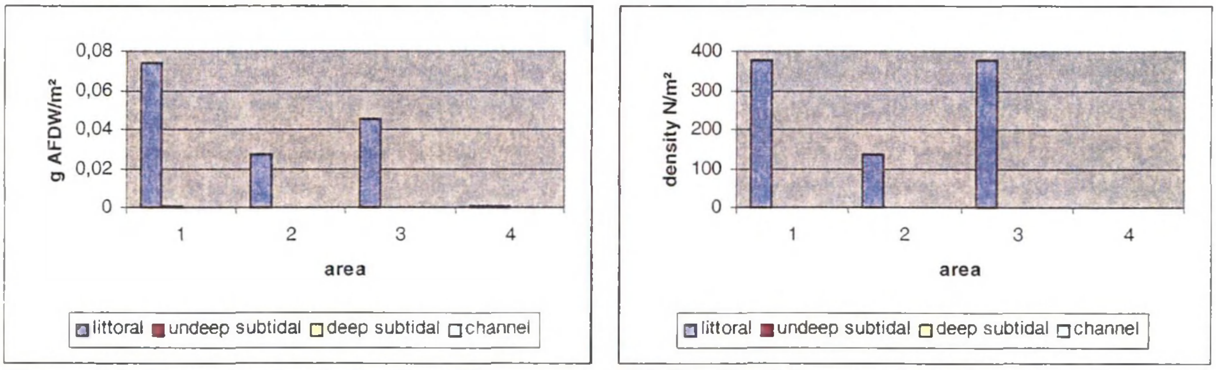


Figure 5.1. Mean density (ind m⁻²) and biomass (g AFDW m⁻²) of C. arenarium along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline ; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

C. arenarium was equally present in spring and autumn (Table 5.2). Density was in general higher in autumn as compared to spring, with exception of salinity region 2 where a slightly higher density was observed in spring. The ratio density:biomass indicated larger individuals found in spring, and most probably more new recruits, being much smaller, in summer.

Table 5.2. Spring (Mar - May) versus autumn (Aug - Oct) occurrence (presence/absence), density (ind m⁻²) and biomass (g AFDW m⁻²) of the Cockle in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone).

LITTORAL		1	2	3	4
Presence	Spring	22,7 % (n=97)	18,3 % (n= 169)	17,0 % (n=147)	0,0 % (n= 33)
	Autumn	24,4 % (n=135)	15,6 % (n=218)	21,7 % (n=249)	0,9 % (n= 214)
Density	Spring	201	197	163	0
	Autumn	551	146	586	1,4
Biomass	Spring	0,065	0,049	0,066	0,0
	Autumn	0,089	0,020	0,030	0,0001

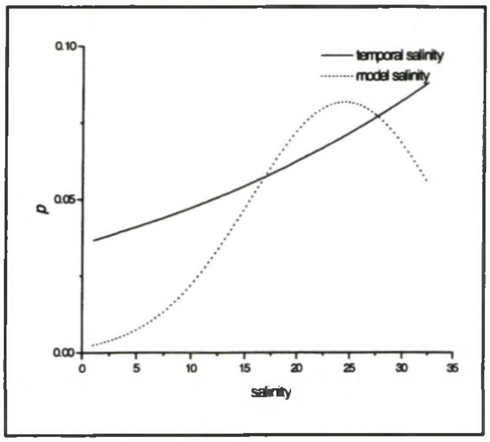
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Only the linear term of temporal salinity was included in the model, whereas both the linear and quadratic term were included in the model salinity model. Based on model salinity, *C. arenarium* showed an optimum in the polyhaline zone at a salinity around 25 psu. Below a salinity of 20 psu there was a steep decline in occurrence. The response curve based on temporal salinity showed a linear decrease in chance of occurrence from the polyhaline zone towards the meoshaline zone.

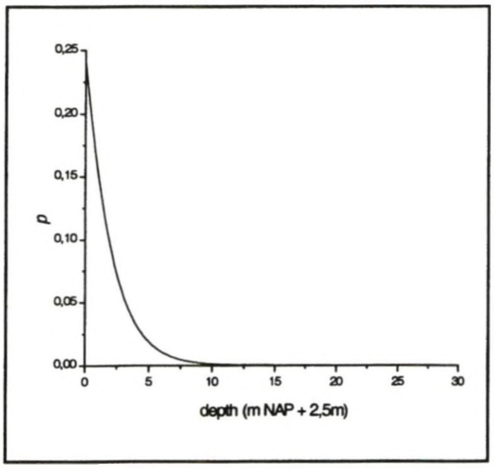
Corophium arenarium	*Term*	*Regression coefficient*	*Standard error*
present: 190 absent: 2922			
	Intercept	-3,3022	0,2203
	Temporal salinity	0,0296	0,0104
	Temporal salinity²	-	-
	Concordance	53,90%	
	Intercept	-6,3350	0,8704
	Model salinity	0,3200	0,0849
	Model salinity²	-0,00654	0,00199
	Concordance	50,20%	



Depth

Only the linear term of depth was included in the model. As *C. arenarium* was typically observed in the intertidal zone (see Table 5.1), a steep decreasing (sigmoidal) response was observed with increasing depth.

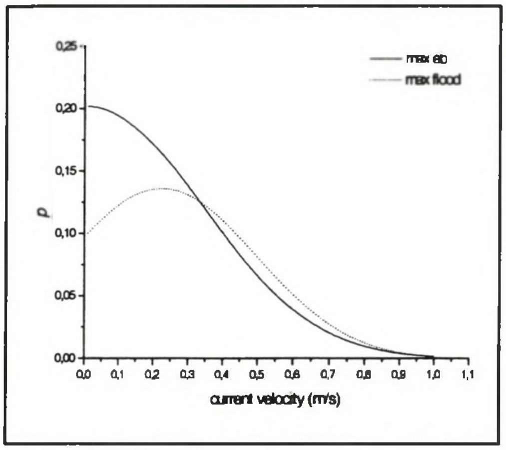
Corophium arenarium	*Term*	*Regression coefficient*	*Standard error*
present: 148 absent: 2726			
	Intercept	-1,1454	0,1397
	Depth	-0,5638	0,0614
	depth²	-	-
	Concordance	83,00%	



Maximum ebb and flood current velocities (m.s^{-1})

Only the quadratic term of maximum ebb current velocity was included in the model, whereas both the linear and quadratic terms were included in the maximum flood current velocity model. This resulted in a more or less unimodal response curve for maximum flood current velocity with an optimum around 0.25 m.s^{-1}. Based on the maximum ebb current velocity, a sigmoidal decrease in response was observed with increasing current velocities.

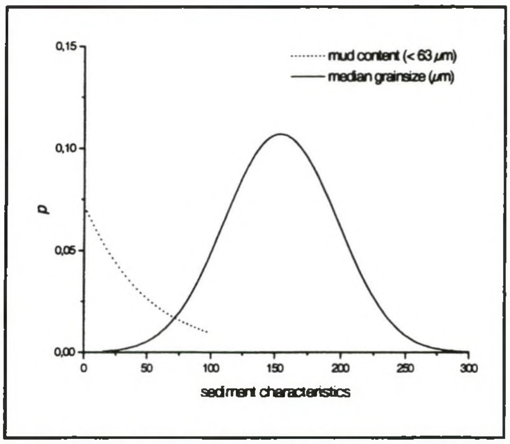
Corophium arenarium	*Term*	*Regression coefficient*	*Standard error*
present: 178 absent: 2859			
	Intercept	-1,3746	0,1164
	Maxeb	-	-
	Maxeb²	-5,1007	0,5257
	Concordance	79,20%	
	Intercept	-2,2320	0,2760
	Maxfl	3,4138	1,4656
	Maxfl²	-7,6230	1,6942
	Concordance	76,50%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Both the linear and quadratic term were included in the median grain size model, whereas only the linear term was included in the mud content model. *C. arenarium* clearly prefered relatively sandy sediments, showing a unimodal response curve for median grain size with an optimum at ± 160 μm. This is clearly in between the preference of *C. volutator* and *Bathyporeia sps.*, which prefer more muddy and more sandy sediments respectively.

Corophium arenarium	*Term*	*Regression coefficient*	*Standard error*
present: 78 absent: 1424			
	intercept	-8,9815	1,3626
	median	0,0892	0,0177
	median²	-0,00029	0,000056
	concordance	73,60%	
present: 74 absent: 1312			
	intercept	-2,5604	0,1468
	mud	-0,0210	0,00728
	mud²	-	-
	concordance	49,80%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, only model salinity and depth (both the linear as the quadratic term) as maximum ebb current velocity (only linear term) were included in the regression model (Table 5.3), with the linear term of maximum ebb current velocity (but removed and again included afterwards), depth and model salinity adding most to the change in deviance. The model with sediment characteristics performed equally well, with median grain size (linear and quadratic term) and mud content (linear term only) included in the model. The linear term of maximum flood current velocity and mud content, and the quadratic term of median grain size added most to the change of deviance in this model.

Table 5.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Corophium arenarium	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	Without sediment Presence: 144 absence: 2683			with sediment Presence: 68 Absence: 1225		
	Intercept	-6,3340	1,0144	Intercept	-5,5340	2,0134
	Model salinity	0,5422	0,1058	Temporal salinity	0,0799	0,0251
	Model salinity^2	-0,0108	0,00253	Depth	-0,6590	0,1327
	Depth	-0,7501	0,0992	Depth^2	0,0190	0,00559
	Depth^2	0,0122	0,00221	Median	0,0564	0,0230
	Maxeb	-1,6721	0,6448	Median^2	-0,00019	0,000067
				Mud	-0,0571	0,0185
	Concordance	87,3%		concordance	85,1%	

Percent correct predictions

The logistic regression model, without or with sediment characteristics, included, predicts overall 93 % of the responses correctly (Table 5.4). However, only 33,3 % of the modelled (or predicted) presences were also actually observed in the field. When including sediment characteristics in the model, this percentage was even lower (25,0 %).

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 5.4. Comparative statistics on the predicted and observed occurrence of Corophium arenarium in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model).

Corophium arenarium
(p=0,22)
(without sediment characteristics)

Response Observed	Model Pm	 Am	 Total	% **correct**
Po	48	96	144	33,3
Ao	96	2587	2683	96,0
Total	144	2683	2827	93,1

Difference between proportions	0,298	
95% CI	-1,000 to 0,362	(normal approximation)

Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)

Corophium arenarium
(p=0,23)
(with sediment characteristics)

Response Observed	Model Pm	 Am	 Total	% **correct**
Po	17	51	68	25,0
Ao	51	1293	1344	96,0
Total	68	1344	1412	92,8

Difference between proportions	0,212	
95% CI	-1,000 to 0,299	(normal approximation)

Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)

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ECOPROFILE OF COROPHIUM VOLUTATOR

INTRODUCTION

Corophium volutator was the most important *Corophium* species observed in the Schelde estuary and it was by far the most abundant species in the intertidal, β-mesohaline zone of the estuary (± 40% of the total density observed). It also constituted 16% of the total biomass in this zone. In the α-mesohaline zone *C. volutator* was less dominant, but was still the third important species (15%) in terms of density.

AUTO-ECOLOGY

COROPHIUM VOLUTATOR (PALLAS, 1766)	Arthropoda, Amphipoda, Corophiidae

General

C. volutator is a benthic amphipod, widely distributed in the shallow coastal areas of the North Temperate Zone. This euryhaline species inhabits U-shaped burrows in estuarine sediments and lives up to six cm deep, mainly in muddy or muddy-sandy sediments. As an important component in the estuarine food web, *C. volutator* is an important link, feeding on bacteria/diatoms, and in turn forming a major constituent in the diet of fish and waders.

Habitat preferences

Salinity: *C. volutator* tolerates a minimal salinity of about 2, showing experimentally a maximal growth rate in salinities 5-30 and a salinity preference range of 10-30 (McLUSKY, 1967; 1968a,b; 1970), with a clear influence of temperature on the salinity tolerance (MILLS & FISH, 1980). Below a salinity of 5 *C. volutator* is scarce in the field, and breeding occurred only in salinities greater than 7.5 (McLUSKY, 1968a).

Sediment type: The preferred substratum of *C. volutator* is noted as mud (SEGERSTRALE, 1940), soft bottom (THAMDRUP, 1935), finer soils (WATKIN, 1941), with a 37-38 % silt-clay content (GEE, 1961; MEADOWS, 1964a,b,c). *C. volutator* is relatively resistent to anaerobic conditions (GAMBLE, 1970).

Feeding

C. volutator is a selective surface deposit feeder, although suspension feeding and epipsammic browsing may also occur, feeding mainly on bacteria and epipelic diatoms. Food is collected by filtering particles from the current generated through the U-shaped burrow by the beating pleopods, or by using the antennae to scrape material into this current (MEADOWS & REID, 1966). For more detailed studies on the food selection by *C. volutator* see FENCHEL *et al.* (1975), NIELSEN & KOFOED (1982), MILLER (1984), MURDOCH *et al.* (1986), GERDOL & HUGHES (1994a), and SMITH *et al.* (1996).

Population dynamics and life history

In general, *C. volutator* is observed in low densities and biomasses in winter and spring, followed by a rapid increase in the summer period. Later in the year, densities and biomasses drop again to a winter level. In winter, density observed varies between studies and between study sites. McLUSKY (1968a) found in the Ythan estuary (UK) an overwintering population, characterized by low to very low densities, depending on the salinity; highest density was observed at the study site with a winter salinity > 10 psu (8000 ind.m^{-2}), whereas at a winter salinity < 1 psu, *C. volutator* was absent. PEER *et al.* (1986) found in the Bay of Fundy (Canada) maximum overwintering densities of 3500 ind.m^{-2}. However, in some stations *C. volutator* was totally absent during the winter which was attributed to severe ice scouring. MÜLLER & ROSENBERG (1982) found on the west coast of Sweden a high variation in winter density, ranging from 0 to 12000 ind.m^{-2}. Also here ice formation was the main cause for the absence of *C. volutator*. OMORI & TANAKA (1984) observed relatively high densities during the winter months (23000-35000 ind.m^{-2}) but this was probably due to the relatively high winter temperatures. In summer, peak densities of 25000-30000 ind.m^{-2} (McLUSKY, 1968; OLAFSSON & PERSSON, 1986) up to 100000 ind.m^{-2} (GERDOL & HUGHES, 1993) are observed, but mostly different (smaller) mesh sizes for sieving are used (often 0,5 mm).

C. volutator is generally believed to be bivoltine, , with a long-lived overwintering generation and a short-lived spring-summer generation (WATKIN, 1941; FISH & MILLS, 1979; GRATTO, 1979; MÜLLER & ROSENBERG, 1982; PEER, 1986; MEIßNER & BICK, 1997), although some studies record one (McLusky, 1968a) to four (Muus, 1967; OMORI & TANAKA, 1984) generations per year. The overwintering generation breeds from May to June, which give rise to a subsequent summer-breeding generation which reproduces between the beginning of July and September. However, some studies record one to four generations per year.

C. volutator has, like all amphipods, no larval stage. Small amphipods hatch from eggs retained in a ventral thoracic brood pouch. Within the brood pouch four clearly defined stages can be recognized (PEER *et al.*, 1986). The newly hatched amphipods remained in the brood pouch for 1-3 days according to HUGHES (1988) and up to five days according to FISH & MILLS (1979), but are able to move in or out at will. FISH & MILLS (1979) estimated the time from copulation to the release of young being ± 14 days, while PEER *et al.* (1986) recorded 19 days between the observation of the first gravid females and the first young. MÖLLER & ROSENBERG (1982) gives a hatching time of ± 2 weeks for the first generation. *C. volutator* is known to have a semi-lunar rhythm of release of young (FISH & MILLS, 1979). Also PEER (1986) observed the release of young occurring during the time of the highest tides associated with the full moon at perigree. After the escape from the brood pouch by the young, they remain in the parental burrow for a few hours before constructing their own burrow (HUGHES, 1988). Based on these short laboratory observations, HUGHES (1988) concluded that there was no direct evidence that juveniles swim or crawl from the parental burrow immediately after release from the brood pouch.

Biotic interactions

JENSEN (1985) demonstrated that increasing densities of *Cerastoderma edule* negatively affected *C. volutator* densities by observing an increase in migration behaviour and a decrease in survival, growth and reproduction *of C. volutator.* In a series of experiments, COMMITO (1982) and AMBROSE (1982, 1984a,b) showed that *Nereis virens* had a negative impact on *C. volutator* and they attributed this impact to predation. High densities of *Nereis diversicolor* reduce the density of *C. volutator*, mainly through the effect of disturbance and not predation (OLAFSSON & PERSSON, 1986), although RÖNN *et al.* (1988) and BICK & ARLT (1993) have shown that *N. diversicolor*, depending on its abundance, exercises predation pressure on *C. volutator*, simultaneously inducing its emigration. Cage experiments showed that the density of recruits of *C. volutator* was negatively affected by adult individuals of its own species, by *C. arenarium*, by *Macoma balthica* and by *N. diversicolor* (JENSEN, 1988; JENSEN & KRISTENSEN, 1990). However, in recolonizing experiments FLACH (1992) concluded that neither the presence of *M. balthica* nor that of *N. diversicolor* significantly affected the abundance of *C. volutator.* A strongly negative effect was found of *C. edule* when present in high densities, whereas *A. marina* negatively affected *C. volutator* abundances already at relatively low densities.

Population crashes of *C. volutator* are reported more than once. Parasite infestation is often mentioned as being the main cause for a suddenly dramatical decimation of the population in the summer period (MUUS, 1967; OLAFSSON & PERSSON, 1986; LAUCKNER, 1987; JENSEN & MOURITSEN, 1992; MEIßNER & BICK, 1997). Also predation by waders can cause a tempory decrease of the numbers of *C. volutator* (PEER 1986). RAFFAELLI *et al.* (1991) observed a dramatical decline of *C. volutator* in the Ythan estuary throughout those parts of the estuary affected by macroalgal mats. Under a high biomass of weed, *C. volutator* disappeared almost completely.

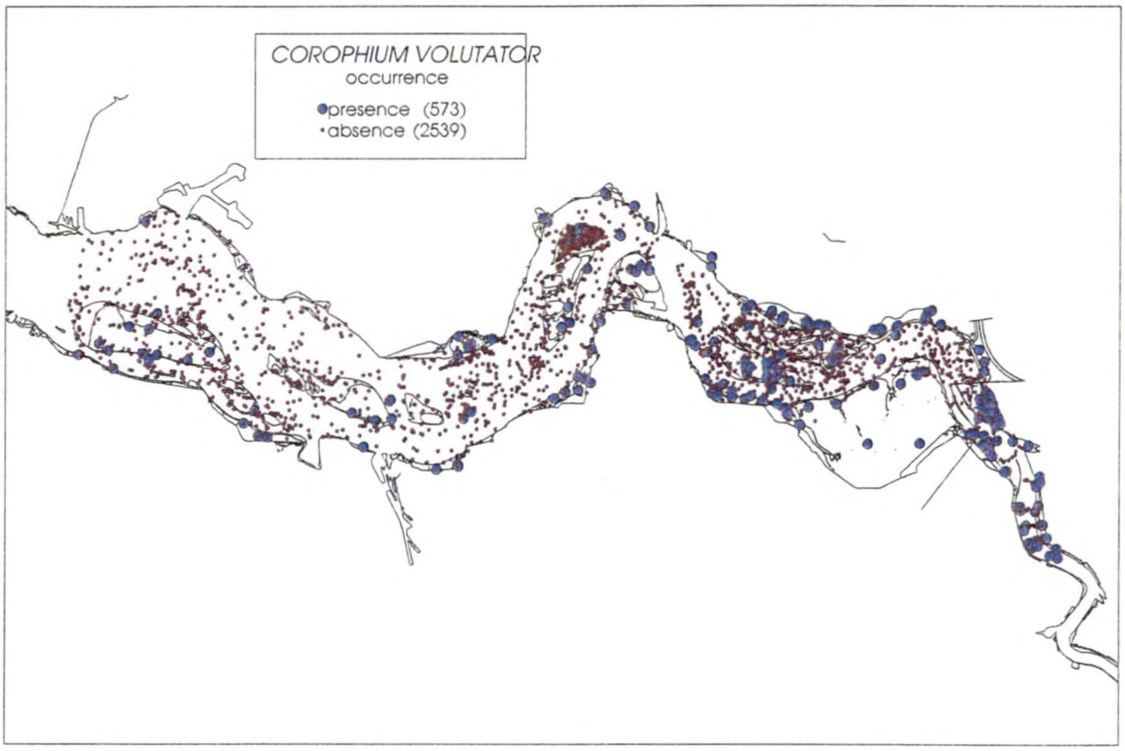
Role of *C. volutator* in stabilisation of sediments

The presence of *C. volutator* may have significant impact on sediment topography, sediment stability and erosion/sedimentation processes (REISE, 1978; MEADOWS *et al.*, 1990; JENSEN & MOURITSEN, 1992). In the literature both stabilising as destabilising forces were ascribed for *C. volutator. C. volutator* may increase directly sediment stability by binding particles with the secretions used to construct their tubes or burrow walls (MEADOWS & TAIT, 1989; MEADOWS *et al.*, 1990). Indirectly, by grazing upon the benthic microalgae, species like *C. volutator* will negatively influence sediment stability (DABORN et al., 1993; GERDOL & HUGHES, 1994b).

Pelagic occurrence

C. volutator seemingly have little need to leave their burrow, except to find a mate, and in laboratory studies this has rarely been seen (HUGHES, 1988). FISH & MILLS (1979) found that as the tide ebbs, adult males emerge from the sediment and crawl across the mud surface, probably searching for burrows occupied by adult, receptive females.

C. volutator has been found in plankton samples, and the pelagic occurrence has been demonstrated both under laboratory conditions (HOLMSTRÖM & MORGAN, 1979, 1983a,b,c) and *in situ* observations (HUGHES, 1980; ESSINK *et al.*, 1989; HUGHES & HORSFALL, 1990). Swimming behaviour of C. volutator was demonstrated to have a rhythmicity with circadian, semi-lunar and seasonal components, but with geographical DIFFERENCES (HUGHES & HORSFALL, 1990).



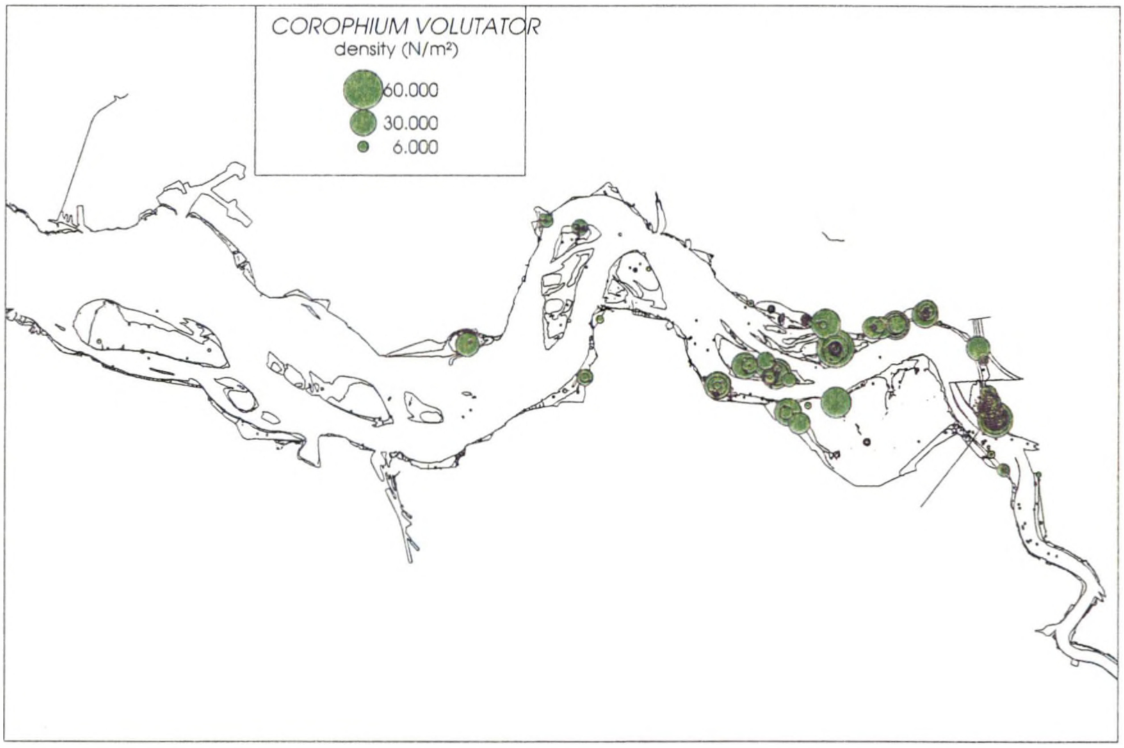


Figure 6.2. Geographical distribution maps of Corophium volutator in the Schelde estuary with presence/absence data (top) and density (ind m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

Corophium volutator showed a significant increase in occurrence from salinity region 1 towards salinity region 4 (Table 6.1). In the β-mesohaline zone (salinity region 4) the species occurred in 82% of all sampling occasions, being the most frequently observed species here. In the subtidal zone, *C. volutator* was nearly absent, except for salinity region 4 were also subtidally this species occurred.

Mean density and biomass in the intertidal zone significantly increased towards salinity region 4 (Figure 6.1). In the subtidal zone density and biomass were very low in all salinity regions. The geographical distribution of *C. volutator* in the Schelde estuary is shown in Figure 6.2.

Table 6.1. Occurrence (p/a) of C. volutator along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone).

	1	2	3	4
Littoral	7,6 % (n=262)	13,3 % (n= 503)	39,4 % (n=485)	82,2 % (n= 287)
Undeep subtidal	2,0 % 'n=151)	3,3 % (n=153)	2,4 % (n=127)	13,7 % (n=51)
Deep subtidal	0,0 % (n=123)	2,3 % (n=130)	2,7 % (n=112)	17,9 % (n=67)
Channel	0,5 % (n=186)	0,0 % (n=173)	1,7 % (n=232)	25,7 % (n=70)

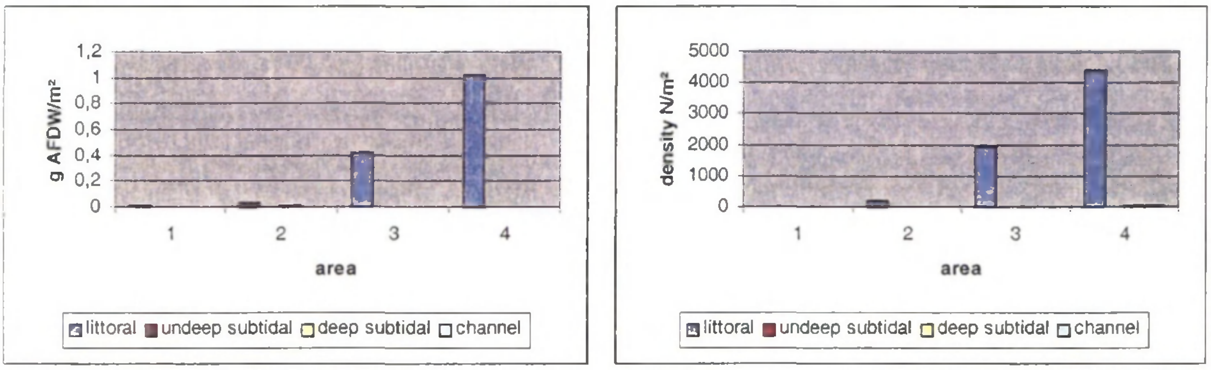


Figure 6.1. Mean density (ind m⁻²) and biomass (g AFDW m⁻²) of C. volutator along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline ; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

C. volutator occurred more in autumn samples as compared to spring samples (Table 6.2). Especially mean density and biomass were much higher in autumn.

Table 6.2. Spring (March - May) versus autumn (Augustus - October) occurrence (presence/absence), density (ind m⁻²) and biomass (g AFDW m⁻²) of C. volutator in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone).

LITTORAL		1	2	3	4
Presence	Spring	1,0 % (n=97)	13,0 % (n= 169)	27,9 % (n=147)	60,6 % (n= 33)
	Autumn	13,3 % (n=135)	15,1 % (n=218)	38,2 % (n=249)	83,6 % (n= 214)
Density	Spring	2	66	274	324
	Autumn	41	321	3143	4964
Biomass	Spring	0,0005	0,03	0,13	0,17
	Autumn	0,01	0,06	0,57	1,05

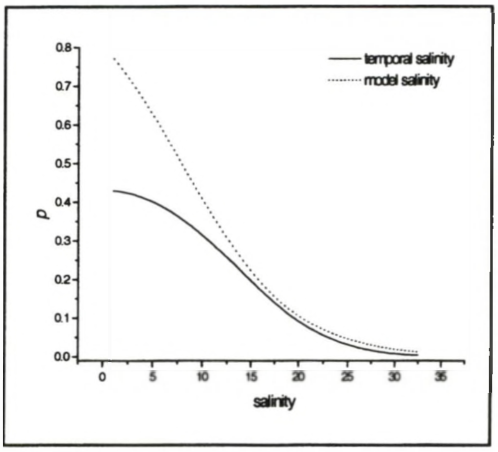
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed for each abiotic variable seperately. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, *C. volutator* was considered as being present.

Model salinity and temporal salinity

Only the quadratic term was included in the 'temporal salinity' model, whereas for model salinity only the linear term was included. The response of *C. volutator* to salinity was a relatively monotonic one, with an increasing chance of occurrence with decreasing salinity.

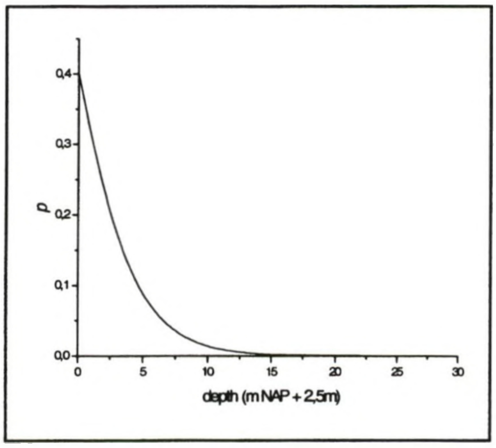
Corophium volutator	*Term*	*Regression coefficient*	*Standard error*
Present: 462			
Absent: 2650			
	Intercept	-0,2788	0,0842
	Temporal salinity	-	-
	Temporal salinity^2	-0,00505	0,000308
	Concordance	77,90%	
	Intercept	1,3865	0,1484
	Model salinity	-0,1766	0,00898
	Model salinity^2	-	-
	Concordance	80,10%	



Depth

Both the linear and quadratic term were included in the depth model. However, the response showed a rather linear decrease in chance of occurrence of *C. volutator* with increasing depth.

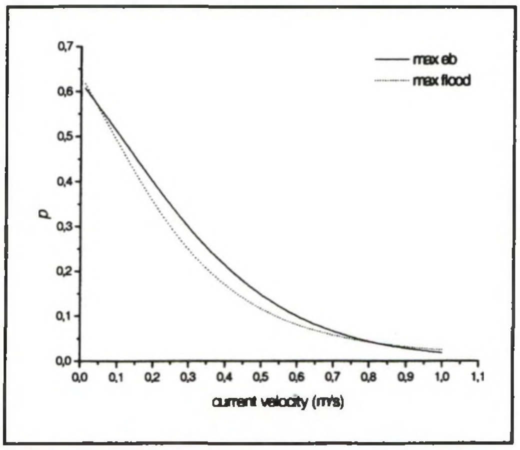
Corophium volutator	*Term*	*Regression coefficient*	*Standard error*
present: 411			
absent: 2463			
	Intercept	0,3489	0,1031
	Depth	-0,6970	0,0434
	Depth^2	0,0118	0,000973
	Concordance	87,00%	



Maximum ebb and flood current velocities

Only the linear term was included in the maximum ebb current velocity model, whereas both the linear and quadratic term were included in the maximum flood current velocity model. However, more or less similar linear curves for maximum ebb and flood current velocity were observed, showing a high chance of occurrence at small current velocities and a gradual decreasing chance of occurrence with increasing current velocities.

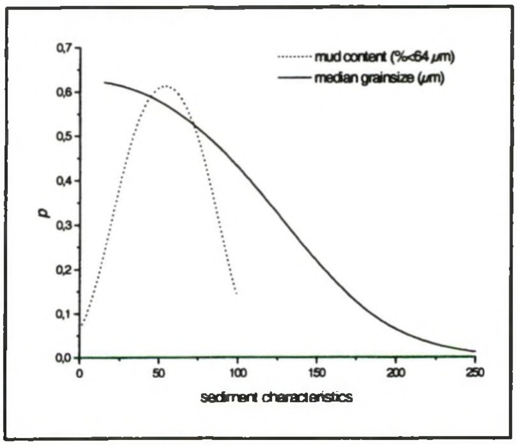
Corophium volutator	*Term*	*Regression coefficient*	*Standard error*
Present: 429 absent: 2608			
	Intercept	0,4807	0,1212
	Maxeb	-4,4698	0,2593
	Maxeb^2	-	-
	Concordance	79,30%	
	Intercept	0.5384	0,1554
	Maxfl	-6,0559	0,6976
	Maxfl^2	1,8435	0,6076
	Concordance	80,70%	



Sediment characteristics: median grainsize and mud content

Only the linear term was included in the median grain size model, whereas in the mud content model both the linear and the quadratic term were included. This resulted in a sigmoidal curve for median grain size, showing a high chance of occurrence in muddy and very fine sand sediments (small μm for median grain size), and an unimodal response curve for mud content, with an optimum at 55%, but with a relatively broad tolerance.

Corophium voluator	*Term*	*Regression coefficient*	*Standard error*
Present: 344 absent: 1158			
	Intercept	0,5151	0,1109
	Median	-	-
	median^2	-0,00008	5,642E-6
	Concordance	83,0%	
present: 341 absent: 1045			
	Intercept	-2,6872	0,1407
	Mud	0,1171	0,0102
	mud^2	-0,00109	0,000137
	Concordance	79,90%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

BINARY LOGISTIC REGRESSION MODEL

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data. The overall model is significant at the .05 level according to the Model chi-square statistic.

In the regression model without sediment characteristics, both the linear as the quadratic term were included for model salinity and depth (Table 6.3). Also the linear term for maximum ebb current velocity was included. The linear term of model salinity, maximum ebb current velocity and depth added most to the change of deviance in this model.
The model with sediment characteristics performed equally, with the linear term of median grain size also included. The linear term of median grain size, maximum ebb current velocity and model salinity added most to the change of deviance in this model.

Table 6.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Corophium volutator	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment			with sediment		
	Presence: 394			presence: 313		
	Absence: 2433			absence: 1089		
	Intercept	6,6438	0,6181	intercept	6,2743	1,5958
	Model salinity	-0,4245	0,0641	Model salinity	-0,1884	0,1389
	Model salinity^2	0,00582	0,00176	Depth	-0,4738	0,00413
	Depth	-0,4134	0,0456	Depth^2	0,0145	0,00488
	Depth^2	0,00755	0,00111	Maxeb	-3,3653	0,0569
	Maxeb	-3,2311	0,4195	Median	-0,0111	0,6413
	Concordance	92,5%		concordance	92,7%	

PERCENT CORRECT PREDICTIONS

The logistic regression model, without sediment characteristics, included, predicts overall 78,1 % of the responses correctly (Table 6.4). With 64,7 % of the modelled (or predicted) presences being also actually observed in the field the model performed very well. When including sediment characteristics in the model, this percentage decreased a little to 56,3%.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 6.4. Comparative statistics on the predicted and observed occurrence of Corophium volutator in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model).

Corophium volutator (p=0,33)
(without sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	255	139	394	64,7
Ao	139	2294	2433	94,3
Total	394	2433	2827	90,2

Difference between proportions 0,590
95% CI -1,000 to 0,630 (normal approximation)

Fisher exact test: 1-tailed p <0.0001 (exact)
(observed by model: Po<Ao)

Corophium volutator (p=0,15)
(with sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	235	78	313	75,1
Ao	78	1011	1089	92,8
Total	313	1089	1402	88,9

Difference between proportions 0,452
95% CI -1,000 to 0,500 (normal approximation)

1-tailed p <0.0001 (exact)

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ECOPROFILE OF ETEONE LONGA

INTRODUCTION

Eteone longa is a regularly observed species in the intertidal, polyhaline and α-mesohaline zone of the Schelde estuary. Density and biomass are low and the contribution of *E. longa* to the overall macrobenthic density and biomass of the estuary is small.

AUTO-ECOLOGY

ETEONE LONGA	Annelida, Polychaeta

General

Eteone longa is a North-Atlantic species that also is often observed in estuaries. Its vertical distribution goes from the eulittoral up to a depth of 1700 m.

Habitat preferences

Salinity: *E. longa* is a North-Atlantic species which penetrates the estuaries until about 10 g Cl^-/l at high tide during average river discharge, where it has to withstand periods of lower salinity during high river discharge (WOLFF, 1973). MUUS (1967) also observed its main distribution in shallow water in salinities over 10 g Cl^-/l.

Sediment type: According to most authors *E. longa* is observed in all kinds of sediments (SCHMIDT, 1951, MUUS, 1967, REINECK *et al.*, 1968, ...). In the Delta area *E. longa* prefers fine and muddy, less well sorted sand (WOLFF, 1973).

Feeding

E. longa is a predator, crawling on or just beneath the sediment surface (RASMUSSEN, 1973), looking for prey. *E. longa* predates on different species of Annelida. Known preys are *Spio filicornis* and *Scolelepis squamata* (BEHRENDS & MICHAELIS, 1977).

Population dynamics and life history

Shortly before spawning, *E. longa* performs a swimming behaviour at night and during high tide (HAMMOND, 1966). The pelagic spawning occurs from March to May (HARTMANN-SCHRÖDER, 1971) and is induced by sudden increases in temperature (RASMUSSEN, 1956). The pelagic, larval phase is very short (THORSON, 1946).

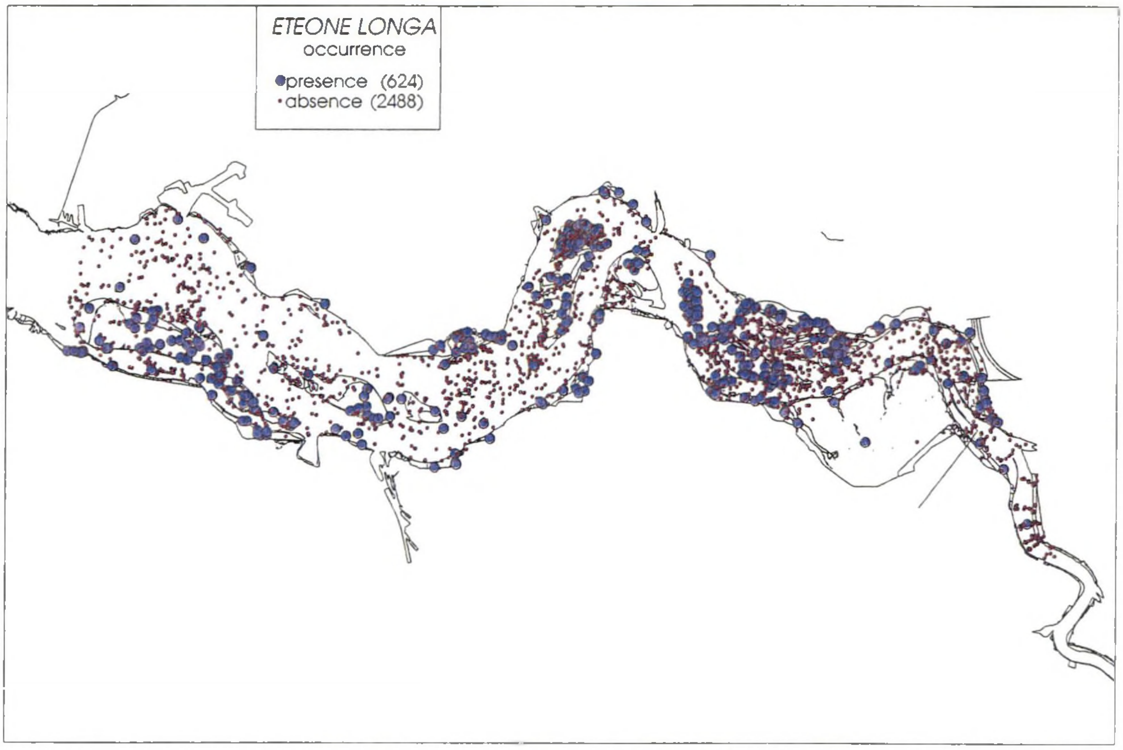


Figure 7.2. Geographical distribution maps of Eteone longa in the Schelde estuary with presence/absence data (top) and density (ind m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

E. longa occurred most in the intertidal zone of salinity region 1, being present in half of the sampling occassions (Table 7.1). In salinity region 2 and 3 this occurrence decreased to a 40%, and in the β-mesohaline zone (salinity region 4) the species was nearly absent. In the *subtidal E. longa* was only observed irregularly.

Mean biomass and density of *E. longa* followed the same trend as the pattern of occurrence, with highest values in salinity region 1 (Figure 7.1). However, values were in general low and the contribution of *E. longa* to the overall density and biomass is therefore small. The geographical distribution of *E. longa* in the Schelde estuary is shown in Figure 7.2.

Table 7.1. Occurrence (p/a) of E. longa along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	52,3 % (n=262)	37,2 % (n= 503)	37,3 % (n=485)	4,5 % (n= 287)
Undeep subtidal	6,0 % 'n=151)	5,9 % (n=153)	6,3 % (n=127)	2,0 % (n=51)
Deep subtidal	4,9 % (n=123)	6,2 % (n=130)	8,0 % (n=112)	4,5 % (n=67)
Channel	3,8 % (n=186)	2,9 % (n=173)	16,8 % (n=232)	2,9 % (n=70)

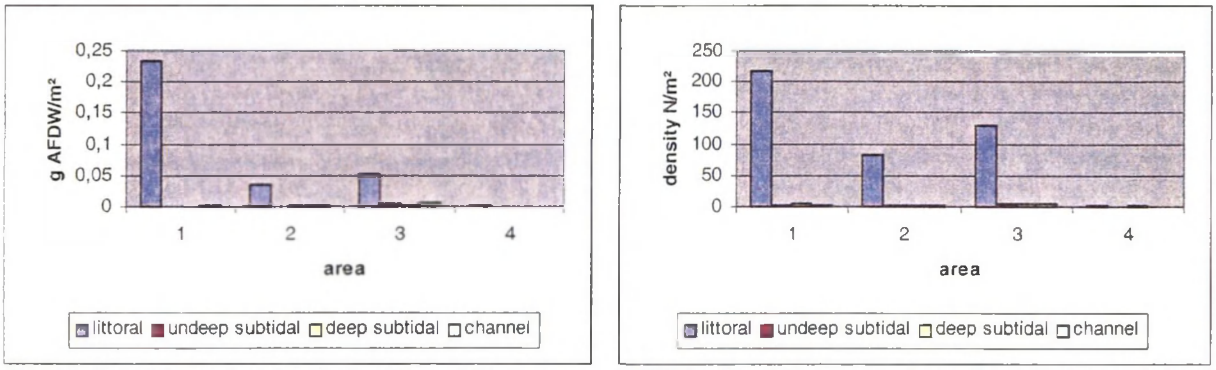


Figure 7.1. Mean density (ind m⁻²) and biomass (g AFDW m⁻²) of E. longa along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline zone; 3&4: mesohaline zone).

Seasonal variations: Spring versus autumn occurrence

E. longa occurred more in autumn samples as compared to spring samples, with a 10-20% higher occurrence (Table 7.2). This was reflected in the mean density, with a highest increase from spring to autumn in salinity region 3. However, mean biomass did not show this trend, and especially in salinity region 1 higher biomass values were observed in spring.

Table 7.2. Spring (March - May) versus autumn (Augustus - October) occurrence (presence/absence), density (ind m⁻²) and biomass (g AFDW m⁻²) of E. longa in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone)

LITTORAL		1	2	3	4
Presence	Spring	42,3 % (n=97)	32,0 % (n= 169)	21,1 % (n=147)	6,1 % (n= 33)
	Autumn	61,5 % (n=135)	42,2 % (n=218)	41,8 % (n=249)	5,1 % (n= 214)
Density	Spring	138	51	14	6
	Autumn	269	117	175	3
Biomass	Spring	0,351	0,033	0,012	0,004
	Autumn	0,168	0,039	0,061	0,002

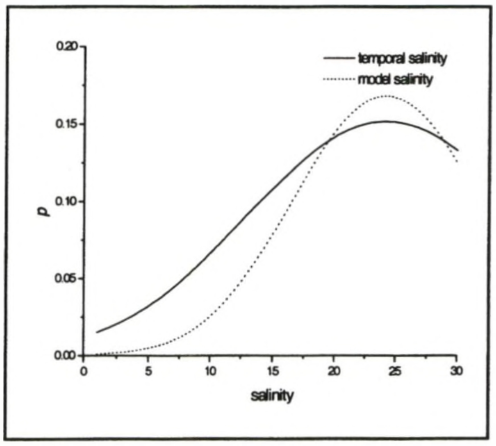
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Both the linear and quadratic term were included in both salinity models. *E. longa* showed an optimum in the polyhaline zone at a salinity of 24. Below a salinity of 15 psu there was a steep decline in chance of occurrence, and from a salinity of ± 10 psu the species became nearly absent. The model based on temporal salinity showed a somewhat higher probability of occurrence in the lower salinity region.

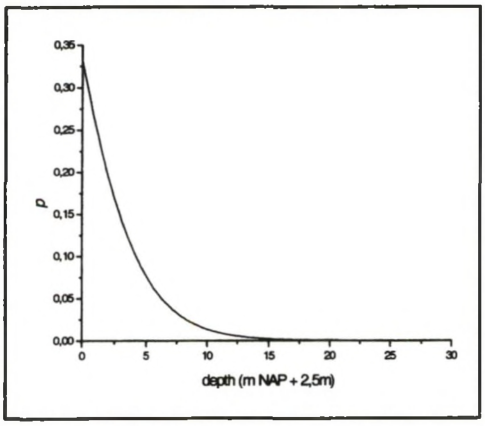
Eteone longa	*Term*	*Regression coefficient*	*Standard error*
present: 359 absent: 2753			
	Intercept	-4,4046	0,4486
	Temporal salinity	0,2217	0,0482
	Temporal salinity²	-0,00458	0,00123
	Concordance	56,80%	
	Intercept	-7,5659	0,7858
	Model salinity	0,4934	0,0742
	Model salinity²	-0,0102	0,00170
	Concordance	58,90%	



Depth

Only the linear term of depth was included in the model. As *E. longa* was mostly observed in the intertidal zone (see Table 7.1), a decreasing (sigmoidal) response was observed with increasing depth.

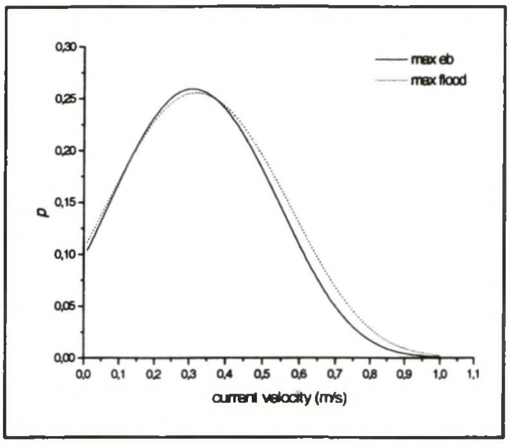
Eteone longa	*Term*	*Regression coefficient*	*Standard error*
present: 308 absent: 2566			
	intercept	-0,6993	0,0969
	depth	-0,3582	0,0292
	depth²	-	-
	concordance	77,30%	



Maximum ebb and flood current velocities

Both the linear and quadratic terms were included in both current velocity models, resulting in a unimodal response curve with an optimum around 0,30 m.s^{-1}. Both at low and especially at high current velocities the chance of occurrence of *E. longa* decreased substantially.

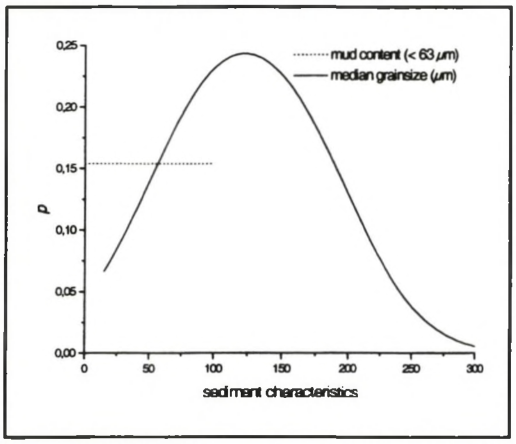
Eteone longa	*Term*	*Regression coefficient*	*Standard error*
present: 347 absent: 2690			
	Intercept	-2,2338	0,3016
	Maxeb	7,6833	1,4740
	Maxeb²	-12,4701	1,6913
	Concordance	77,00%	
	Intercept	-2,1425	0,2328
	Maxfl	6,7511	1,1868
	Maxfl²	-10,6249	1,3347
	Concordance	78,70%	



Sediment characteristics: median grainsize and mud content

Both the linear and quadratic terms were included in the median grain size model, whereas in the mud content model no terms were included. This resulted in a unimodal response curve for median grain size with an optimum around 125 µm, but with a similar tolerance in the range 75-175 µm. In finer and coarser sediments, the chance of occurrence of *E. longa* is very low.

Eteone longa	*Term*	*Regression coefficient*	*Standard error*
present: 221 absent: 1281			
	intercept	-3,0924	0,3747
	median	0,0319	0,00570
	median²	-0,00013	0,00002
	concordance	69,2%	
present: 213 absent: 1173			
	intercept	-1,7060	0,0745
	mud	-	-
	mud²	-	-
	concordance	-	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, linear and/or quadratic terms were included for all abiotic explanatory variables (Table 7.3). The linear term of maximum flood current velocity, model salinity and depth added most to the change of deviance in the model. The model with sediment characteristics had a similar performance, as indicated by the concordance, with the linear and quadratic term of median grain also size included in the model. The quadratic term of maximum flood current velocity and the linear term of temporal salinity added most to the change of deviance in this model.

Table 7.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Eteone longa	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment presence: 301 absence: 2526			with sediment presence: 197 absence: 1205		
	Intercept	-7,4407	0,8847	Intercept	-8,2733	1,0778
	Temporal salinity	0,0628	0,0173	Temporal salinity	0,0651	0,0213
	Model salinity	0,5041	0,0843	Model salinity	0,3650	0,1389
	Model salinity^2	-0,0112	0,00201	Model salinity^2	-0,00800	0,00274
	Depth	-0,3861	0,0563	Depth	-0,2229	0,0625
	Depth^2	0,00663	0,00131	Maxfl	9,6220	2,3346
	Maxeb^2	-1,2397	1,5509	Maxfl^2	-12,2741	2,6998
	Maxfl	4,9387	1,4632	Median	0,0212	0,00653
	Maxfl^2	-6,0626	1,5509	Median^2	-0,00008	0,000021
	concordance	87,0%		concordance	85,7%	

Percent correct predictions

The logistic regression model, without or with sediment characteristics, included, predicts overall 87,5 % of the responses correctly (Table 7.4). However, only 41,5 % of the modelled (or predicted) presences were also actually observed in the field. When including sediment characteristics in the model, this percentage was similar (41,1 %).

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 7.4. Comparative statistics on the predicted and observed occurrence of Eteone longa in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model).

Eteone longa (p=0,334)
(without sediment characteristics)

Response Observed	Model Pm	Am	Total	% **correct**
Po	125	176	301	41,5
Ao	176	2350	2526	93
Total	301	2526	2827	87,5

Difference between proportions	0,346	
95% CI	-1,000 to 0,393	(normal approximation)
Fisher exact test: 1-tailed p (observed by model: Po<Ao)	<0.0001 (exact)	

Eteone longa (p=0,38)
(with sediment characteristics)

Response Observed	Model Pm	Am	Total	% **correct**
Po	81	116	197	41,1
Ao	116	1008	1124	89,7
Total	197	1124	1321	82,4

Difference between proportions	0,308	
95% CI	-1,000 to 0,368	(normal approximation)
Fisher exact test: 1-tailed p (observed by model: Po<Ao)	<0.0001 (exact)	

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ECOPROFILE OF *HETEROMASTUS FILIFORMIS*

INTRODUCTION

Heteromastus filiformis is the most common species in the Schelde estuary, being observed in all salinity regions and all depth strata. It is the most important annelid species in the estuary, contributing substantially to both the overall macrobenthic density and biomass in the intertidal zone of all salinity regions.

AUTO-ECOLOGY

HETEROMASTUS FILIFORMIS	Annelida, Polychaeta

General

Heteromastus filiformis is known as a cosmopolitic and opportunistic species, often very dominant in marine benthic communities (ROSENBERG, 1972; BOESH et al., 1976; SHAFFER, 1983). The species is observed from the eulittoral up to 1000 m (HARTMAN & FAUCHALD, 1971), but with a clear preference for the intertidal zone. In the eighties *H. filiformis* showed a remarkable increase in the Dutch and German Wadden Sea, which was related to an increase in eutrophication of the area (DÖRJES *et al.*, 1986; BEUKEMA, 1989). Therefore, *H. filiformis* is often considered as an indicator for organic pollution.

Habitat preferences

Salinity: *H. filiformis* is able to withstand low salinities. The limit of its occurrence is about the isohaline of 3 g Cl^-/l at high tide during average river discharge (WOLFF, 1973), but it becomes rarer already beyond the isohaline of 10 g Cl^-/l under similar conditions (WOLFF, 1973). MUUS (1967) also observed the species less frequently at salinities below 10 g Cl^-/l.

Sediment type: *H. filiformis* prefers less well sorted, muddy sediments, but also the species occurs regularly in fine and median sands (WOLFF, 1973, CADÉE, 1979).

Feeding

H. filiformis is a non selective deposit feeder (MUUS, 1967). RHOADS (1974) describes *H. filiformis* as a 'conveyer-belt feeder'. They feed 'head-down' at a certain depth beneath the sediment surface and the faeces are deposited at the sediment surface (CADÉE, 1979). *H. filiformis* is a well known prey of *Nephtys hombergii* (BEUKEMA, 1987).

Population dynamics and life history

Spawning occurs in spring. Larvae are pelagic. Of the juveniles appearing in spring, only half are sexually mature the next winter and are therefore capable to reproduce in their first year of life (SHAFFER, 1983). The other half only reproduce in spring of their second year of life. *H. filiformis* reproduces only once and dies most of the time shortly after spawning (BUCHANAN & WARWICK, 1974).

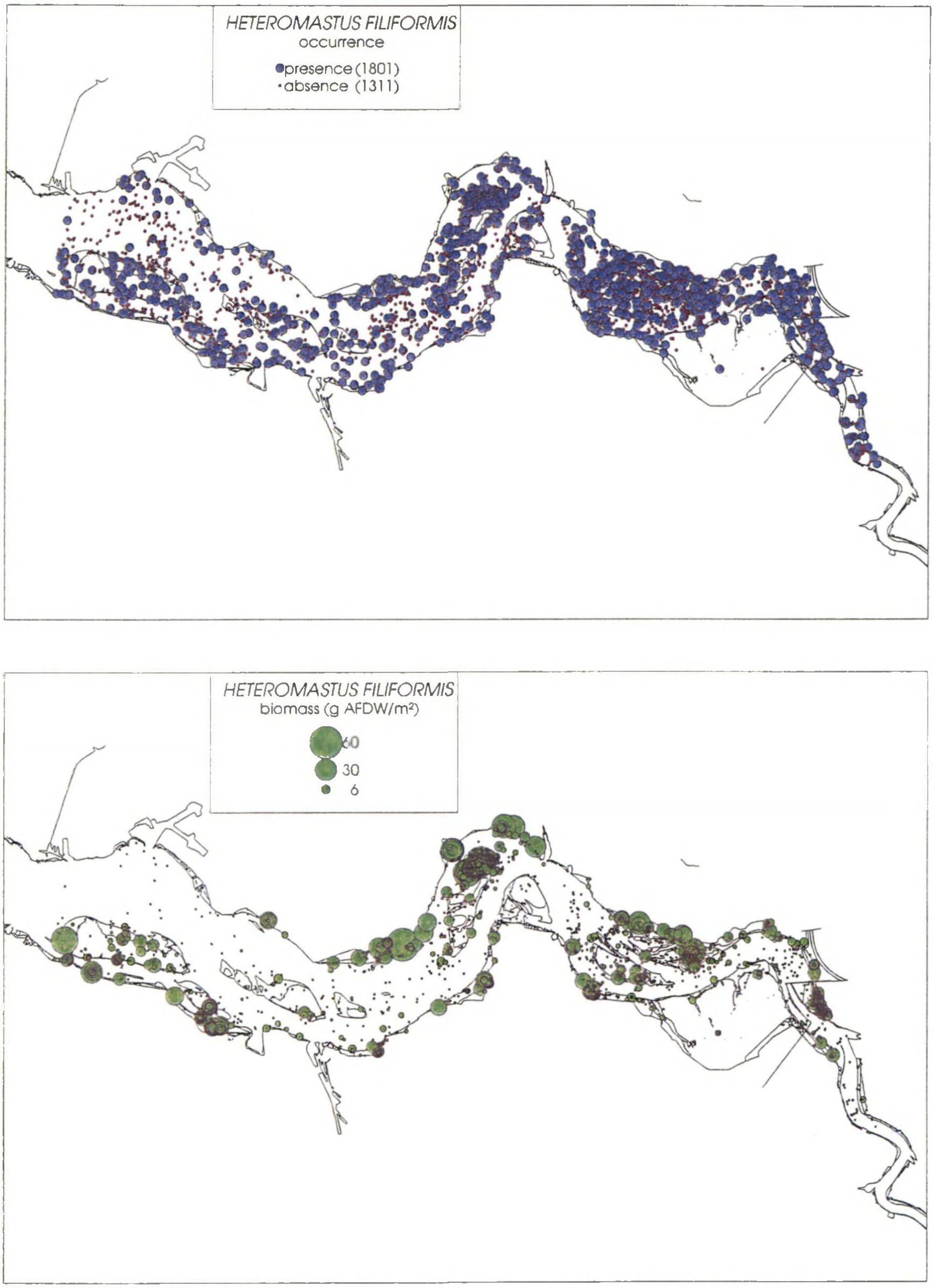


Figure 8.2. Geographical distribution maps of Heteromastus filiformis in the Schelde estuary with presence/absence data (top) and biomass (g AFDW m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

H. filiformis was the most observed species in the Schelde estuary, being commonly present in all salinity regions and all depth strata (Table 8.1). The highest frequencies of occurrence are observed in the intertidal zones of all salinity regions.

Mean biomass and mean density were significantly higher in the intertidal zone (Figure 8.1), contributing substantially to both the overall macrobenthic density and biomass in the intertidal zone of all salinity regions. The geographical distribution of *H. filiformis* in the Schelde estuary is shown in Figure 8.2.

Table 8.1. Occurrence (p/a) of H. filiformis along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone).

	1	2	3	4
Littoral	67,2 % (n=262)	86,5 % (n= 503)	75,9 % (n=485)	68,3 % (n= 287)
Undeep subtidal	29,8 % (n=151)	39,2 % (n=153)	53,5 % (n=127)	37,3 % (n=51)
Deep subtidal	17,1 % (n=123)	44,6 % (n=130)	56,3 % (n=112)	55,2 % (n=67)
Channel	20,4 % (n=186)	43,4 % (n=173)	46,6 % (n=232)	48,6 % (n=70)

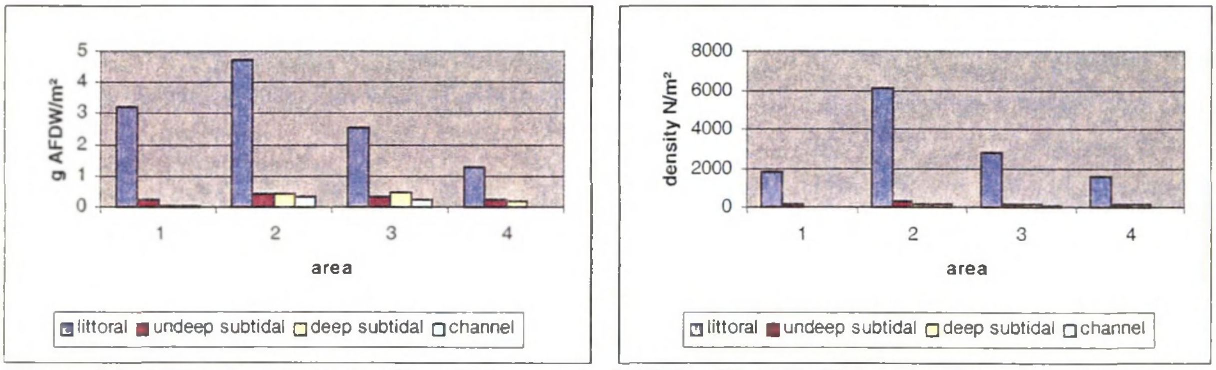


Figure 8.1. Mean density (ind m^{-2}) and biomass (g AFDW m^{-2}) of H. filiformis along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline ; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

Spring and autumn occurrence were comparable in the polyhaline zone (salinity regions 1 and 2) and the α-mesohaline zone (salinity region 3) (Table 8.2). In the β-mesohaline zone the species was less frequently observed in spring, probably due to the lower salinity conditions during this period. Both density and biomass were much higher in autumn as compared to spring.

Table 8.2. Spring (March - May) versus autumn (Augustus - October) occurrence (p/a), density (ind m^{-2}) and biomass (g AFDW m^{-2}) of H. filiformis in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone).

LITTORAL		1	2	3	4
Presence	Spring	65,0 % (n=97)	84,0 % (n= 169)	69,4 % (n=147)	33,3 % (n= 33)
	Autumn	66,7 % (n=135)	83,0 % (n=218)	75,9 % (n=249)	79,0 % (n= 214)
Density	Spring	985	2957	1448	253
	Autumn	2462	7177	3183	2066
Biomass	Spring	1,81	3,06	0,83	0,41
	Autumn	4,02	5,37	2,85	1,60

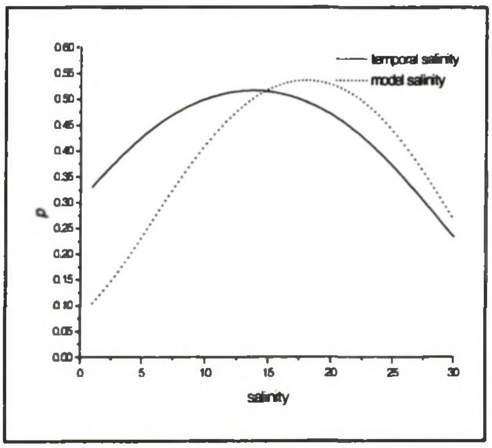
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Both the linear and quadratic term were included in both salinity models. This resulted in unimodal response curves for *H. filiformis*, however with a very broad tolerance, indicating a high probability of occurrence along the complete salinity gradient. This is in accordance with Table 8.1. The response curve based on the model for temporal salinity was somewhat broader; especially towards the lower salinities there was a higher probability of occurrence as compared to the curve based on the model for model salinity. This was probably the result of *H. filiformis* being observed at high frequencies, not only in autumn, but also in spring, when in general lower (temporal) salinities are observed (Table 8.2).

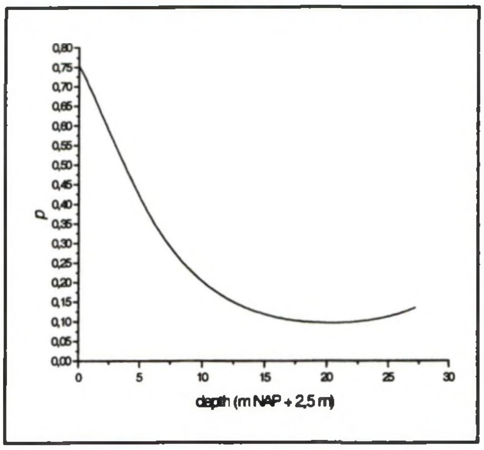
Heteromastus filliformis	*Term*	*Regression coefficient*	*Standard error*
Present: 1333 absent: 1779			
	Intercept	-0,8323	0,1935
	Temporal salinity	0,1310	0,0237
	Temporal salinity^2	-0,00476	0,000665
	Concordance	59,20%	
	Intercept	-2,4277	0,2879
	Model salinity	0,2869	0,0317
	Model salinity^2	-0,00799	0,00081
	Concordance	59,20%	



Depth

Both the linear and quadratic term was included in the depth model for *H. filiformis*. However, no unimodal response curve was obtained, but it can be concluded that the chance of occurrence of *H. filiformis* was highest in the intertidal zone, but also in the subtidal zone the species could be observed, although less frequently.

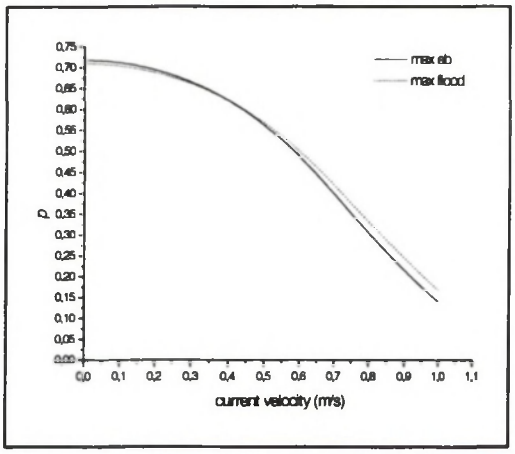
Heteromastus filiformis	*Term*	*Regression coefficient*	*Standard error*
Present: 1190 absent: 1684			
	Intercept	1,1226	0,0781
	Depth	-0,3303	0,0183
	depth^2	0,00811	0,000698
	Concordance	75,30%	



Maximum ebb and flood current velocities (m.s^{-1})

Only the linear term was included in both current velocity models. This resulted in more or less similar sigmoidal response curves for both models with a decrease in chance of occurrence with increasing current velocities, but with a broad tolerance up to 0.4-0.5 m.s^{-1}. At higher current velocities, a linear decrease in chance of occurrence was noticed.

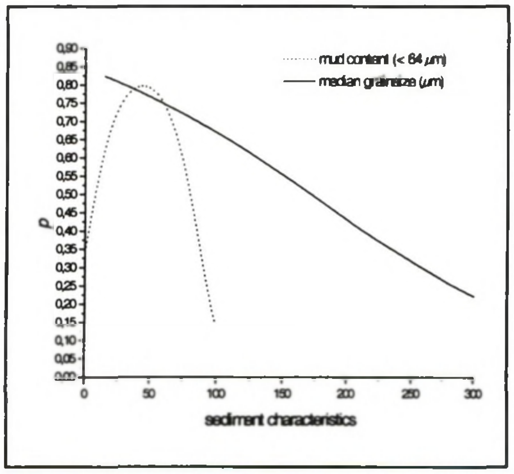
Heteromastus filiformis	*Term*	*Regression coefficient*	*Standard error*
Present: 1293 absent: 1744			
	Intercept	0,9316	0,0645
	Maxeb	-	-
	Maxeb²	-2,7518	0,1299
	Concordance	75,40%	
	Intercept	0,8926	0,0611
	Maxfl	-	-
	Maxfl²	-2,4952	0,1122
	Concordance	76,80%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Only the linear term was included in the median grain size model, whereas in the mud content model both the linear and the quadratic term were included. This resulted in a linear curve for median grain size, showing a high chance of occurrence in muddy and very fine sand sediments (small μm for median grain size), and an unimodal response curve for mud content, with an optimum at 45%, but with a very broad tolerance.

Heteromastus filiformis	*Term*	*Regression coefficient*	*Standard error*
present: 777 absent: 725			
	intercept	1,6892	0,1366
	median	-0,00984	0,000765
	median²	-	-
	concordance	71,40%	
present: 744 absent: 642			
	intercept	-0,6586	0,0877
	mud	0,0919	0,00917
	mud²	-0,00104	0,000129
	concordance	70,90%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, both the linear as the quadratic term were included for all abiotic explanatory variables, except the linear term of maximum flood current velocity (Table 8.3), with the linear term of maximum flood current velocity (maxfl) adding most to the change in deviance of the model (but removed). The model with sediment characteristics had a better performance, as indicated by the concordance, with the quadratic term of median grain size included in the model. The linear terms of maximum flood current velocity (but removed), depth, median and model salinity added most to the change of deviance in this model.

Table 8.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Heteromastus filiformis	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment presence: 1164 absence: 1663			with sediment Presence: 686 Absence: 607		
	intercept	-2,2298	0,3763	Intercept	-7,5618	1,0637
	Temporal salinity	0,1147	0,0334	Temporal salinity	0,3599	0,0686
	Temporal salinity^2	-0,00426	0,00105	Temporal salinity^2	-0,0129	0,00230
	Model salinity	0,3433	0,0471	Model salinity	0,4851	0,1009
	Model salinity^2	-0,00845	0,00131	Model salinity^2	-0,00845	0,00286
	Depth	-0,1261	0,0238	Depth	-0,2340	0,0494
	Depth^2	0,00448	0,000796	Depth^2	0,00732	0,00186
	Maxeb^2	-0,7335	0,2175	Maxeb	7,7127	1,3858
	Maxfl^2	-1,7250	0,1794	Maxeb^2	-4,9373	1,0796
				Maxfl	-2,9286	0,4725
				Median	-0,00552	0,00205
				Mud	0,1073	0,0181
				Mud^2	-0,00114	0,000219
	concordance	82,3%		concordance	89,2%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 90,0 % of the responses correctly (Table 8.4). 69,9 % of the modelled (or predicted) presences were also actually observed in the field, indicating a good performance of the model. When including sediment characteristics in the model, this percentage increased up to 82,5 %, indicating a very good performance of the model. So the model performed better when the sediment characteristics were included in the model.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 8.4. Comparative statistics on the predicted and observed occurrence of H. filiformis in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model).

Heteromastus filiformis (p=0,505)
(without sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	814	350	1164	69,9
Ao	350	1313	1663	80
Total	1164	1663	2827	75,2

Difference between proportions	0,489	
95% CI	-1,000 to 0,516	(normal approximation)
Fisher exact test: 1-tailed p (observed by model: Po<Ao)	<0.0001 (exact)	

Heteromastus filiformis (p=0,56)
(with sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	566	120	686	82,5
Ao	120	487	607	80,2
Total	686	607	1293	81,4

Difference between proportions	0,627	
95% CI	-1,000 to 0,663	(normal approximation)
Fisher exact test: 1-tailed p (observed by model: Po<Ao)	<0.0001 (exact)	

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ECOPROFILE OF HYDROBIA ULVAE

INTRODUCTION

Hydrobia ulvae is the most common observed gastropod on soft sediments in the Schelde estuary. Locally this species can reach very high densities, and in salinity region 2 *H. ulvae* makes up about 10% of the total intertidal density. Biomass values were low and therefore the contribution to the overall macrobenthic biomass in the Schelde estuary is small.

AUTO-ECOLOGY

HYDROBIA ULVAE (Pennant, 1777)	Mollusca, Gastropoda

General

The prosobranch *Hydrobia ulvae* is a widely distributed inhabitant of the intertidal zone of lagoons and estuaries throughout Europe and other geographical regions (GRAHAM, 1988). *H. ulvae* often demonstrates a typically cyclic behaviour of crawling, digging in, and floating (by means of a mucous raft). NEWELL (1962) interpreted this behaviour as a way of exploiting food just under the sediment surface, whereas SCHÄFER (1972) and BARNES (1981c) rather interpreted this behaviour as a protection against desiccation and predation. Many authors interpret the floating behaviour as a mechanism for active dispersion (NEWELL, 1962; ANDERSON, 1971; LEVENTION, 1979). BARNES (1981a,b,c) AND LITTLE & NIX (1970) could not observe any cyclic floating behaviour. According to BARNES (1981c) only a very small part of the population (1%), and probably only accidentally, will disperse by floating during each tide. Sediment transport through currents and wave action has a much larger impact on the dispersion of H. ulvae then the floating behaviour (SIEGISMUND & HYLLEBERG, 1987). LAPPALAINEN (1979) ascribed a decrease in *H. ulvae* in an undeep area of the Baltic Sea to a change (increase) in water movements in the area.

Habitat preferences

Salinity: *H. ulvae* is a marine species penetrating into the brackish part of the estuaries until a salinity of 10 g Cl^-/l at high tide during average river discharge or about 3 g Cl^-/l during high river discharges (WOLFF, 1973). NEWELL (1964) observed experimentally a salinity of about 3,5 g Cl^-/l as the lower limit of the physiological tolerance of *H. ulvae*. In the Baltic Sea MUUS (1967) observed a lower salinity tolerance of 5-6 g Cl^-/l. Towards the North Sea, however, H. ulvae most probably is limited by the increased water movements at the exposed shores (WOLFF, 1973)

Sediment type: *H. ulvae* seems to be rather indifferent about the nature of the substratum, but seems more influenced by the water movements (currents, waves). As a result, *H. ulvae* is most often observed in fine (BARNES & GREENWOOD, 1978) or muddy sediments (NEWELL, 1962; CHATFIELD, 1972; WOLFF, 1973*)*. *H. ulvae* is also often observed in hughe densities in seagrass meadows and saltmarshes.

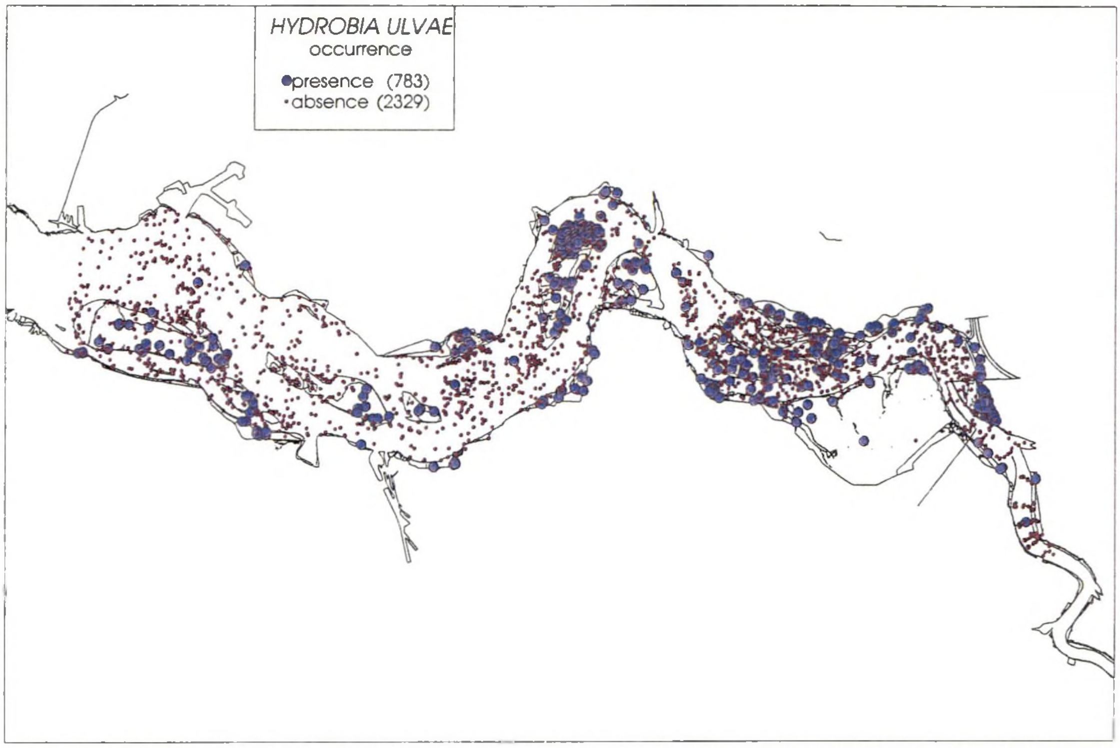
Feeding

H. ulvae is both a deposit feeder (FENCHEL & KOFOED, 1971) as a grazer (LOPEZ & KOFOED, 1980), which mainly feeds on benthic diatoms and to a certain extent also on bacteria (NEWELL, 1965; HYLLEBERG & RIIS-VESTERGAARD, 1984). *H. ulvae* grazes on the sediment surface by means of its proboscis.

Population dynamics and life history

Reproduction occurs, like with all prosobranch Mollusca, through copulation after which the fertilised eggs are deposited by the female on the shells of the own species, but also on dead shells, sand grains and green macroalgae (ANDERSON, 1971; FISH & FISH, 1974; BACHELET & YACINE-KASSAB, 1987). Egg capsules are deposited whole year round, with the most important period being April-July. *H. ulvae* is the only species from the Hydrobiidae which have pelagic larvae (HYLLEBERG, 1986). However, the nature of the larvae, that may be non-planktotrophic, planktonic and lecithotrophic, or planktotrophic (Barnes, 1988) and the life in the plankton, that could last from only some hours or some days (THORSON, 1946; PILKINGTON, 1971) to several weeks (Fish & Fish, 1977), are especially controversial. Once settled, they can be transported again through passive migration (e.g. currents, waves) to other areas (SIEGISMUND & HYLLEBERG, 1987). Other studies reveal that the length of larval life or the reproductive strategy of the species could be environmentally induced (BARNES, 1988, 1990, 1994). For more details on the population dynamics of *H. ulvae* see e.g. BARNES (1988,1990,1994) and SOLA (1996).

Parasite infestation is often mentioned as being responsible for changes in the behaviour of *H. ulvae* (MINCHELLA, 1985; HUXHAM ET AL., 1995); trematodes may also infect the gonads and other glands, thus originating a special morphology and an abnormal increase in the size of the snail (MOURITSEN & JENSEN, 1994; HUXHAM ET AL., 1995; SOLA, 1996). This infestation may result in a dramatical decimation of the population in the summer period (JENSEN & MOURITSEN, 1992).



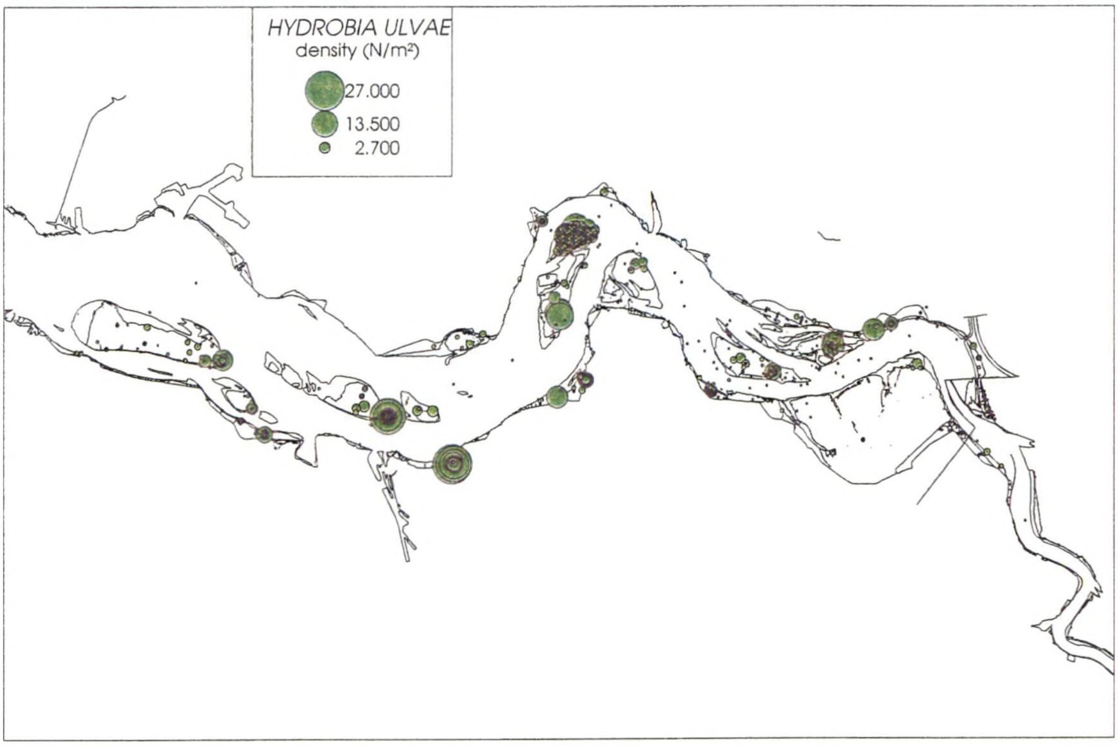


Figure 9.2. Geographical distribution maps of Hydrobia ulvae in the Schelde estuary with presence/absence data (top) and density (ind m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

H. ulvae was commonly observed in the intertidal zone of all salinity regions (Table 9.1), but clearly preferred the polyhaline/mesohaline transition zone (salinity regions 2 and 3). In this zone also subtidally the species was observed, although not common.

Mean biomass and mean density of *H. ulvae* were highest in salinity region 2 (Figure 9.1), making up in this zone about 10% of the total intertidal density. Biomass values were low and therefore the contribution to the overall macrobenthic biomass in the Schelde estuary is small. The geographical distribution of *H. ulvae* in the Schelde estuary is shown in Figure 9.2.

Table 9.1. Occurrence (p/a) of H. ulvae along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	34,7 % (n=262)	66,0 % (n= 503)	44,1 % (n=485)	30,0 % (n= 287)
undeep subtidal	2,0 % 'n=151)	4,6 % (n=153)	6,3 % (n=127)	2,0 % (n=51)
deep subtidal	0,0 % (n=123)	4,6 % (n=130)	8,0 % (n=112)	1,5 % (n=67)
channel	0,5 % (n=186)	4,1 % (n=173)	6,9 % (n=232)	1,4 % (n=70)

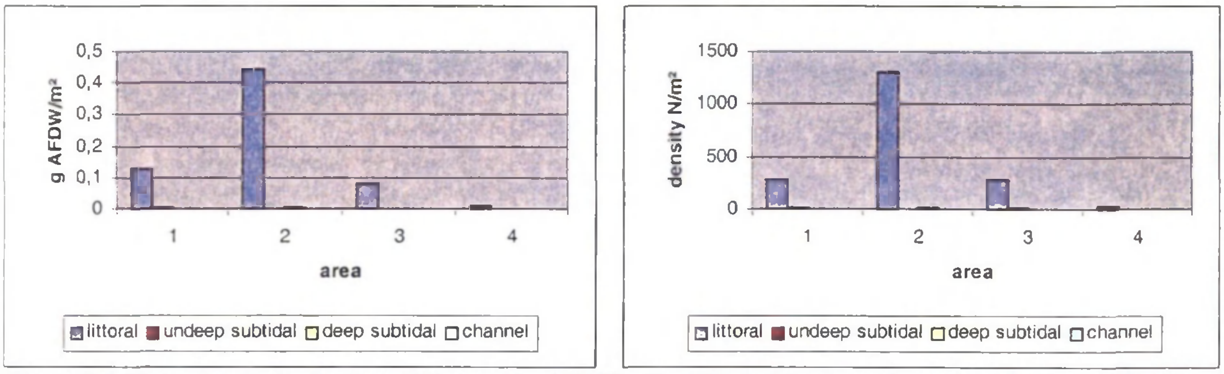


Figure 9.1 Mean density (ind m⁻²) and biomass (g AFDW m⁻²) of Hydrobia ulvae along the salinity and depth gradient in the Schelde estuary (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone).

Seasonal variations: spring versus autumn occurrence

Spring and autumn occurrence were comparable in the polyhaline zone (salinity regions 1 and 2) and the α-mesohaline zone (salinity region 3) (Table 9.2). In the β-mesohaline zone the species was less frequently observed in spring, probably due to the lower salinity conditions during this period. Both density and biomass doubled more or less in autumn as compared to spring.

Table 9.2. Spring (March - May) versus autumn (Augustus - October) occurrence (presence/absence), density (ind m⁻²) and biomass (g AFDW m⁻²) of Hydrobia ulvae in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone).

LITTORAL		1	2	3	4
Presence	Spring	34,0 % (n=97)	63,3 % (n= 169)	36,7 % (n=147)	12,1 % (n= 33)
	Autumn	32,6 % (n=135)	60,1 % (n=218)	47,0 % (n=249)	36,0 % (n= 214)
Density	Spring	235	1024	216	8
	Autumn	315	1832	375	45
Biomass	Spring	0,0993	0,3493	0,0539	0,0015
	Autumn	0,1453	0,6862	0,0845	0,0091

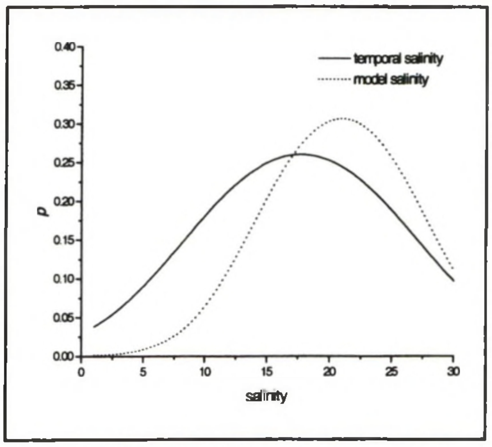
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Both the linear and quadratic term were included in both salinity models, giving unimodal response curves for both models. An optimum is observed in the poly/mesphaline zone, being around 17 psu and 21 psu for -'temporal salinity' and 'model salinity' respectively. The 'model salinity' model showed a more narrow tolerance with an optimum which shifted towards a higher salinity as compared to the 'temporal salinity' model. The 'temporal salinity' model showed a much broader response curve, extending more into the mesohaline zone. This difference in response was probably the result of the lower salinities occurring in winter and spring in the poly-/mesohaline zone (when *H. ulvae* was also frequently observed, see Table 9.2), which were dedected with the 'temporal salinity' model (see Material & Methods), and not with the 'model salinity' model, since this model does not take into account seasonal variations of salinity.

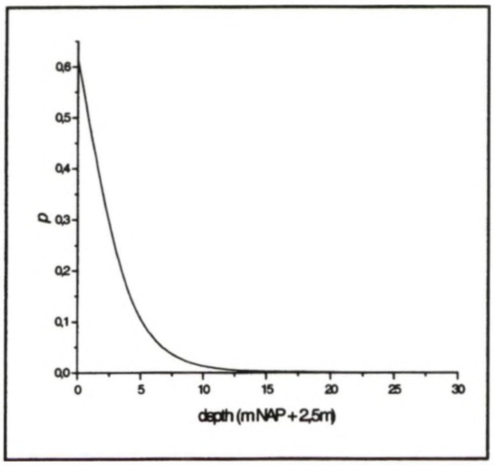
Hydrobia ulvae	*Term*	*Regression coefficient*	*Standard error*
present: 603 absent: 2509			
	Intercept	-3,5035	0,3146
	Temporal salinity	0,2279	0,0366
	Temporal salinity²	-0,00785	0,000995
	Concordance	58,70%	
	Intercept	-7,6278	0,6499
	Model salinity	0,6499	0,0568
	Model salinity²	-0,0155	0,00136
	Concordance	69,10%	



Depth

Both the linear and quadratic term were included in the depth model. However, the response showed a rather linear decrease in chance of occurrence of *H. ulvae* with increasing depth, clearly reflecting the littoral preference of this species.

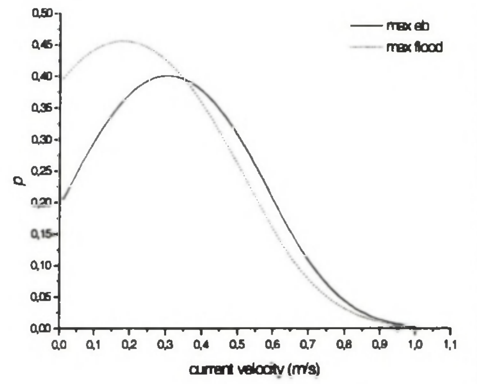
Hydrobia ulvae	*Term*	*Regression coefficient*	*Standard error*
present: 527 absent: 2347			
	Intercept	0,4673	0,0931
	Depth	-0,5655	0,0345
	depth²	0,00868	0,00154
	Concordance	83,10%	



Maximum ebb and flood current velocities (m.s^{-1})

Both the linear and quadratic terms were included in both current velocity models, resulting in an unimodal response curve for both models with an optimum around 0,3 and 0.18 m.s^{-1} for maximum ebb and maximum flood current velocity respectively. However, a relatively broad tolerance was observed up to current velocities of 0,5 m.s^{-1}. At higher current speeds a linear and steep decrease in chance of occurrence of *H. ulvae* was observed.

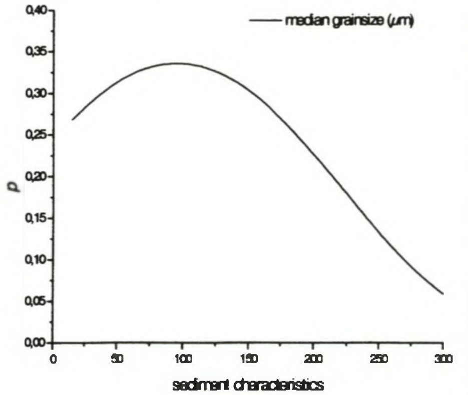
Hydrobia ulvae	*Term*	*Regression coefficient*	*Standard error*
Present: 582 Absent: 2455			
	Intercept	-1,4178	0,2391
	Maxeb	6,6523	1,1100
	Maxeb^2	-10,9256	1,2036
	Concordance	77,40%	
	Intercept	-0,4466	0,1810
	Maxfl	3,0057	0,9678
	Maxfl^2	-8,4305	1,1323
	Concordance	84,70%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Both the linear and quadratic terms were included in the median grain size model, whereas no terms were included in the mud content model. This resulted in an unimodal response curve with an optimum around 100 μm for median grain size. However, the response curve was rather broad and *H. ulvae* seemed rather tolerant concerning median grain size. Only in very coarse sediments, the chance of occurrence of *H. ulvae* was very low.

Hydrobia ulvae	*Term*	*Regression coefficient*	*Standard error*
present: 396 absent: 1106			
	Intercept	-1,1361	0,2376
	Median	0,00952	0,00329
	median^2	-0,00005	0,000011
	Concordance	63,70%	
present: 613 absent: 773			
	Intercept	-0,9163	0,0595
	Mud	-	-
	mud^2	-	-
	Concordance		



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, both the linear as the quadratic term were included for all abiotic explanatory variables, except for the quadratic terms of maximum flood (maxfl) and maximum ebb (maxeb) current velocities (Table 9.3). The linear terms of maximum flood current velocity and depth, and the linear and quadratic term of model salinity added most to the change of deviance in the model. The model with sediment characteristics had a similar performance, as indicated by the concordance, with the linear term of median grain size included in the model. The same terms as the model without sediment characteristics were responsible for the largest change of deviance in this model.

Table 9.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Hydrobia ulvae	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment presence: 515 absence: 2312			with sediment Presence: 370 Absence: 1032		
	Intercept	-8,5258	0,6652	Intercept	-8,9867	0,8517
	Temporal salinity	0,1491	0,0548	Temporal salinity	0,0411	0,0197
	Temporal salinity^2	-0,00379	0,00170	Model salinity	0,9189	0,1003
	Model salinity	0,8541	0,0831	Model salinity^2	-0,0207	0,00260
	Model salinity^2	-0,0194	0,00221	Depth	-0,4817	0,0759
	Depth	-0,5680	0,0543	Maxeb	8,5542	2,0397
	Depth^2	0,0099	0,00118	Maxeb^2	-4,4185	2,1189
	Maxeb	1,7631	0,4958	Maxfl	-5,2032	0,6484
	Maxfl	-4,0569	0,4140	Median	-0,0085	0,00154
	Concordance	91,9%		concordance	91,7%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 88,3 % of the responses correctly (Table 9.4). 67,9 % of the modelled (or predicted) presences were also actually observed in the field, indicating a good performance of the model. When including sediment characteristics in the model, this percentage increased up to 72,7 %. So the model performed better when the sediment characteristics were included in the model.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 9.4. Comparative statistics on the predicted and observed occurrence of H. ulvae in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model).

Hydrobia ulvae (p=0,474)
(without sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	349	165	514	67,9
Ao	165	2147	2312	92,9
Total	514	2312	2826	88,3

Difference between proportions	0,608	
95% CI	-1,000 to 0,643	(normal approximation)
Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)	

Hydrobia ulvae (p=0,50)
(with sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	269	101	370	72,7
Ao	101	931	1032	90,2
Total	370	1032	1402	85,6

Difference between proportions	0,629	
95% CI	-1,000 to 0,670	(normal approximation)
Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)	

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ECOPROFILE OF MACOMA BALTHICA

INTRODUCTION

Macoma balthica is the most common bivalve species in the Schelde estuary. It is very common in the intertidal zone along the complete salinity gradient of the Schelde estuary. It contributes substantially to the overall macrobenthic biomass in the intertidal zone of the Schelde estuary.

AUTO-ECOLOGY

MACOMA BALTHICA (LINNEAUS, 1758	Mollusca, Bivalva, Tellinidae

General

The Baltic Tellin *Macoma Balthica* shows a wide arctic-boreal distribution along the coasts of the Norhtern Ice Sea and both sides of the Northern Atlantic. It is a very common species along the coasts and estuaries of northern Europe and its distribution extends from the White Sea and other parts of northern Russia (BEUKEMA & MEEHAN, 1985) to the Gironde estuary (BACHELET, 1980) in SW France where the species reaches its southern limit of its geographical range. In North America the species is found from the Hudson Bay (GREEN, 1973) in North America to as far south as Chesapeake and San Francisco Bays (NICHOLS & THOMPSON, 1982). The occurrence of *M. balthica* is normally limited to shallow coastal areas (up to about 25 m depth) and intertidal areas. In the Baltic Sea the species is observed to a depth of 150 m.

Macoma balthica lives horizontally (for migrating individuals) or vertically in the sediments. The inhalant siphon is long and can be extended above the surface (at low tide) where it moves round and round. The exhalant siphon is much shorter and does not come out of the substrate (REISE, 1985). The siphons keep on growing (READING & MCGRORTY, 1978), which means that older animals will live deeper than juveniles (VASSALLO, 1977; ZWARTS & WANINK, 1989). Depth distribution is seasonally determined (READING & MCGRORTY, 1978; ZWARTS & WANINK, 1989), with *M. balthica* living deeper in autumn and winter than in spring and summer. However, at high summer temperatures *M. balthica* reacts also by burrowing deeper into the sediment.

M. balthica has been subject of numerous papers because of its common occurrence and its role as an important link between primary producers and fish and shorebirds.

Habitat preferences

Salinity: *M. balthica* is a typical euryhaline species with a large salinity tolerance (from full sea water to less 3 ‰ S) but shows reduced growth rates and thin shells at low salinities. In the estuaries of the Delta area it reaches the isohaline of 2 g Cl^-/l at high tide during normal river discharge (WOLFF, 1973).

Sediment type: *M. balthica* inhabits all types of sandy sediments, but also shows a preference for the finer sediments with a median grain size of 150-225 µm and 0,5-10% of mud (WOLFF, 1973). NEWELL (1965) showed that large populations may occur in very fine sediments

Feeding

M.balthica is in the first place a selective deposit feeder (GILBERT, 1977; REISE, 1983), which is able to switch to filter feeding in sandy sediments (OLAFSSON, 1986; HUMMEL, 1985). When deposit feeding, also suspended algae can be taken up (HUMMEL, 1985; BEUKEMA & CADÉE, 1991; THOMPSON & NICHOLS, 1988). Also in the course of the year *M. balthica* is able to switch between feeding techniques. In spring and early summer, when phytoplankton blooms occur, food uptake occurs mainly through the water column by filter feeding. In summer and autumn, *M. balthica* shifts more towards deposit feeding and in winter it is almost inactive. Also the presence of large densities of congeners and/or other species can cause shifts in feeding techniques used (LIN & HINES, 1994; KAMERMANS, 1994). Food exists both of benthic and planktonic microalgae, but also detritus with bacteria and protozoa (REISE, 1985).

Population dynamics and life history

Populations of *M. balthica* are characterised by a relatively low variability in time and space, compared to other estuarine species (BEUKEMA *et al.*, 1983). This relative constancy is the result of a long life span, the large tolerance towards different environmental variables, and the use of different feeding mechanisms (MCLUSKY & ELLIOT, 1981). It also has an opportunistic reproductive strategy (HARVEY & VINCENT, 1989).

M. balthica is a gonochoristic species with comparable numbers of male and females. Duration, timing and number of spawning periods varies from year to year (GILBERT, 1978; BACHELET, 1980, 1986; HARVEY & VINCENT, 1989) and differ from place to place (e.g. WARWICK & PRICE, 1975; CHAMBERS & MILNE, 1975; BACHELET, 1980) and depends on water temperature and age (e.g. HONKOOP & VAN DER MEER, 1997). Main reproduction period is situated in spring (March-May) when water temperature rise above 10 °C. In the more southern areas of its geographical range a second reproduction period can occur in autumn. Macoma balthica has pelagic larvae (Jorgensen, 1946), which settle down at a size of 270-310 μm (BACHELET, 1986).

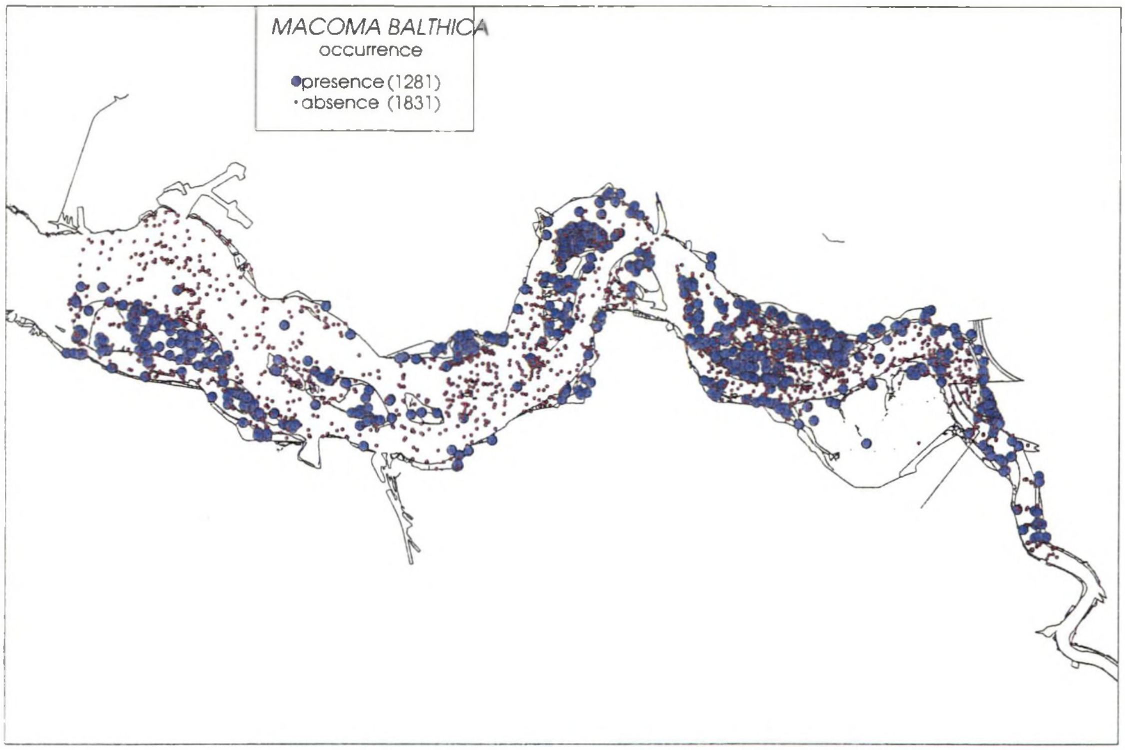
Settling takes place all over the intertidal flats (BOYDEN & LITTLE, 1973; RATCLIFFE *et al.*, 1981). By passive transport through tidal currents a redistribution takes place and the juveniles colonize mainly the areas high in the intertidal zone and near the marsh edge (BEUKEMA, 1981, 1993; BEUKEMA & DE VLAS, 1989). However, primary settlement on the tidal flats seems to be variable in space, and is also observed low in the intertidal zone (GÜNTHER, 1991, 1992; ARMONIES & HELLWIG-ARMONIES, 1992, ARMONIES, 1996). Probably nor tidal height, nor active selection can explain the primary settlement of *M. balthica*, but rather the local hydrodynamical conditions will determine this settlement, therefore considering it as a passive process. During their first winter the juveniles actively migrate by thread-drifting to the lower parts of the intertidal area and to the subtidal zone. The reason for this second (winter)migration is probably the very low winter temperatures and the possibility of ice cover on the mudflats. However, this winter migration is not seen in all areas, but specifically it is already often observed in the Wadden Sea (ARMONIES & HELLWIG-ARMONIES, 1992; BEUKEMA & DE VLAS, 1989; GÜNTHER, 1991; ARMONIES, 1996).

The start and length of the growing season depends on the geographical position. In northern areas growth start later and the duration is shorter. In The Netherlands animals start growing in spring with a duration of approximately four months (March-June) (ZWARTS, 1991). Year to year variations can be very high, depending e.g. on the presence of diatoms (BEUKEMA & CADÉE, 1991). Experimentally it was noticed that growth of *M. balthica* is (intraspecific) density dependent (BREY, 1991) and the effect seems more pronounced with deposit-feeding animals then with suspension-feeding animals (SKILLETER & PETERSON, 1994; PETERSON & SKILLETER, 1994). This density dependent growth is also observed in field studies, based on the growth of the year-rings (VINCENT *et al.*, 1994). Production estimates are given by e.g. ANKAR (1980), BERGH (1974) and CRANFORD *et al.* (1985).

Biotic interactions

Macoma balthica is an important prey-item of many shorebirds like Knot *Calidris canutus*, Dunlin *Calidris alpina*, Redshank *Tringa totanus*, Bar-tailed Godwit and Oystercather *Haematopus ostralegus*. Other important predators are flatfish, gobiids and epibenthic species like shrimps and crabs. Benthic organisms such as *Retusa obtusa* and *Nereis diversicolor* are important predators of young *Macoma balthica* (RATCLIFFE *et al.*, 1981).

Settling of *M. balthica* larvae can be hampered by the activity of sediment reworking invertebrates, such as *Arenicola marina* (FLACH, 1992).



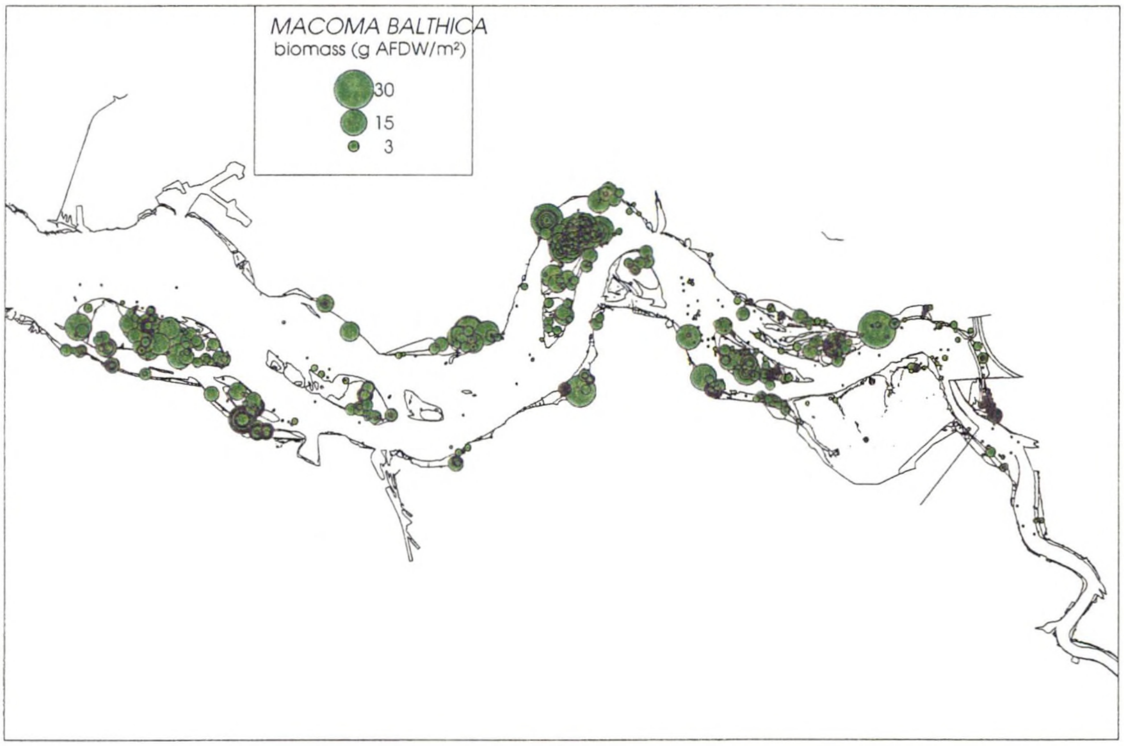


Figure 10.2. Geographical distribution maps of Macoma balthica in the Schelde estuary with presence/absence data (top) and biomass (g AFDW m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

M. balthica was a very common species in the intertidal zone of all salinity regions with a frequency of occurrence between 67 and 76 % (Table 10.1). Also in the subtidal zone *M. balthica* was observed, with a frequency of occurrence between 7,5 and 18 %.

Mean biomass was significantly higher in the polyhaline zone as compared to the mesohaline zone, and clearly decreased in upstream direction (Figure 10.1). This trend was not observed in the mean density, indicating larger individuals found in the polyhaline zone. Mean biomass and density in the subtidal zone were very low. The geographical distribution of *M. balthica* in the Schelde estuary is shown in Figure 10.2.

Table 10.1. Occurrence (p/a) of M. balthica along the salinity and depth gradients of the Schelde estuary. N=number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	66,8 % (n=262)	69,6 % (n= 503)	69,9 % (n=485)	76,3 % (n= 287)
undeep subtidal	16,6 % (n=151)	13,1 % (n=153)	14,2 % (n=127)	15,7 % (n=51)
deep subtidal	8,9 % (n=123)	10,8 % (n=130)	15,2 % (n=112)	10,5 % (n=67)
Channel	8,6 % (n=186)	7,5 % (n=173)	17,6 % (n=232)	11,4 % (n=70)

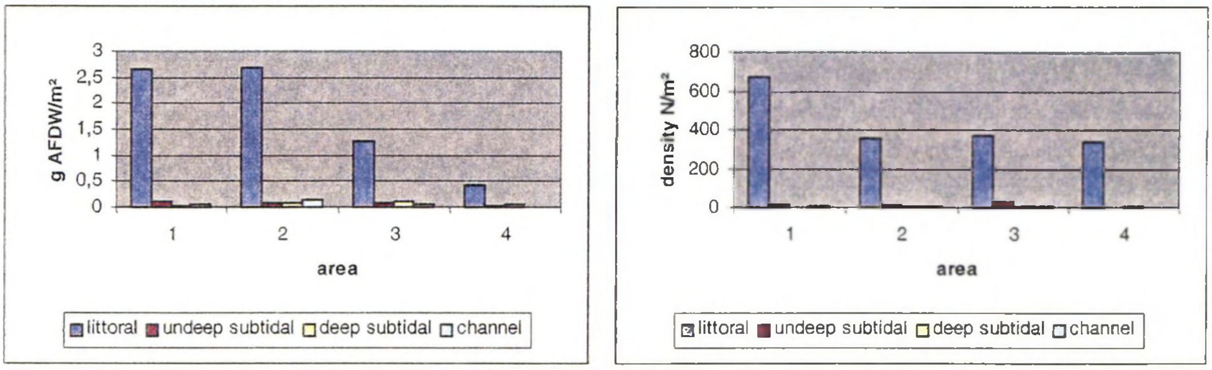


Figure 10.1. Mean density (ind m^{-2}) and biomass (g AFDW m^{-2}) of M. balthica along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline ; 3&4: mesohaline).

Seasonal variations : spring versus autumn occurrence

The occurrence was slightly higher in autumn in the salinity regions 1 to 3, whereas in salinity region 4 *M. balthica* was much less observed in spring samples (Table 10.2). Mean density, and to a lesser extent also mean biomass, were much higher in autumn.

Table 10.2. Spring (March - May) versus autumn (Augustus - October) occurrence (presence/absence), density (ind m^{-2}) and biomass (g AFDW m^{-2}) of M. balthica in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline zone; 3&4: mesohaline zone).

LITTORAL		1	2	3	4
Presence	Spring	53,6 % (n=97)	64,5 % (n= 169)	64,6 % (n=147)	48,5 % (n= 33)
	Autumn	72,6 % (n=135)	71,1 % (n=218)	68,3 % (n=249)	79,4 % (n= 214)
Density	Spring	152	228	137	49
	Autumn	923	462	438	380
Biomass	Spring	1,65	2,84	1,15	0,24
	Autumn	3,00	2,66	1,10	0,43

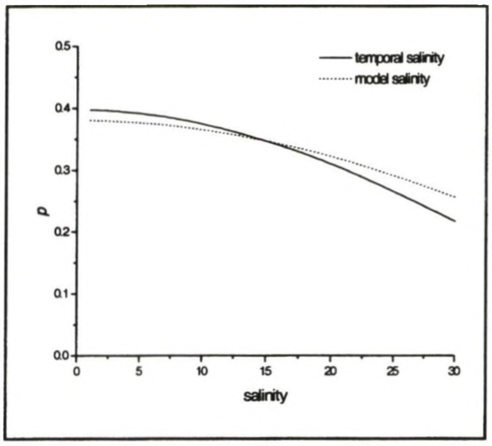
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Only the quadratic term of both 'temporal salinity' and 'model salinity' were included in the models. *M. balthica* showed no clear response for salinity, indicating a very high tolerance for salinity (see also Table 10.1).

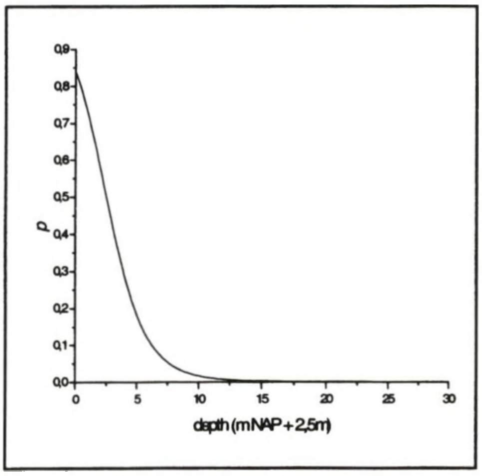
Macoma balthica	*Term*	*Regression coefficient*	*Standard error*
present: 973 absent: 2139			
	intercept	-0,4171	0,0676
	Temporal salinity	-	-
	Temporal salinity²	-0,00096	0,000149
	Concordance	56,50%	
	Intercept	-0,4889	0,0750
	Model salinity	-	-
	Model salinity²	-0,00064	0,000141
	Concordance	54,20%	



Depth

Both the linear and quadratic term were included in the depth model. However, the response showed a rather linear decrease in chance of occurrence of *M. balthica* with increasing depth (see also Table 10.2).

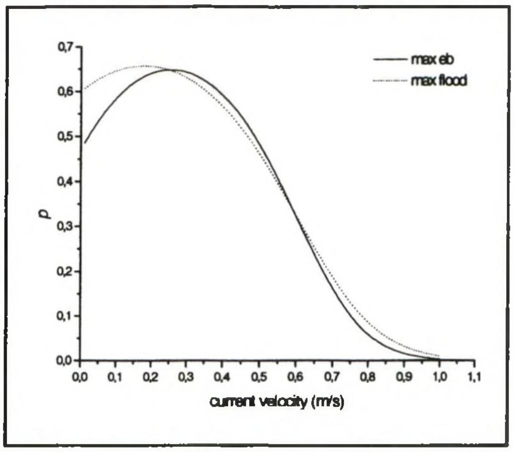
Macoma balthica	*Term*	*Regression coefficient*	*Standard error*
present: 840 absent: 2043			
	intercept	1,6521	0,0963
	depth	-0,6899	0,0307
	depth²	0,0115	0,000881
	concordance	88,60%	



Maximum ebb and flood current velocities (m.s^{-1})

Both the linear and quadratic terms were included in both current velocity models, resulting in an unimodal response curve for both models with an optimum around 0,175-0,275 m.s^{-1}. However, a relatively broad tolerance was observed up to current velocities of 0,5 m.s^{-1}. At higher current speeds a linear and steep decrease in probability of occurrence of *M. balthica* was observed.

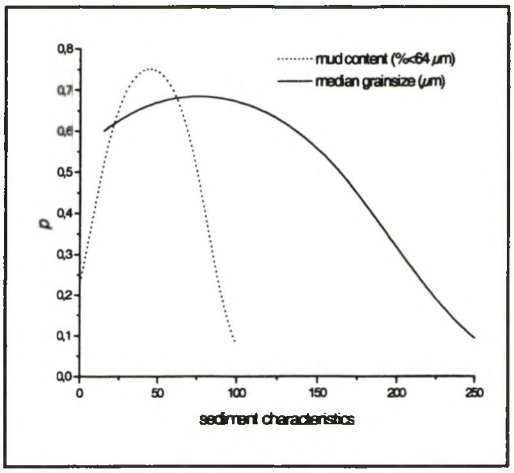
Macoma balthica	*Term*	*Regression coefficient*	*Standard error*
present: 936 absent: 2101			
	Intercept	-0,1159	0,2252
	Maxeb	5,7402	1,0365
	Maxeb²	-11,3351	1,1194
	Concordance	84,40%	
	Intercept	0,4058	0,1720
	Maxfl	2,7547	0,8376
	Maxfl²	-7,7741	0,8919
	Concordance	84,90%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Both the linear and quadratic terms were included in both the median grain size as the mud content models, resulting in an unimodal response curve with an optimum around 75 μm and 45% for median grain size and mud content respectively. However, the response curve was very broad and *M. balthica* seemed rather tolerant concerning median grain size and mud content. Only at very coarse sediments, as indicated by the median grain size model, the chance of occurrence of *M. balthica* was very low.

Macoma balthica	*Term*	*Regression coefficient*	*Standard error*
present: 629 absent: 873			
	intercept	0,2037	0,2564
	median	0,0151	0,00405
	median²	-0,0001	0,000015
	concordance	78,80%	
present: 613 absent: 773			
	intercept	-1,2070	0,0942
	mud	0,1040	0,00917
	mud²	-0,00117	0,00013
	concordance	73,50%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, no terms concerning salinity were included in the model (Table 10.3). The linear terms of maximum flood current velocity and depht added most to the change of deviance in the model. The model with sediment characteristics had a slightly better performance, as indicated by the concordance, with the quadratic term of median grain size included in the model. The linear term of maximum flood current velocity, the quadratic term of median grain size and the linear term of depth added most to the change of deviance in this model.

Table 10.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Macoma balthica	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment			with sediment		
	presence: 820			Presence: 562		
	absence: 2007			Absence: 731		
	intercept	0,4229	0,2790	Intercept	0,6798	0,6948
	Depth	-0,4422	0,0372	Temporal salinity	0,3963	0,0840
	Depth^2	0,00823	0,000971	Temporal salinity^2	-0,0159	0,00293
	Maxeb	3,6948	1,4378	Model salinity	-0,3009	0,1170
	Maxeb^2	-4,7585	1,4702	Model salinity^2	0,0140	0,00351
	Maxfl	3,5401	1,1828	Depth^2	-0,0980	0,0143
	Maxfl^2	-5,8467	1,2245	Maxfl	7,1246	1,9453
				Maxfl^2	-10,5546	2,2932
				Median^2	-0,00006	5,489E-6
	concordance	91,1%		concordance	94,0%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 85,5 % of the responses correctly (Table 10.4). 75,0 % of the modelled (or predicted) presences were also actually observed in the field, indicating a very good performance of the model. When including sediment characteristics in the model, this percentage increased up to 85,4 %, indicating a very good performance of the model. So the model performed better when the sediment characteristics were included in the model.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 10.4. Comparative statistics on the predicted and observed occurrence of M. balthica in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model).

Macoma balthica (p=0,605)
(without sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	615	205	820	75
Ao	205	1802	2007	89,8
Total	820	2007	2827	85,5

Difference between proportions 0,648
95% CI -1,000 to 0,675 (normal approximation)

Fisher exact test: 1-tailed p <0.0001 (exact)
(observed by model: Po<Ao)

Macoma balthica (p=0,605)
(with sediment characteristics)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	480	82	562	85,4
Ao	82	649	731	88,8
Total	562	731	1293	87,3

Difference between proportions 0,742
95% CI -1,000 to 0,773 (normal approximation)

Fisher exact test: 1-tailed p <0.0001 (exact)
(observed by model: Po<Ao)

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ECOPROFILE OF MYA ARENARIA

INTRODUCTION

Mya arenaria was not very common in the Schelde estuary. Only in the intertidal, polyhaline/mesohaline transition zone the species was observed regularly and here *M. arenaria* contributed about 10% to the overall intertidal macrobenthic biomass. However, its patchy distribution and very deep occurrence in the sediment of the larger individuals, makes this species very difficult to sample and therefore probably an underestimation has been made of the total biomass of this species.

AUTO-ECOLOGY

***MYA ARENARIA** (Linnaeus, 1758)*	Mollusca, Bivalva,

General

The Sandgaper *Mya arenaria* has a boreal amphi-atlantic distribution, which at present also occurs in the Pacific (Japan, Alaska). This American species was introduced in Europe in the 16-17th century.

M. arenaria lives in a vertical position in the sediment to a depth of 40 cm, depending on the age and the length of the two siphons (ZWARTS & WANINK, 1989). Through these siphons the species is in contact with the overlying water. The burrowing capacity diminishes with age (KÜHL, 1983). To a size of 5 cm *M. arenaria* is able to burrow again after being washed out, whereas older and bigger *M. arenaria* loose this burrowing capacity because the relative shorter foot is no longer able to get the shell in a vertical position, which is necessary for burrowing.

A detailed ecoprofile on *M. arenaria* can be found in STEUR *et al.* (1996) (in Dutch).

Habitat preferences

Salinity: *M. arenaria* is a typical euryhaline species, which penetrates estuaries to the low salinity zones. *M. arenaria* is well adapted to low and strongly fluctuating salinities. In the Delta area (SW Netherlands) small specimens reach nearly the isohaline of 2 g Cl^-/l during high tide at normal river discharge, but larger individuals only occur at higher salinities (WOLFF, 1973). In the Baltic *M. arenaria* occurs down to salinities of 2.5-3 g Cl^-/l (MUUS, 1967). In the Loire estuary ROBINEAU (1987) classifies the species as typically brackish. The seaward extension is not restricted by salinity, but by other factors, such as its slow pumping rate resulting in shortage of food in offshore waters (WOLFF, 1973).

Sediment type: *M. arenaria* is found in almost all sediment types (KÜHL, 1983), except in anaerobic mud and very coarse sand (MUUS, 1967; DANKERS & BEUKEMA, 1983). However, this species mainly prefer fine and muddy sediments (WOLFF, 1973). NEWELL & HIDU (1982) experimentally demonstrated that juvenile *M. arenaria* grew fasted in fine and muddy sediments. *M. arenaria* is relatively resistent to oxygen deficiency, long exposure times and severe winter weather (MUUS, 1967). *M. arenaria* has an aggregrated distribution pattern. It is suggested that, as in the case of sediment particles, hydrodynamic forces are primarily responsible for the zonation of *Mya* populations in intertidal areas (MATTHIESSEN, 1960).

Feeding

M. arenaria is a suspension feeder which feeds on small plankton (flagellates) and detritus (WOLFF, 1973; KÜHL, 1983). The pumping rate is lower than in many other suspension feeders. Deposit feeding has been observed in *Mya*, particularly when there is only a thin water film on the substrate. Food uptake is highest in the months April-May when also the phytoplankton bloom is observed (KAMERMANS, 1994).

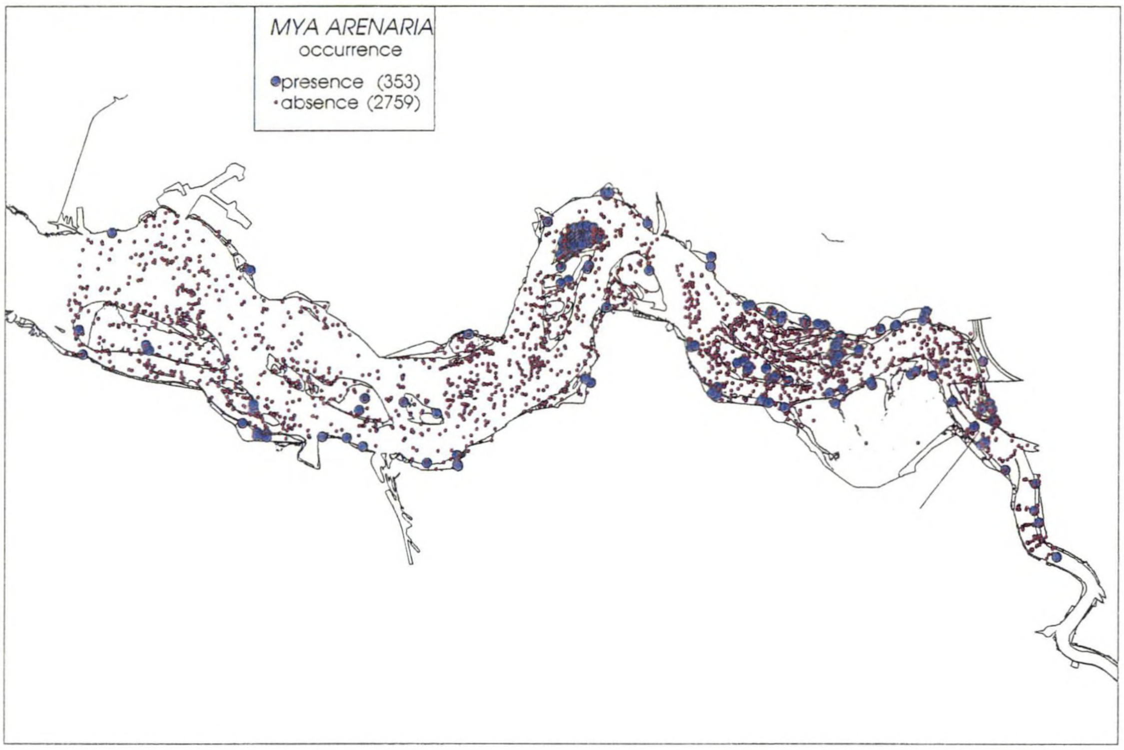
Population dynamics and life history

M. arenaria has separate sexes, although sometimes hermaphroditic individuals are observed (APPELDOORN & SANDERS, 1988). The species reproduces and spawns in summer from May/June until September (Wolff, 1973; KÜHL, 1983; MÖLLER & ROSENBERG, 1983; WARWICK & PRICE, 1975). The eggs (70-80 μm) are fertilised in the exhalant siphon or in the mantle cavity of the female. The larvae (150-225 μm) swim freely in the water column for about two weeks and undergo a metamorphosis at a size of 240-300 μm. These veliconcha larvae settle by means of byssus threads which they anchor to sand grains and algae (GREEN, 1968). There is some evidence that the presence of adult benthic suspension feeders, like *Cerastoderma edule* and *M. arenaria*, when present in high densities, might significantly reduce settlement success of bivalve larvae, and hence may limit recruitment of new individuals (MÖLLER, 1986; ANDRÉ & ROSENBERG, 1991). The mechanism proposed is that adults filter settling larvae out of the water column (WOODIN, 1976). Disturbance of the top layer of the sediment by the bioturbater *Arenicola mariana* may also negatively affect the occurrence of juvenile *M. arenaria* (FLACH, 1992). Settling preferably occurs in fine sediments in the lower parts of the intertidal zone (GÜNTHER, 1992). In a later phase the animals burrow into the sediment. Growth rate can reach 10 to 15 mm in the first year (THAMDRUP, 1935; WARWICK & PRICE, 1975). *M. arenaria* can become very large (> 10 cm) and very old (> 15 years). As in *Cerastoderma edule*, *M. arenaria* often have a good spatfall after severe winters (BEUKEMA, 1982, 1992).

The growing season of *M. arenaria* is situated between April and August in Dutch waters. However, in Scandinavia juveniles may grow until November (GÜNTHER, 1992). Length and weight increase simultaneously with highest growth speed in the months May-June (ZWARTS, 1991). From autumn to winter the flesh weight of M. arenaria diminish by half (ZWARTS, 1991; , 1992).

High suspended matter in the water column in areas like the Dollard (Ems estuary) and the eastern part of the Westerschelde might hamper the growth of the suspension feeding *M. arenaria* (ESSINK & BOS, 1985; GRANT & THORPE, 1991).

Mortality is highest in the first year of life. The juveniles are situated relatively high near the sediment surface, being exposed to predation and unfavourable weather conditions (KÜHL, 1981; BEAL *et al.*, 1995). Only 0,1% survives the first winter.



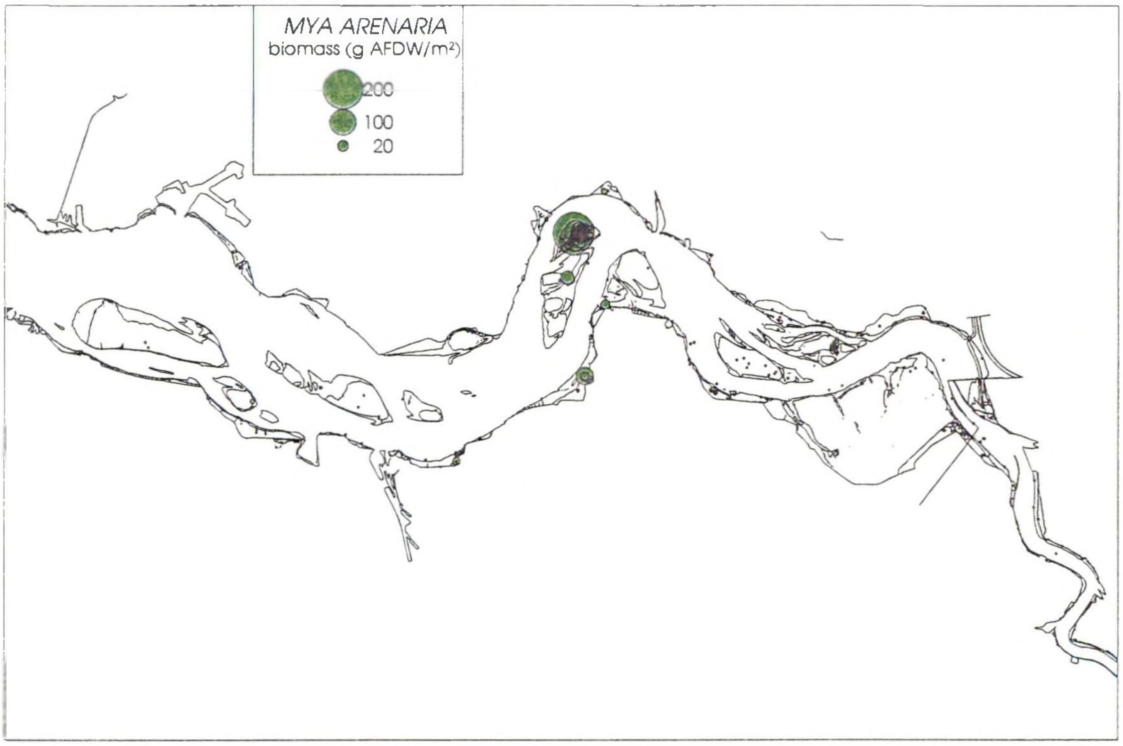


Figure 11.2. Geographical distribution maps of Mya arenaria in the Schelde estuary with presence/absence data (top) and biomass (g AFDW m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

M. arenaria was mainly observed in the intertidal zone of the poly-/mesohaline transition zone (salinity regions 2 and 3) (Table 11.1). Both in salinity region 1 and salinity region 4 the species was nearly absent. Mean density and biomass were highest in salinity region 2 (Figure 11.1), and here *M. arenaria* accounted for 10% of the overall intertidal macrobenthic biomass observed here. The geographical distribution of *M. arenaria* in the Schelde estuary is shown in Figure 11.2. It was very striking to see that high biomass values only were observed on the Molenplaat, a tidal flat which was extensively studied during the Ecoflat project. The patchy distribution and very deep occurrence in the sediment of the larger individuals makes this species very difficult to sample and therefore probably an underestimation has been made of the occurrence and total biomass of this species.

Table 11.1. Occurrence (p/a) of M. arenaria along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	11,1 % (n=262)	32,0 % (n= 503)	26,0 % (n=485)	4,2 % (n= 287)
Undeep subtidal	1,3 % 'n=151)	2,6 % (n=153)	1,6 % (n=127)	3,9 % (n=51)
Deep subtidal	0,0 % (n=123)	0,8 % (n=130)	0,9 % (n=112)	3,0 % (n=67)
Channel	0,5 % (n=186)	0,0 % (n=173)	2,2 % (n=232)	7,1 % (n=70)

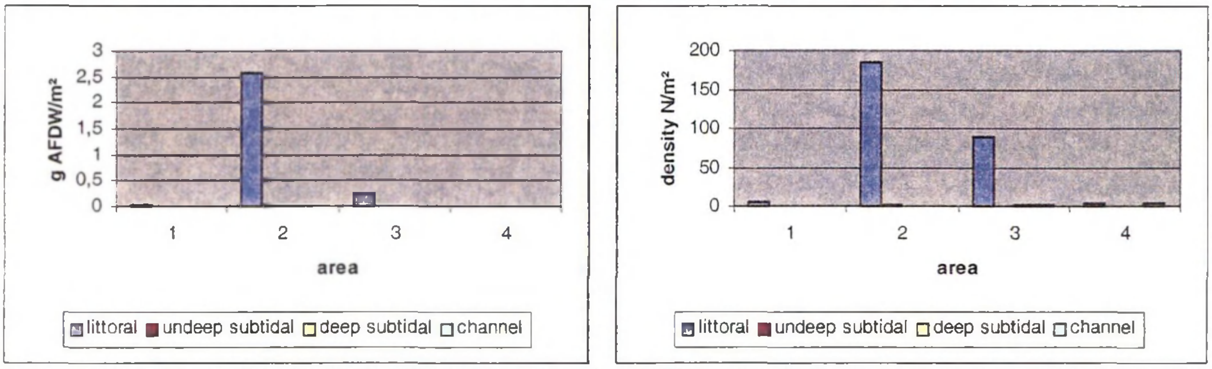


Figure 11.1. Mean density (ind m^{-2}) and biomass (g AFDW m^{-2}) of M. arenaria along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

Spring and autumn occurrence were comparable in all salinity regions (Table 11.2). However, mean density was much higher in autumn as compared to spring, indicating spatfall of this species in summer. Mean biomass in salinity region 2 was much higer in autumn.

Table 11.2. Spring (March - May) versus autumn (Augustus - October) occurrence (p/a), density (ind m^{-2}) and biomass (g AFDW m^{-2}) of M. arenaria in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

LITTORAL		1	2	3	4
Presence	Spring	7,2 % (n=97)	25,4 % (n= 169)	24,5 % (n=147)	3,0 % (n= 33)
	Autumn	12,6 % (n=135)	33,0 % (n=218)	25,3 % (n=249)	5,1 % (n= 214)
Density	Spring	985	2957	1448	253
	Autumn	2462	7177	3183	2066
Biomass	Spring	0,0392	0,9102	0,1167	0,41
	Autumn	0,0354	4,0366	0,3127	0.0024

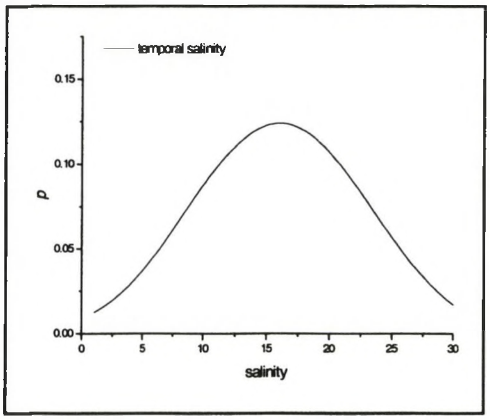
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Both the linear and quadratic term were included in the 'temporal salinity' model, whereas no terms were included in the 'model salinity' model. This resulted in an unimodal response curve for temporal salinity with an optimum at a salinity around 17. Below a salinity of 10 psu and above a salinity of 22,5 psu the probability of occurrence of *M. arenaria* decreased.

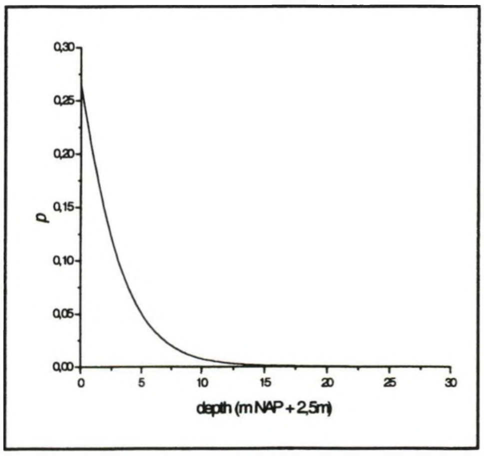
Mya arenaria	*Term*	*Regression coefficient*	*Standard error*
present: 245 absent: 2867			
	Intercept	-4,6947	0,4910
	Temporal salinity	0,3424	0,0591
	Temporal salinity²	-0,0107	0,00168
	Concordance	59,6	
	Intercept	-2,4598	0,0666
	Model salinity	-	-
	Model salinity²	-	-
	Concordance	-	



Depth

Only the linear term was included in the depth model. The response showed a rather linear decrease in probability of occurrence of *M. arenaria* with increasing depth.

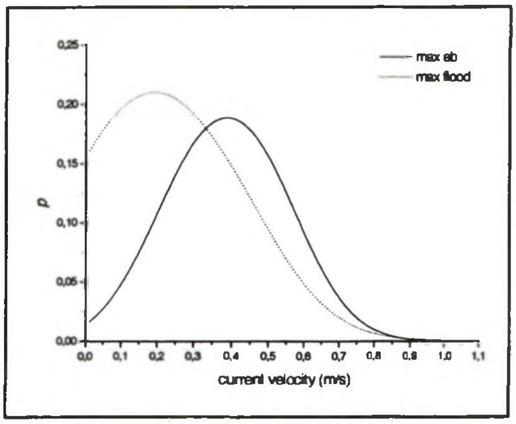
Mya arenaria	*Term*	*Regression coefficient*	*Standard error*
present: 225 absent: 2649			
	intercept	-1,0204	0,1103
	depth	-0,3831	0,0361
	depth²	-	-
	concordance	77,30%	



Maximum ebb and flood current velocities ($m.s^{-1}$)

Both the linear and quadratic terms were included in both current velocity models, resulting in an unimodal response curve for both models with an optimum around 0,4 and 0,2 $m.s^{-1}$ for maximum ebb and maximum flood current velocity respectively.

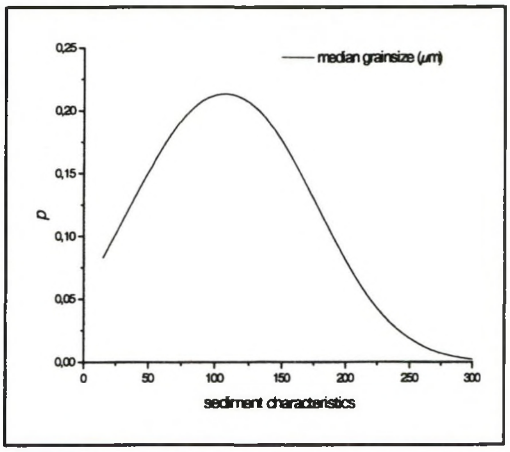
Mya arenaria	*Term*	*Regression coefficient*	*Standard error*
present: 243 absent: 2794			
	Intercept	-4,2368	0,4462
	Maxeb	14,3481	2,1036
	$Maxeb^2$	-18,5355	2,3710
	Concordance	79,10%	
	Intercept	-1,6880	0,2473
	Maxfl	3,7942	1,4422
	$Maxfl^2$	-9,9149	1,8690
	Concordance	82,90%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Both the linear and quadratic terms were included in the median grain size model, whereas no terms were included in the mud content model. This resulted in an unimodal response curve with an optimum around 110 μm for median grain size. Especially in very coarse sediments, the chance of occurrence of *M. arenaria* was very low.

Mya arenaria	*Term*	*Regression coefficient*	*Standard error*
present: 191 absent: 1311			
	Intercept	-2,7921	0,3753
	Median	0,0278	0,00604
	$median^2$	-0,00013	0,000023
	concordance	69,30%	
present: 199 absent: 1187			
	intercept	-1,8458	0,0783
	mud	-	-
	mud^2	-	-
	concordance	-	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, no terms concerning salinity were included in the model (Table 11.3). The linear term (but removed) and the quadratic term of maximum flood current velocity added most to the change of deviance in the model. The model with sediment characteristics had a slightly better performance, as indicated by the concordance, with the quadratic term of median grain size included in the model. The linear term of maximum flood current velocity, the linear and quadratic term of model salinity and the quadratic term of median grain size added most to the change of deviance in this model.

Table 11.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Mya arenaria	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment presence: 224 absence: 2603			with sediment Presence: 175 Absence: 1118		
	intercept	-3,6768	0,4762	Intercept	-14,1739	1,5489
	Depth	-0,1560	0,0488	Model salinity	1,2698	0,1596
	Maxeb	13,6226	2,2750	Model salinity^2	-0,0313	0,00414
	Maxeb^2	-12,9912	2,6683	Maxeb	19,3107	4,1154
	Maxfl^2	-5,3594	0,6933	Maxeb^2	-17,5379	4,6675
				Maxfl	-10,6339	2,3516
				Maxfl^2	5,0399	2,4605
				Median^2	-0,00005	6,778E-6
	Concordance	88,0%		concordance	91,4%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 90,7 % of the responses correctly (Table 11.4). However, only 40,6% of the modelled (or predicted) presences were also actually observed in the field. When including sediment characteristics in the model, this percentage was similar with 40,1%, indicating a similar performance of both models

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 11.4. Comparative statistics on the predicted and observed occurrence of M. arenaria in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model). Fisher exact one-tailed test (observed by model: Po<Ao).

Mya arenaria (p=0,28)
(without sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	91	133	**224**	40,6
Ao	133	2512	**2645**	95
Total	**224**	**2645**	**2869**	90,7

Difference between proportions	0,356	
95% CI	-1,000 to 0,410	(normal approximation)
Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)	

Mya arenaria (p=0,38)
(with sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	75	112	**187**	40,1
Ao	112	1140	**1252**	91,1
Total	**187**	**1252**	**1439**	84,4

Difference between proportions	0,312	
95% CI	-1,000 to 0,372	(normal approximation)
Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)	

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ECOPROFILE OF NEPHTYS CIRROSA

INTRODUCTION

Nephtys cirrosa is the most common *Nephtys* species, together with *Nephtys hombergii*. *Nephtys cirrosa* is more restricted to the subtidal zone then *N. hombergii* and in this zone it is one of the most important species. *N. hombergii* was mainly observed in the polyhaline zone.

AUTO-ECOLOGY

NEPHTYS CIRROSA	Annelida, Polychaeta

General

The polychaete *N. cirrosa* is, in comparison with *N. hombergii*, a southern species with northern limits in Scotland (MCINTYRE & ELEFTHERIOU, 1968). At severe winters in the Delta area the population of *N. cirrosa* can die and it takes 3-4 years before the species appears again (WOLFF, 1971).

Habitat preferences

Salinity: *N. cirrosa* penetrates the estuaries up to the isohalines of 10-15 g Cl^-/l (WOLFF, 1973).

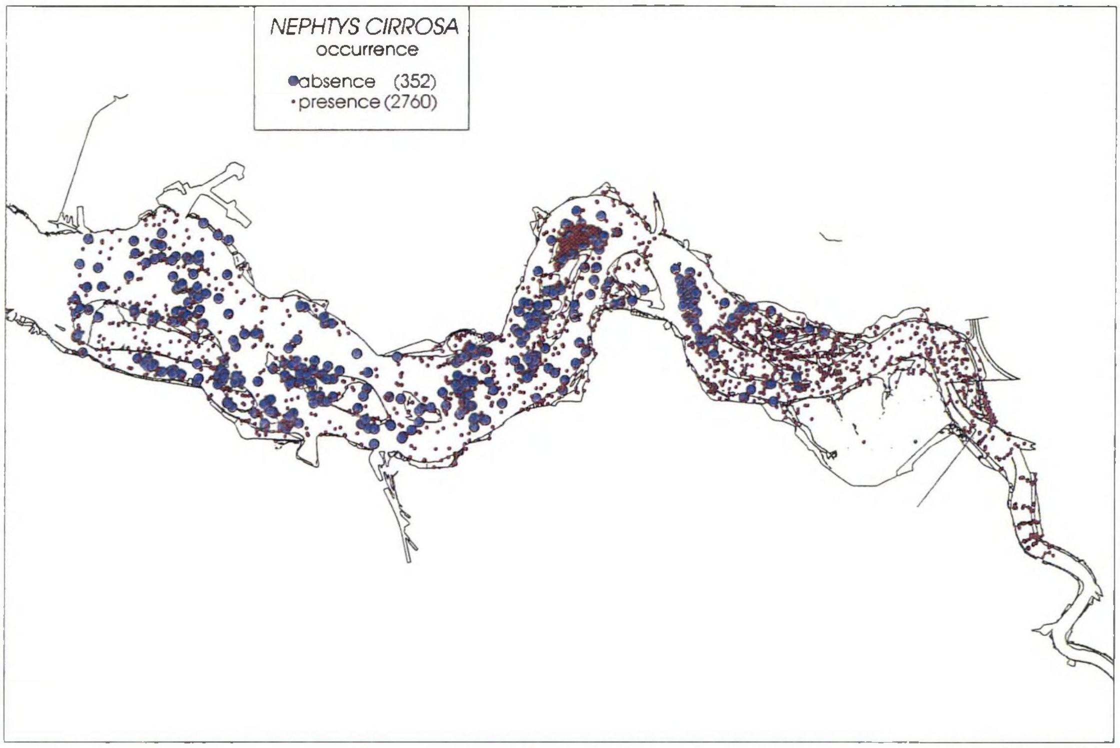
Depth distribution and sediment type: *N. cirrosa* is, in comparison to *N. hombergii*, a typical sublittoral species, prefering sandy sediments (CLARK & HADERLIE, 1960; WOLFF, 1971).

Feeding

N. cirrosa lives in non-permanent burrows (HARTMANN-SCHRÖDER, 1971) and is a predator/carnivor (CLARK, 1962), feeding on other polychaete species like *Scoloplos armiger*, *Heteromastus filiformis*, etc. (COMMITO & AMBROSE, 1985).

Population dynamics and life history

N. cirrosa is a polytelic species. Spawning occurs in the open water during swimming of the adults. The larvae are planctonic.



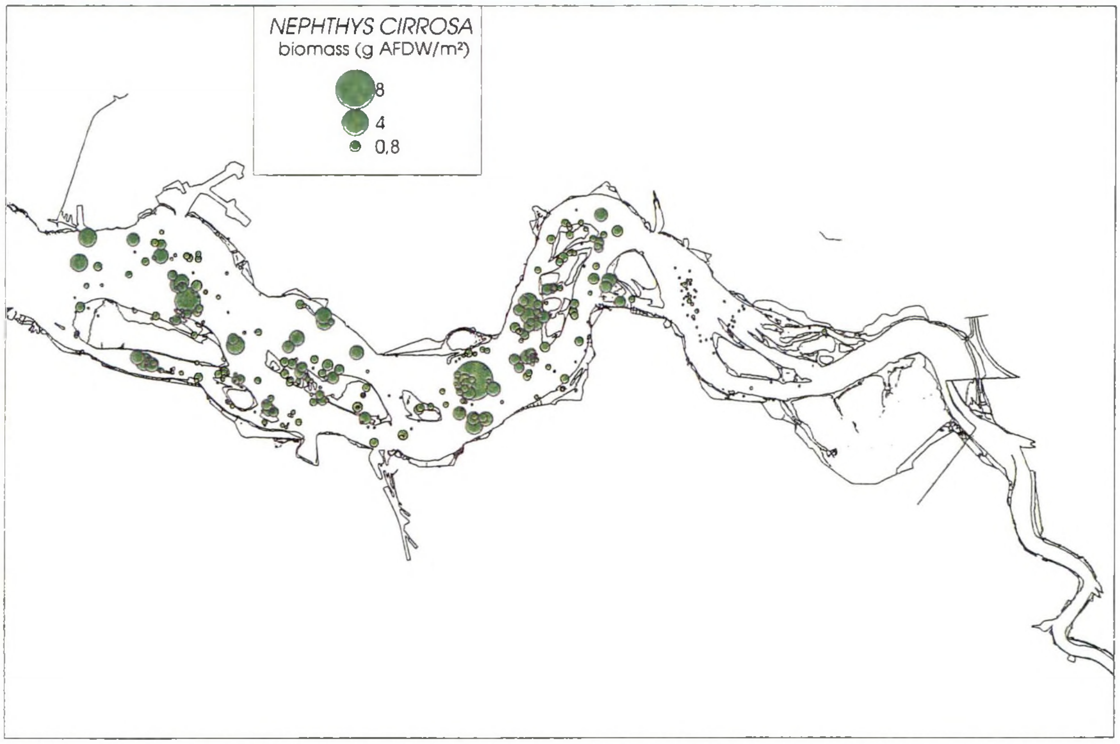


Figure 12.2 Geographical distribution maps of Nephtys cirrosa in the Schelde estuary with presence/absence data (top) and biomass (g AFDW m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

The presence of *N. cirrosa* is mainly restricted to the polyhaline (salinity region 1 and 2), subtidal zone (Table 12.1.). Here, the species was observed in all three subtidal depth strata. In the α-mesohaline zone (salinity region 3), the species was observed irregularly, with most observations in the channel. In the β-mesohaline zone (salinity region 4) the species is completely absent. In the intertidal zone *N. cirrosa* was nearly absent, except for salinity region 1 where in 10% of the sampling occasions the species was observed. Both mean biomass and density were highest in salinity region 1 and 2, with highest biomass values in the deep subtidal and the channel (Figure 12.1). The geographical distribution of *N. cirrosa* in the Schelde estuary is shown in Figure 12.2.

Table 12.1 Occurrence (p/a) of N. cirrosa along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	10,3 % (n=262)	2,8 % (n= 503)	1,0 % (n=485)	0 % (n= 287)
Undeep subtidal	28,5 % 'n=151)	24,8 % (n=153)	3,2 % (n=127)	0 % (n=51)
Deep subtidal	43,9 % (n=123)	26,2 % (n=130)	6,3 % (n=112)	0 % (n=67)
Channel	26,3 % (n=186)	24,3 % (n=173)	15,1 % (n=232)	0 % (n=70)

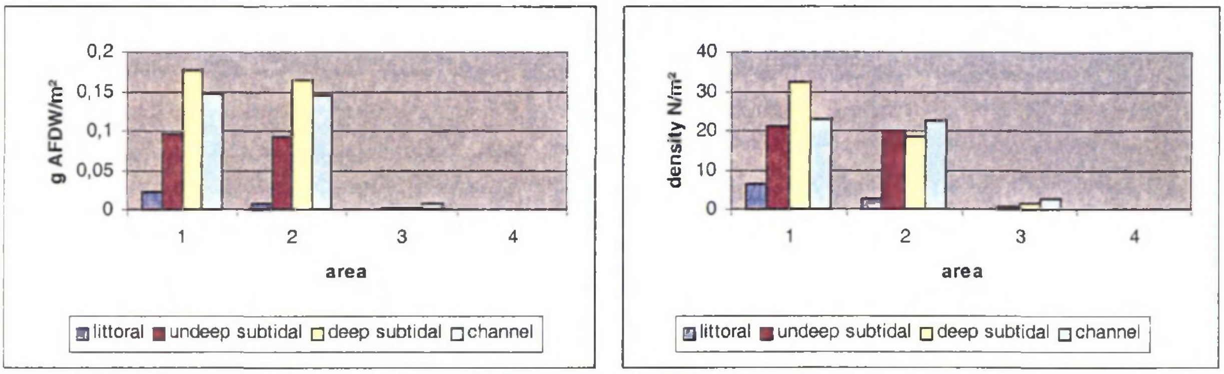


Figure 12.1. Mean density (ind m^{-2}) and biomass (g AFDW m^{-2}) of N. cirrosa along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

In the polyhaline, subtidal zone *N. cirrosa* was observed more frequently in autumn as compared to spring, but mean density and biomass were comparable in both seasons (Table 12.2). In the β-mesohaline zone (salinity region 3) this trend was even more pronounced, *with N. cirrosa* being nearly absent in spring, and appearing in autumn in 13,6% of the sampling occassions, which probably is explained by the lower salinities occurring in winter and spring in this salinity region, which caused more unfavourable conditions for this species.

Table 12.2. Spring (Mar-May) versus autumn (Aug-Oct) occurrence (presence/absence), density (ind m^{-2}) and biomass (g AFDW m^{-2}) of N. cirrosa in the subtidal zone of the Schelde estuary (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

SUBTIDAL		1	2	3	4
Presence	Spring	25,7 % (n=187)	19,7 % (n= 203)	0,7 % (n=140)	0,0 % (n= 33)
	Autumn	36,6 % (n=268)	29,2 % (n=243)	13,6 % (n=331)	0,0 % (n= 155)
Density	Spring	21	17	0,5	0
	Autumn	28	24	2,2	0
Biomass	Spring	0,14	0,11	0,0018	0
	Autumn	0,14	0,15	0,0056	0

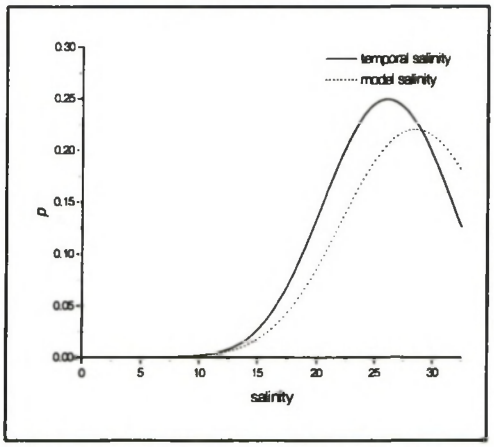
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed.

Model salinity and temporal salinity

Both the linear and quadratic term were included in both salinity models, giving unimodal response curves for both models. An optimum is observed in the polyhaline zone, being around 26 psu and 28,5 psu for 'temporal salinity' and 'model salinity' respectively. The 'temporal salinity' optimum shifted slightly towards a lower salinity as compared to the 'model salinity' optimum, but both curves were comparable. This shift was much less pronounced as compared to e.g. *Arenicola marina*.

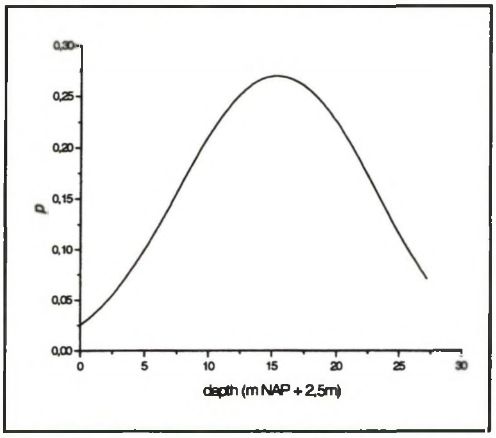
Nephtys cirrosa	*Term*	*Regression coefficient*	*Standard error*
present: 352 absent: 2760			
	Intercept	-14,9834	1,4903
	Temporal salinity	1,0643	0,1289
	Temporal salinity²	-0,0204	0,00274
	Concordance	77,00%	
	Intercept	-13,6466	1,6386
	Model salinity	0,8705	0,1374
	Model salinity²	-0,0153	0,00284
	Concordance	74,60%	



Depth

Both the linear and quadratic term of depth were included in the model, giving an unimodal, bell-shaped response curve for depth. *N. cirrosa* showed an optimum around 12,5 m NAP (15m NAP on the graph), but showed a relatively broad tolerance.

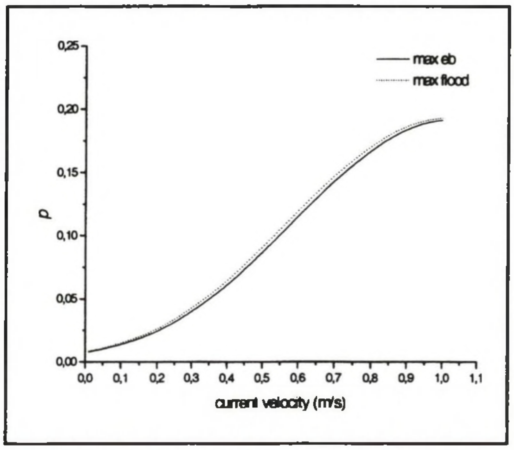
Nephtys cirrosa	*Term*	*Regression coefficient*	*Standard error*
present: 344 absent: 2530			
	Intercept	-3,6365	0,1692
	Depth	0,3439	0,0332
	depth²	-0,0112	0,00139
	Concordance	71,50%	



Maximum ebb and flood current velocities (m.s^{-1})

Both the linear and quadratic terms were included in the maximum ebb and flood current velocity models. The response curves were very similar for both models, showing a sigmoidal response with an increase in probability of occurrence with increasing current velocity. *N. cirrosa* is one of the few common species in the Schelde estuary showing this pattern. Compared with *N. hombergii, N. cirrosa* clearly preferred higher current velocities.

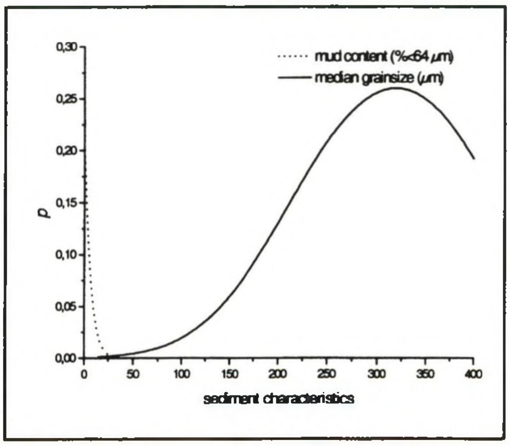
Nephtys cirrosa	*Term*	*Regression coefficient*	*Standard error*
present: 346 absent: 2691			
	Intercept	-4,9120	0,3735
	Maxeb	6,7694	0,9944
	Maxeb²	-3,3002	0,6259
	Concordance	65,70%	
	Intercept	-4,8131	0,3266
	Maxfl	6,6613	0,8577
	Maxfl²	-3,2807	0,5321
	Concordance	66,70%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Both the linear and quadratic term were included in the median grain size model, whereas only the linear term was included in the mud content model. *N. cirrosa* clearly prefered very coarse sediments, showing an unimodal response curves for median grain size with an optimum at ± 320 μm. For mud content the change of occurrence decreased steeply with increasing mud content.

Nephtys cirrosa	*Term*	*Regression coefficient*	*Standard error*
present: 125 absent: 1377			
	intercept	-7,1578	0,8036
	median	0,0383	0,00698
	median²	-0,00006	0,000015
	concordance	73,60%	
present: 109 absent: 1277			
	intercept	-1,3400	0,1426
	mud	-0,1701	0,0300
	mud²	-	-
	concordance	78,10%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, linear and quadratic terms of temporal and model salinity and of maxium ebb current velocity (maxeb) were included in the model (Table 12.3), with the linear term of temporal salinity, the linear term of maximum ebb current velocity (maxeb), the quadratic term of temporal salinity adding most to the change in deviance. The model with sediment characteristics performed better with a concordance of 91,1 %, with the linear term of depth, the linear term of temporal salinity and the quadratic term of depth adding most to the change of deviance in the model.

Table 12.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Nepthys cirrosa	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment Presence: 339 Absence: 2488			with sediment presence: 102 absence: 1191		
	Intercept	-19,6625	1,9184	intercept	-13,8353	2,6926
	Temporal salinity	0,7573	0,1426	Temporal salinity	0,8223	0,2374
	Temporal salinity^2	-0,0151	0,00315	Temporal salinity^2	-0,0154	0,00523
	Model salinity	0,4195	0,1633	Depth	0,5568	0,0810
	Model salinity^2	-0,00728	0,00349	Depth^2	-0,0181	0,00333
	Maxeb	7,4088	1,2172	Maxeb^2	-0,8913	0,3886
	Maxeb^2	-3,6803	0,7592	Mud	-0,1074	0,0302
	concordance	82,2%		concordance	91,1%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 84,0 % of the responses correctly (Table 12.4). However, only 33,3 % of the modelled (or predicted) presences were also actually observed in the field. When including sediment characteristics in the model, this percentage increased up to 48,0 %.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 12.4. Comparative statistics on the predicted and observed occurrence of N. cirrosa. in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model). Fisher exact one-tailed test (observed by model: Po<Ao).

Nephtys cirrosa (p=0,316)
(without sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	113	226	**339**	33,3
Ao	226	2262	**2488**	90,9
Total	**339**	**2488**	**2827**	84

Difference between proportions	0,242	
95% CI	-1,000 to 0,286	(normal approximation)

Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)

Nephtys cirrosa (p=0,192)
(with sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	49	53	**102**	48
Ao	53	1138	**1191**	95,6
Total	**102**	**1191**	**1293**	91,8

Difference between proportions	0,436	
95% CI	-1,000 to 0,518	(normal approximation)

1-tailed p **(observed by model: Po<Ao)**	-<0.0001 (exact)

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ECOPROFILE OF NEPHTYS HOMBERGII

INTRODUCTION

Nephtys hombergii was a relatively common species in the polyhaline zone of the estuary and it is one of few common species which was observed both in the intertidal as in the subtidal zone.

AUTO-ECOLOGY

NEPHTYS HOMBERGII	Annelida, Polychaeta

General

The polychaete *N. hombergii* is a cosmpolitic species, very common along the Atlantic coasts. *N. hombergii* is very winter sensitive with high mortalities during severe winters (BEUKEMA, 1979; BEUKEMA & ESSINK, 1986).

In contrast to *Nereis diversicolor, N. hombergii* lives in non permanent and therefore non fixed burrows up to 20 cm deep (HARTMANN-SCHRÖDER, 1971).

Habitat preferences

Salinity: *N. hombergii* penetrates the estuaries up to the isohalines of 10-15 g Cl^-/l (WOLFF, 1973).

Depth distribution and sediment type: *N. hombergii* is found both in the intertidal zone as in the (undeep) subtidal zone, but is most common in the intertidal zone (WOLFF, 1971). *N. hombergii* is found in all sediment types, prefering less well sorted, fine sand sediments (CLARK & HADERLIE, 1960; KIRKEGRAAD, 1969; WOLFF, 1973; GOVAERE, 1978; ALHEIT, 1978). In comparison, *N. cirrosa* prefers more sandy sediments (CLARK & HADERLIE, 1960; WOLFF, 1971).

Feeding

In general, *N. hombergii* is classified as predator/carnivor (CLARK, 1962), feeding on other polychaete species like *Scoloplos armiger*, *Heteromastus filiformis*, and juvenile *Nereis diversicolor*, and nematodes; but also diatoms and detritus are included in its diet (DAVEY & GEORGE, 1986; SHUBERT & REISE, 1986). OLIVE *et al.* (1981) classify *N. hombergii* as a non selective carnivor, whereas WARWICK *et al.* (1979) describe the species as omnivor with microalgae being an important part of the diet.

Population dynamics and life history

N. hombergii is a polytelic species, which reproduce from its second year of life (OLIVE, 1978). Spawning occurs in the open water during swimming of the adults. The larvae are planctonic and settle in the subtidal zone. After three months they migrate to the adult population in the intertidal zone (OLIVE, 1977; WARWICK & PRICE, 1975).

Biotic interactions

N. hombergii negatively affects densities of *Heteromastus filiformis* and *Scoloplos armiger*, consuming on a yearly basis 20-25% of their biomass (SHUBERT & REISE, 1986; BEUKEMA, 1987).

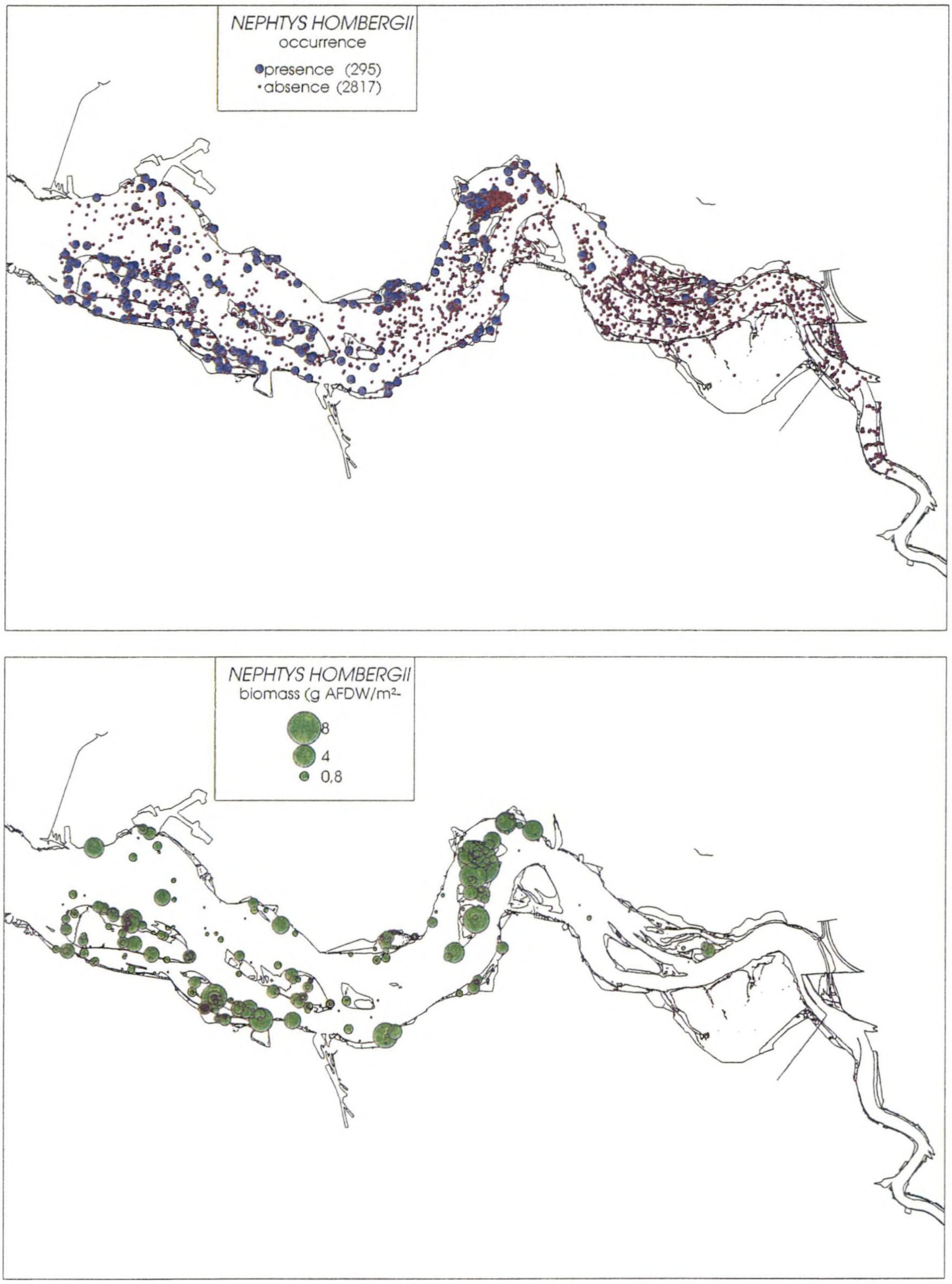


Figure 13.2. Geographical distribution maps of Nephtys hombergii in the Schelde estuary with presence/absence data (top) and biomass (g AFDW m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

The presence of *N. hombergii* is restricted to the polyhaline zone (Table 13.1), with the highest frequency of occurrence in salinity region 1. In the polyhaline zone the species was observed in all depth strata, with a slightly higher preference for the littoral zone. However, *N. hombergii* was the only common species showing a more or less similar occurrence in both the littoral and subtidal zone. In the mesohaline zone the species was almost completely absent.

Both mean biomass and density were highest in salinity region 1 (Figure 13.1). Biomass and density values were comparable between the different depth strata, except for a higher biomass in the littoral zone of salinity region 1. The geographical distribution of *N. hombergii* in the Schelde estuary is shown in Figure 13.2.

Table 13.1. Occurrence (p/a) of N. hombergii along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	35,9 % (n=262)	13,9 % (n= 503)	1,6 % (n=485)	0 % (n= 287)
Undeep subtidal	21,9 % (n=151)	9,8 % (n=153)	1,6 % (n=127)	0 % (n=51)
Deep subtidal	15,4 % (n=123)	6,2 % (n=130)	0,9 % (n=112)	0 % (n=67)
Channel	15,1 % (n=186)	7,5 % (n=173)	1,7 % (n=232)	0 % (n=70)

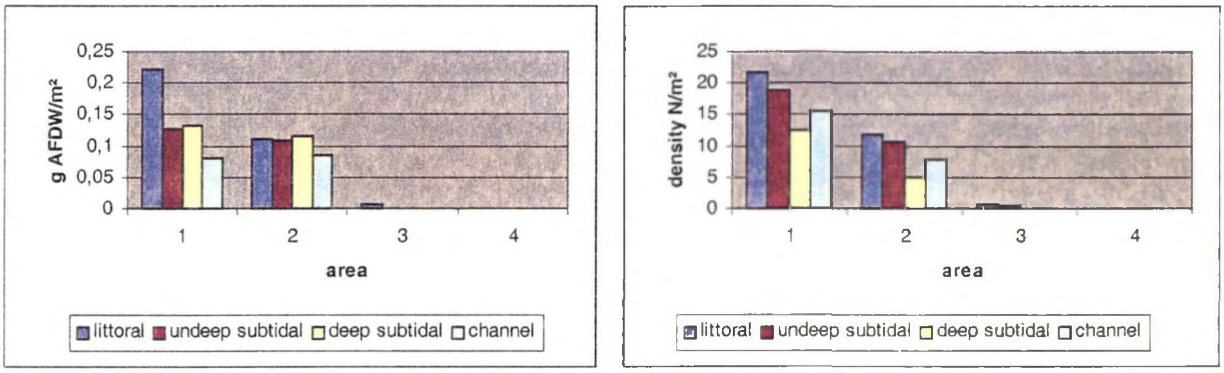


Figure 13.1. Mean density (ind m^{-2}) and biomass (g AFDW m^{-2}) of N. hombergii along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

In the polyhaline, littoral zone *N. hombergii* was observed more frequently in autumn as compared to spring, resulting in a higher mean density and biomass in autumn (Table 13.2). In the mesohaline zone *N. hombergii* was nearly completely absent in both seasons.

Table 13.2. Spring (March - May) versus autumn (Augustus - October) occurrence (p/a), density (ind m^{-2}) and biomass (g AFDW m^{-2}) of N. hombergii in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

LITTORAL		1	2	3	4
Presence	Spring	30,9 % (n=97)	11,2 % (n= 169)	0,6 % (n=147)	0 % (n= 33)
	Autumn	41,5 % (n=135)	20,2 % (n=218)	1,2 % (n=249)	0 % (n= 214)
Density	Spring	17	9	0,5	0
	Autumn	26	18	0,6	0
Biomass	Spring	0,117	0,065	0,001	0
	Autumn	0,281	0,154	0,001	0

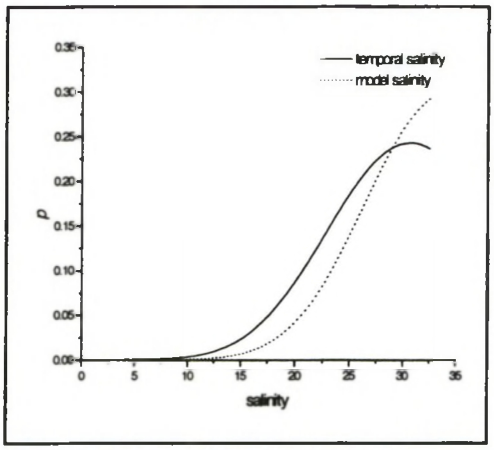
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed.

Model salinity and temporal salinity

Both the linear and quadratic term were included in both salinity models. The response curves showed a sigmoidal increase in probability of occurrence with increasing salinity. Below a salinity of 15 psu the probability of observing *N. cirrosa* became almost zero. Like for several 'polyhaline' species the 'temporal salinity' curve shifted slightly towards a lower salinity as compared to the 'model salinity' curve, but both curves were comparable.

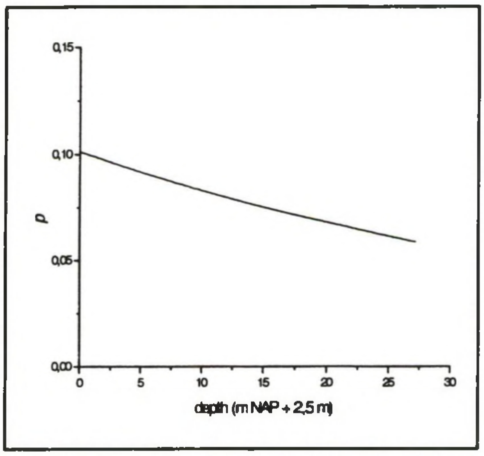
Nephtys hombergii	*Term*	*Regression coefficient*	*Standard error*
Present: 295			
Absent: 2817			
	Intercept	-11,1041	1,3533
	Temporal salinity	0,6500	0,1176
	Temporal salinity²	-0,0106	0,00251
	Concordance	77,20%	
	Intercept	-13,8417	2,2325
	Model salinity	0,7561	0,1804
	Model salinity²	-0,0110	0,00360
	Concordance	79,50%	



Depth

Only the linear term of depth was included in the model, giving a more or less linear, slighty decreasing response with increasing depth. The curve clearly demonstrated *that N. cirrosa* was relatively independent of depth concerning its distribution, wat also could be observed in Table 13.1.

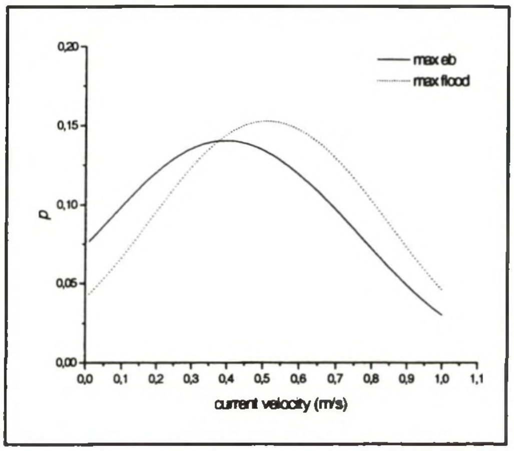
Nephtys hombergii	*Term*	*Regression coefficient*	*Standard error*
Present: 255			
Absent: 2619			
	Intercept	-2,1840	0,0954
	Depth	-0,0217	0,0109
	depth²	-	-
	Concordance	48,00%	



Maximum ebb and flood current velocities (m.s^{-1})

Both the linear and quadratic terms were included in the maximum ebb and flood current velocity models. This resulted in unimodal response curves for maximum ebb and flood current velocity with an optimum around 0.4 and 0.5 m.s^{-1} respectively. However, both curves were broad, indicating a relatively high tolerance for current velocity. Compared with *N. cirrosa, N. hombergii* clearly preferred less high current velocities.

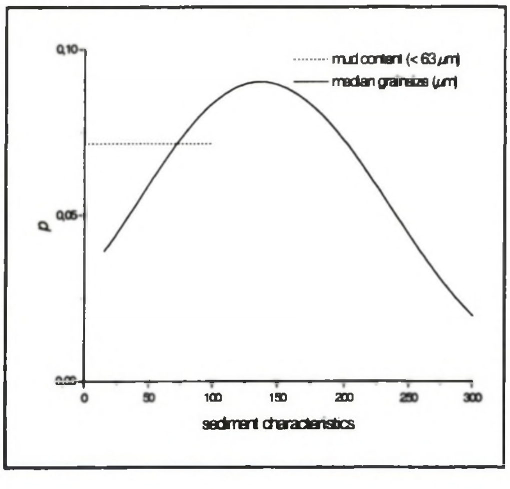
Nephtys hombergii	*Term*	*Regression coefficient*	*Standard error*
present: 281 absent: 2756			
	Intercept	-2,5242	0,2885
	Maxeb	3,5969	1,0891
	Maxeb²	-4,5532	0,9355
	Concordance	64,30%	
	Intercept	-3.1516	0,2527
	Maxfl	5,6340	0,9577
	Maxfl²	-5,5198	0,8033
	Concordance	66,70%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Both the linear and quadratic term were included in the median grain size model, whereas in the mud content model none of both terms were included. An unimodal response curve for median grain size was observed with an optimum at 135 μm. However, *N. hombergii* showed a relatively broad tolerance and only in very coarse or very fine sediments the chance of observing this species became small.

Nephtys hombergii	*Term*	*Regression coefficient*	*Standard error*
present: 107 absent: 1395			
	Intercept	-3,4341	0,4635
	Median	0,0164	0,00613
	Median²	-0,00006	0,000019
	Concordance	59,1%	
present: 341 absent: 1045			
	Intercept	-2,5649	0,1043
	Mud	-	-
	Mud²	-	-
	Concordance	-	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, linear and/or quadratic terms of all abiotic variables were included in the model (Table 13.3), with the quadratic term of maximum ebb current velocity (maxeb) and the linear term of model salinity adding most to the change in deviance. The model with sediment characteristics performed equally, but now only three terms were included in the model with the quadratic term of temporal salinity being the most important.

Table 13.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Nephtys hombergii	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	Without sediment Presence: 248 Absence: 2579			with sediment Presence: 84 Absence: 1318		
	Intercept	-13,8573	1,4990	Intercept	-7,0066	0,7397
	Temporal salinity	0,6095	0,1235	Temporal salinity^2	0,00211	0,00088
	Temporal salinity^2	-0,0135	0,00274	Model salinity	0,1875	0,0431
	Model salinity	0,2077	0,0302	Median^2	-0,00002	5,093E-6
	Depth	0,0607	0,0167			
	Maxeb^2	-1,8681	0,3927			
	Maxfl	3,4719	1,1324			
	Maxfl^2	-3,5303	0,9218			
	Concordance	86,2%		concordance	85,2%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 88,2 % of the responses correctly (Table 13.4). However, only 34,2 % of the modelled (or predicted) presences were also actually observed in the field. When including sediment characteristics in the model, this percentage didn't change.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 13.4. Comparative statistics on the predicted and observed occurrence of N. hombergii in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model). Fisher exact one-tailed test (observed by model: Po<Ao).

Nephtys hombergii (p=0,287)
(without sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**Correct**
Po	85	163	**248**	34,2
Ao	163	2416	**2579**	93,7
Total	**248**	**2579**	**2827**	88,5

Difference between proportions	0,280	
95% CI	-1,000 to 0,330	(normal approximation)
Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001	(exact)

Nephtys hombergii (p=0,285)
(with sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**Correct**
Po	29	55	**84**	34,5
Ao	55	1263	**1318**	95,8
Total	**84**	**1318**	**1402**	92,2

Difference between proportions	0,304	
95% CI	-1,000 to 0,389	(normal approximation)
Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001	(exact)

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ECOPROFILE OF NEREIS DIVERSICOLOR

INTRODUCTION

Nereis diversicolor was a very common polychaete species in the Schelde estuary. Especially in the intertidal mesohaline zone it was one of the constituting species, contributing substantially to both the overall macrobenthic density and biomass. In the β-mesohaline zone *N. diversicolor* made up 53% of the total macrobenthic biomass.

AUTO-ECOLOGY

NEREIS DIVERSICOLOR	Annelida, Polychaeta

General

The polychaete *Nereis diversicolor* is one of the most characteristic species of estuarine tidal areas. Because of its large tolerance for all kinds of abiotic environmental factors (such as temperature, salinity, pollution), *N. diversicolor* has a widespread occurrence, from the cold brackish Baltic Sea to hypersaline lagunes of the Black Sea (METTAM, 1979).

In comparison with *Nepthys hombergii* lives *N. diversicolor* in a branched system of burrows (HARTMANN-SCHRÖDER, 1983), up to a depth of 5-20 cm, extending to 40 cm during severe winters (MUUS, 1967).

Habitat preferences

Salinity: *N. diversicolor* prefers undeep, mesohaline waters (MUUS, 1967; WOLFF, 1973) and the species has a large tolerance against changes in salinity (DALES, 1951b; HARTMANN-SCHRÖDER, 1983).

Sediment type: *N. diversicolor* prefers very fine, muddy sediments (WOLFF, 1973), but in 'black mud' the species is absent.

Feeding

In general, *N. diversicolor* is classified as omnivor, using however different feeding techniques. GOERKE (1966) describes *N. diversicolor* as a deposit feeder, carnivor, scavenger, herbivor and suspension feeder. According to MUUS (1967) *N. diversicolor* feeds mainly on the meiofauna (nematodes, ostracods, and nauplii from harpacticoid copepods) which is uptaken together with the detritus. Also predation on *Corophium volutator* and chironomid larvae was noticed by MUUS (1967). HARTMANN-SCHRÖDER (1971) describes the uptake of plant material (detritus) by *N. diversicolor*. REISE (1969) demonstrated experimentally the uptake of plathelminthes and nematodes, whereas ostracods and copepods were relatively less important. According to COMMITO (1982) *N. diversicolor* mainly feeds on nematodes, Turbellaria and spatfall of *C. edule*.

Population dynamics and life history

N. diversicolor is gonochoristic. The sex ratio is in favour of females (METTAM, 1981). *N. diversicolor* is atocous and oviparous (WOLFF, 1973). Short after spawning the adults die. The time and duration of the spawning is variable (DALES, 1950; MUUS, 1967; CHAMBERS & MILNE, 1975; HEIP & HERMAN, 1979; ...). The larvae come out after a week in the burrows of the adults, on the sediment surface or in the upper layers of the sediment. Seldom or never they are observed in the watercolumn.

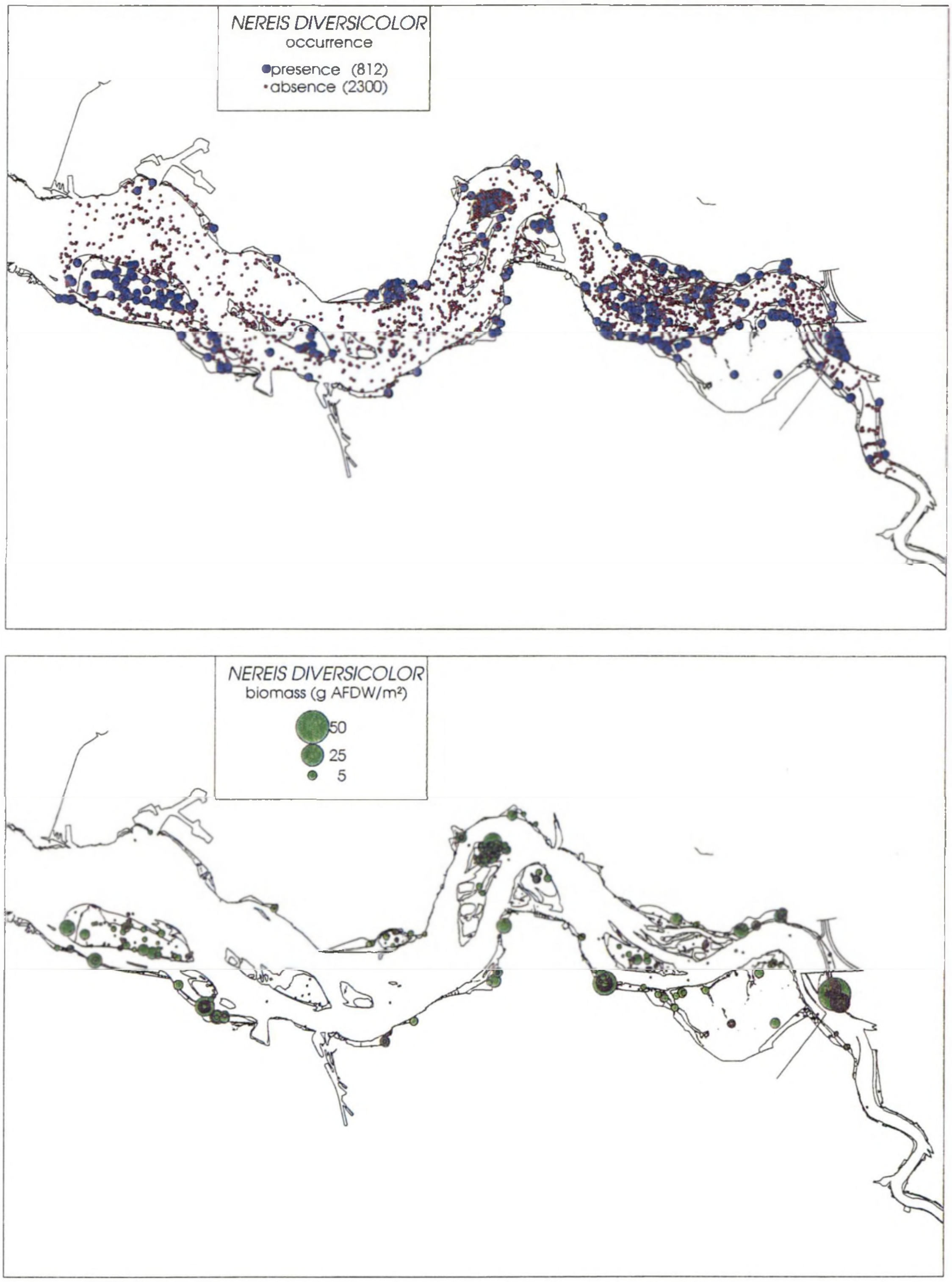


Figure 14.2. Geographical distribution maps of Nereis diversicolor in the Schelde estuary with presence/absence data (top) and biomass (g AFDW m⁻²) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

N. diversicolor was a common species in the littoral, polyhaline and the mesohaline zone, with the highest frequency of occurrence in the β-mesohaline zone (salinity region 4) (Table 14.1). In the subtidal zone *N. diversicolor* was nearly absent.

Mean density and biomass was comparable in the two polyhaline salinity regions 1 and 2 and the α-mesohaline salinity region 3 (Figure 14.1). In the β-mesohaline zone (salinity region 4) mean biomass and density were 3-4x higher then in the other salinity regions, making up 53% of the total biomass here. The geographical distribution of *N. diversicolor* in the Schelde estuary is shown in Figure 14.2.

Table 14.1. Occurrence (p/a) of N. diversicolor along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	54,2 % (n=262)	31,2 % (n= 503)	53,4 % (n=485)	81,5 % (n= 287)
Undeep subtidal	1,3 % 'n=151)	2,0 % (n=153)	3,2 % (n=127)	0,0 % (n=51)
deep subtidal	0,8 % (n=123)	0,0 % (n=130)	1,8 % (n=112)	1,5 % (n=67)
Channel	1,1 % (n=186)	0,0 % (n=173)	2,2 % (n=232)	0,0 % (n=70)

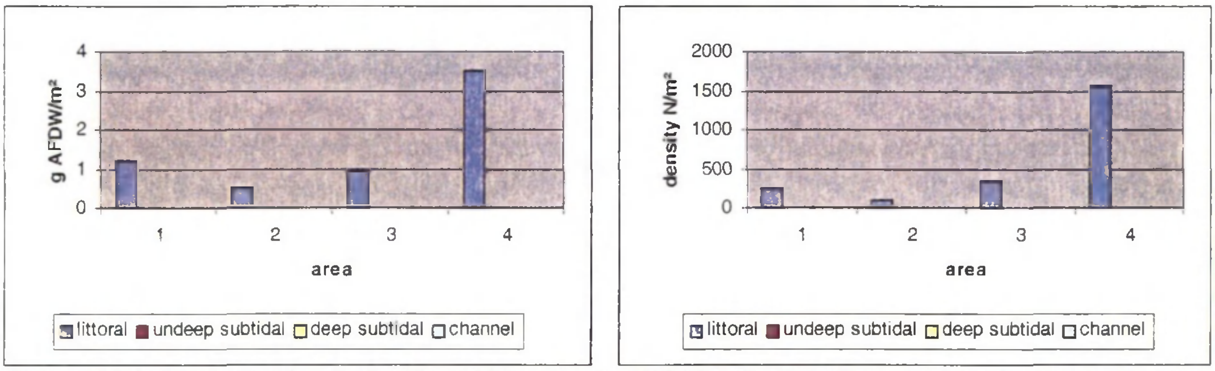


Figure 14.1. Mean density (ind m^{-2}) and biomass (g AFDW m^{-2}) of N. diversicolor along the salinity and depth gradient in the Schelde estuary. (areas: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

The littoral occurrence and density of *N. diversicolor* was comparable between spring and autumn in all salinity regions, except for somewhat higher values in autumn in salinity region 1 (Table 14.2). Mean biomass was higher in spring in all salinity regions, except for salinity region 1 were the opposite was noticed.

Table 14.2. Spring (March - May) versus autumn (Augustus - October) occurrence (p/a), density (ind m^{-2}) and biomass (g AFDW m^{-2}) of Nereis diversicolor in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

LITTORAL		1	2	3	4
Presence	Spring	43,3 % (n=97)	35,5 % (n= 169)	50,3 % (n=147)	75,8 % (n= 33)
	Autumn	61,5 % (n=135)	34,4 % (n=218)	52,6 % (n=249)	79,0 % (n= 214)
Density	Spring	96	107	312	1392
	Autumn	370	139	389	1368
Biomass	Spring	0,78	0,91	1,02	3,83
	Autumn	1,50	0,47	0,79	2,64

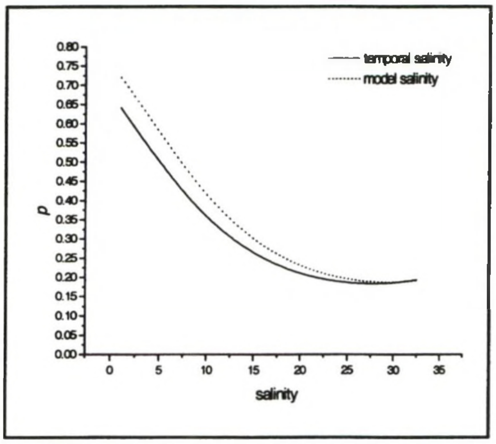
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed.

Model salinity and temporal salinity

Both the linear and quadratic term were included in both salinity models. The response curves showed a sigmoidal increase in probability of occurrence with decreasing salinity. But also in higher salinities the probability of occurrence of *Nereis diversicolor* was still relatively high.

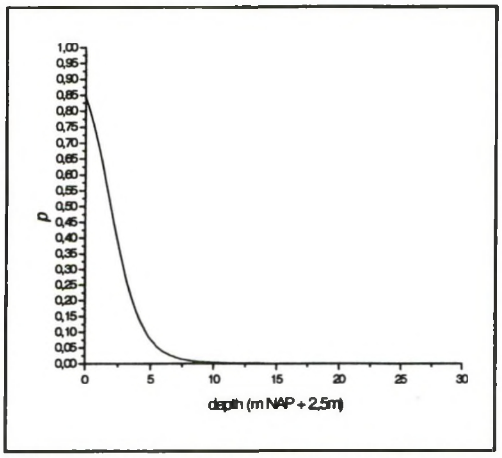
Nereis diversicolor	*Term*	*Regression coefficient*	*Standard error*
present: 812 absent: 2300			
	intercept	0,7385	0,1983
	Temporal salinity	-0,1610	0,0251
	Temporal salinity^2	0,00291	0,000712
	Concordance	62,10%	
	Intercept	1,1206	0,2920
	Model salinity	-0,1758	0,0334
	Model salinity^2	0,00299	0,000867
	Concordance	60,20%	



Depth

Both the linear and quadratic term of depth were included in the model. The response curve showed a very high chance of occurrence in the littoral zone, after which a steep decrease in chance of occurrence was observed. The curve clearly demonstrated the preference of *N. diversicolor* for the littoral zone (see also Table 14.1).

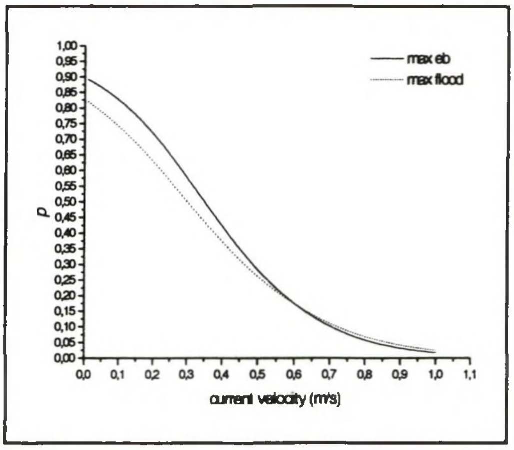
Nereis diversicolor	*Term*	*Regression coefficient*	*Standard error*
present: 682 absent: 2192			
	intercept	1,7040	0,1115
	depth	-0,9131	0,0447
	depth^2	0,0115	0,000983
	concordance	91,00%	



Maximum ebb and flood current velocities (m.s^{-1})

Only the linear term was included in the maximum ebb and flood current velocity models. This resulted in more or less similar sigmoidal curves for maximum ebb and flood current velocity, showing a very high probability of occurrence with small current velocities and a gradual decreasing probability of occurrence with increasing current velocities.

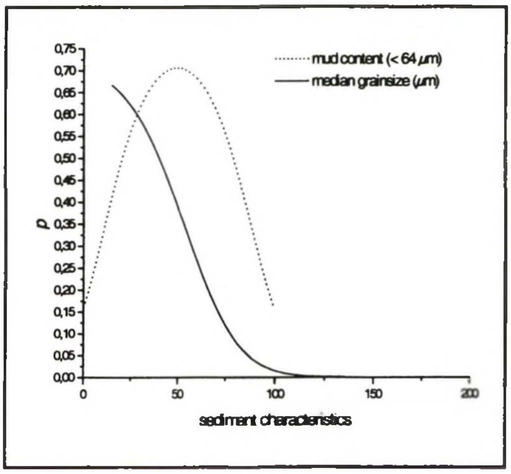
Nereis diversicolor	*Term*	*Regression coefficient*	*Standard error*
present: 771 absent: 2266			
	Intercept	2,1693	0,1269
	Maxeb	-6,2043	0,2603
	Maxeb²	-	-
	Concordance	85,60%	
	Intercept	1,5673	0,1720
	Maxfl	-5,2126	0,2155
	Maxfl²	-	-
	Concordance	85,50%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Only the linear term was included in the median grain size model, whereas in the mud content model both the linear and the quadratic term were included. This resulted in a sigmoidal curve for median grain size, showing a high chance of occurrence in muddy and very fine sand sediments (small μm for median grain size), and an unimodal response curve for mud content, with an optimum at 50%, but with a relatively broad tolerance.

Nereis diversicolor	*Term*	*Regression coefficient*	*Standard error*
present: 523 absent: 979			
	intercept	0,8026	0,1001
	median	-	-
	median²	-0,00005	3,715E-6
	concordance	78,70%	
present: 512 absent: 874			
	intercept	-1,6620	0,1038
	mud	0,1023	0,00917
	mud²	-0,00103	0,000128
	concordance	75,00%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, the linear and quadratic terms of model salinity and depth, and the linear terms of maximum ebb (maxeb) and flood (maxfl) current velocities were included in the model (Table 14.3), with the linear term of maximum flood current velocity and the linear term of depth adding most to the change in deviance. The model with sediment characteristics performed equally well, and now the linear term of maximum ebb current velocity (maxeb), the linear term of median grain size and the linear and quadratic term of depth added most to the chance of deviance in the model.

Table 14.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Nereis diversicolor	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	Without sediment Presence: 660 Absence: 2167			with sediment presence: 454 absence: 839		
	Intercept	7,3822	0,6072	Intercept	9,0758	0,8874
	Model salinity	-0,4199	0,0570	Temporal salinity	-0,3703	0,0764
	Model salinity^2	0,00871	0,00144	Temporal salinity^2	0,0105	0,00229
	Depth	-0,6146	0,0508	Model salinity	-0,0878	0,0236
	Depth^2	0,0106	0,00105	Depth	-0,6606	0,0776
	Maxeb	-2,8955	0,4745	Depth^2	0,0197	0,00299
	Maxfl	-1,1788	0,3880	Maxeb	-3,8073	0,6072
				Median	-0,00954	0,00193
				Mud^2	-0,00024	0,000096
	Concordance	92,9%		Concordance	91,7%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 88,3 % of the responses correctly (Table 14.4). The model performed very well with 75% of the modelled (or predicted) presences which were also actually observed in the field. When including sediment characteristics in the model, this percentage decreased to 65,6%, indicating a better performance of the model excluding sediment characteristics.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 14.4. Comparative statistics on the predicted and observed occurrence of N. diversicolor in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model). Fisher exact one-tailed test (observed by model: Po<Ao).

Nereis diversicolor (p=0,466)
(without sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	495	165	**660**	75
Ao	165	2002	**2167**	92,4
Total	**660**	**2167**	**2827**	88,3

Difference between proportions	0,674
95% CI	-1,000 to 0,703 (normal approximation)
Fisher exact test: 1-tailed p (observed by model: Po<Ao)	<0.0001 (exact)

Nereis diversicolor (p=0,5)
(with sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	298	156	**454**	65,6
Ao	156	683	**839**	81,4
Total	**454**	**839**	**1293**	75,9

Difference between proportions	0,470
95% CI	-1,000 to 0,513 (normal approximation)
1-tailed p (observed by model: Po<Ao)	<0.0001 (exact)

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ECOPROFILE OF NEREIS SUCCINEA

INTRODUCTION

Nereis succinea was much less common in the Schelde estuary then *Nereis diversicolor*. *N. succinea* showed a rather difficult pattern of occurrence in the Schelde estuary. *N. succinea* occurred least in the most outer polyhaline zone. In the middle of the *N. succinea* was a relatively common species in the littoral zone, whereas in the subtidal zone the species was rarely observed. In the β-mesohaline zone the opposite was observed, with *N. succinea* being more common in the subtidal zone. This pattern of occurrence was not reflected in the observed mean biomass and density. In general, values were very low and *N. succinea* does not contribute much to the total macrobenthic density and biomass in the Schelde estuary.

AUTO-ECOLOGY

NEREIS SUCCINEA	Annelida, Polychaeta

General

The polychaete *Nereis succinea* is a typical estuarine species, but is less common as *N. diversicolor*. However, *N. succinea* is observed on a much larger range of different habitats as *N. diversicolor*. *N. succinea* lives normally in U-shaped burrows, open on both sides. *N. succinea* can burrow very fast.

Habitat preferences

Salinity: *N. succinea* penetrates the estuary up to the mesohaline zone, but tolerates less well extreme salinities as *N. diversicolor*. This can probably be explained by the lower tolerance of low salinities of the larvae. In the Westerschelde WOLFF (1973) observed *N. succinea* up to 3 g Cl^-/l. ROBINEAU (1987) describes *N. succinea* as a typical brackish water species in the Loire estuary. However, NEUHOFF (1979) observed from feeding experiments that growth and food conversion at low salinities and temperatures were faster for *N. diversicolor* as compared to *N. succinea*, suggesting that the latter species prefers distinctly higher salinities and temperatures.

Sediment type: *N. succinea* is observed on a wide range of different habitats, going from sand, mud, between shells, on mussel beds, even on piles and harbour constructions (WOLFF, 1973).

Feeding

N. succinea is a non selective deposit feeder, also ingesting detritus (GOERKE, 1971; HARTMANN-SCHRÖDER (1971).

Population dynamics and life history

Swarming epitokous animals can be observed in large numbers between July-September (WOLFF, 1973). At 20-21 °C the free-swimming larvae settle after about 10-14 days.

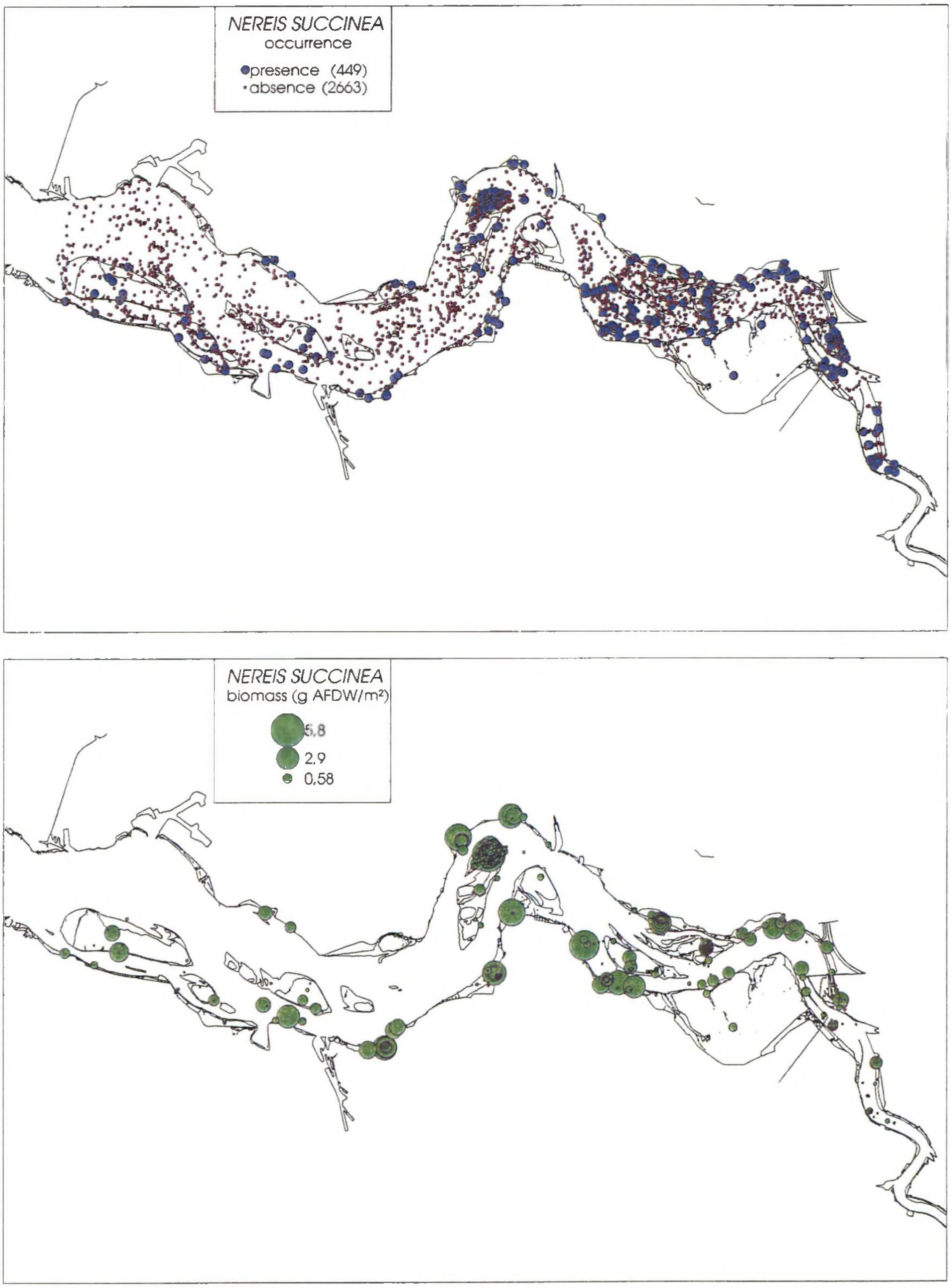


Figure 15.2. Geographical distribution maps of Nereis succinea *in the Schelde estuary with presence/absence data (top) and biomass (g AFDW m^{-2}) data (bottom).*

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

N. succinea showed a rather difficult pattern of occurrence in the Schelde estuary. *N. succinea* occurred least in the most outer polyhaline zone (salinity region 1) (Table 15.1). In the middle of the estuary (poly/mesohaline salinity regions 2 and 3), *N. succinea* was a relatively common species in the littoral zone, whereas in the subtidal zone the species was rarely observed (especially in salinity region 2). In the β-mesohaline zone (salinity region 4) the opposite was observed, with *N. succinea* being more common in the subtidal zone. The pattern of occurrence was not reflected in the observed mean biomass and density (Figure 15.1). In general, values were very low and *N. succinea* does not contribute much to the total macrobenthic density and biomass in the Schelde estuary. The geographical distribution of *N. succinea* in the Schelde estuary is shown in Figure 15.2.

Table 15.1. Occurrence (p/a) of N. succinea along the salinity and depth gradients of the Schelde estuary. N= number of observations (regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	9,2 % (n=262)	37,4 % (n= 503)	27,0 % (n=485)	7,7 % (n= 287)
Undeep subtidal	0 % 'n=151)	3,3 % (n=153)	4,7 % (n=127)	13,7 % (n=51)
deep subtidal	2,4 % (n=123)	1,5 % (n=130)	3,6 % (n=112)	13,4 % (n=67)
channel	2,7 % (n=186)	1,7 % (n=173)	8,6 % (n=232)	28,6 % (n=70)

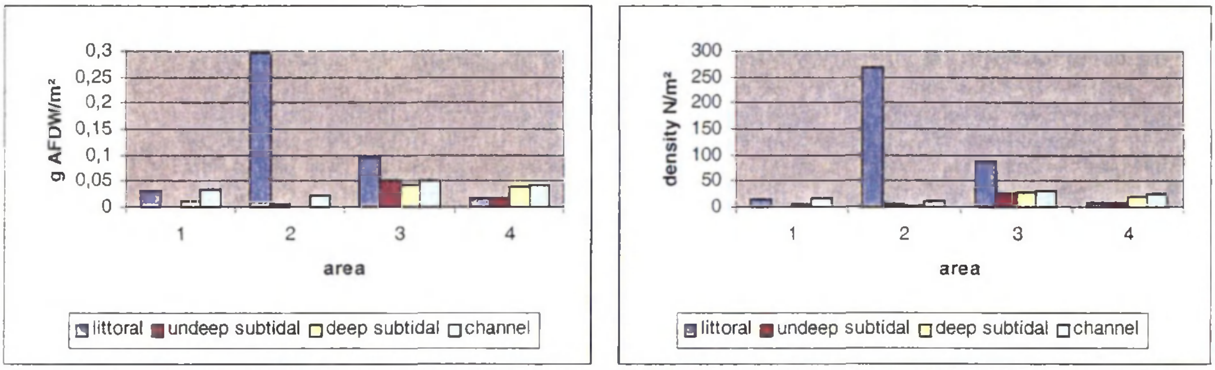


Figure 15.1. Mean density (ind m⁻²) and biomass (g AFDW m⁻²) of Nereis succinea along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

In general, a higher occurrence of *N. succinea* was observed in autumn as compared to spring in the littoral zone (Table 15.2). This was reflected in the mean biomass and density, being higher in autumn, except in salinity region 3 where comparable values were observed for both autumn and spring. A spring-autumn comparison for the subtidal zone of salinity region 4 is difficult to make since too few spring data were available.

Table 15.2. Spring (Mar - May) versus autumn (Aug - Oct) occurrence (p/a), density (ind m⁻²) and biomass (g AFDW m⁻²) of N. succinea in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

LITTORAL		1	2	3	4
Presence	Spring	6,2 % (n=97)	29,6 % (n= 169)	23,8 % (n=147)	3,0 % (n= 33)
	Autumn	13,3 % (n=135)	39,0 % (n=218)	28,9 % (n=249)	9,8 % (n= 214)
Density	Spring	3	142	90	4
	Autumn	26	318	100	10
Biomass	Spring	0,019	0,238	0,115	0,011
	Autumn	0,048	0,312	0,089	0,021

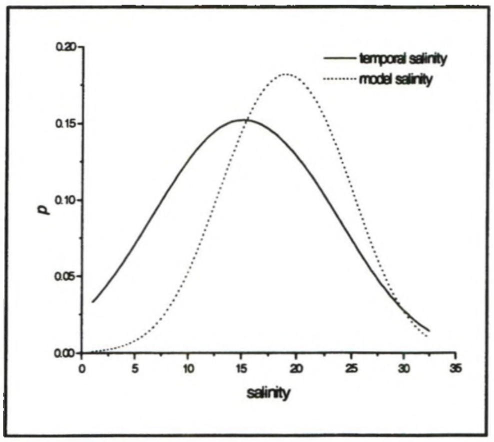
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Both the linear and quadratic term were included in both salinity models, giving unimodal response curves for both models. An optimum is observed in the poly/mesphaline zone, being around 15 psu and 19 psu for -'temporal salinity' and 'model salinity' respectively. The 'model salinity' model showed a more narrow tolerance with an optimum which shifted towards a higher salinity as compared to the 'temporal salinity' model. The 'temporal salinity' model showed a much broader response curve, extending more into the mesohaline zone. This difference in response, observed for many species, was probably the result of the fact that the 'temporal salinity' model did take into account the seasonal variation in salinity.

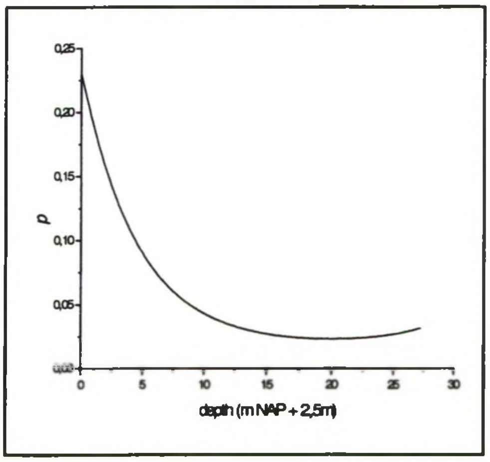
Nereis succinea	*Term*	*Regression coefficient*	*Standard error*
present: 321 absent: 2791			
	Intercept	-3,6232	0,3805
	Temporal salinity	0,2523	0,0467
	Temporal salinity²	-0,00835	0,00134
	Concordance	58,10%	
	Intercept	-7,6936	0,6940
	Model salinity	0,6526	0,0722
	Model salinity²	-0,0172	0,00181
	Concordance	64,10%	



Depth

Both the linear and quadratic term of depth were included in the model. The response showed a (shallow) decrease in chance of occurrence with increasing depth, but the slope suggested also the presence of *N. succinea* in the subtidal zone.

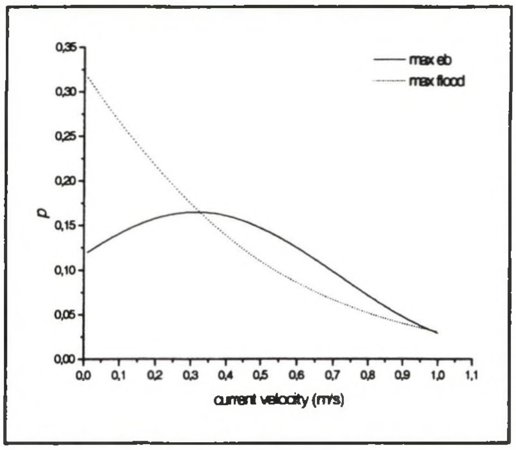
Nereis succinea	*Term*	*Regression coefficient*	*Standard error*
present: 292 absent: 2582			
	Intercept	-1,2077	0,1015
	Depth	-0,2525	0,0280
	depth²	0,00629	0,00102
	Concordance	68,60%	



Maximum ebb and flood current velocities (m.s^{-1})

Both the linear and quadratic term were included in the maximum ebb current velocity model (maxeb), whereas only the linear term was included in the maximum flood current velocity model (maxfl). This resulted in two different response curves: an unimodal response curve for maximum ebb current velocity with an optimum around 0.30-0.35 m.s^{-1}, but with a very broad tolerance, and a linear logit response for maximum flood current velocity with a decrease in probability of occurrence with increasing current velocity. However, it was clear from both response curves that *N. succinea* did not prefer very high current velocities.

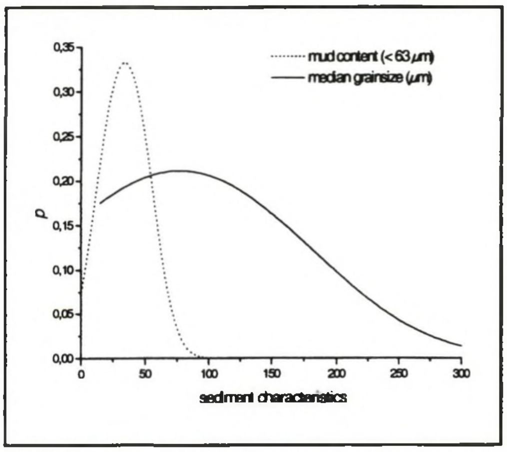
Nereis succinea	*Term*	*Regression coefficient*	*Standard error*
present: 315 absent: 2722			
	Intercept	-2,0212	0,2608
	Maxeb	2,5264	1,0120
	Maxeb^2	-4,0152	0,8881
	Concordance	67,60%	
	Intercept	-0,7451	0,1083
	Maxfl	-2,7050	0,2157
	Maxfl^2	-	-
	Concordance	73,30%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Both the linear and quadratic term were included in the median grain size model and the mud content model. *N. succinea* clearly prefered fine to very fine sandy sediments, showing unimodal response curves for median grain size with an optimum at ± 75 μm and for mud content with an optimum of 35%. However, *N. succinea* showed a relatively broad tolerance and only in very coarse sediments and in sediments with a very high mud content the chance of observing this species was very small.

Corophium voluator	*Term*	*Regression coefficient*	*Standard error*
present: 217 absent: 1285			
	intercept	-1,6760	0,2964
	median	0,00926	0,00450
	median^2	-0,00006	0,000016
	concordance	65,90%	
present: 214 absent: 1172			
	intercept	-2,5173	0,1431
	mud	0,1076	0,0132
	mud^2	-0,00159	0,000214
	concordance	71,20%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, linear and/or quadratic terms of all abiotic variables were included in the model (Table 15.3), with the linear term of maximum flood current velocity (maxfl), the linear and quadratic term of maxium ebb current velocity (maxeb and maxeb^2) and the quadratic term of depth adding most to the change in deviance. The model with sediment characteristics performed slightly better, with the linear term of maximum flood current velocity (maxfl), the linear and quadratic term of model salinity, and the linear term of mud content adding most to the change of deviance in the model.

Table 15.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Nereis succinea	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment			with sediment		
	presence: 288			Presence: 209		
	absence: 2539			Absence: 1084		
	intercept	-7,3157	0,7048	Intercept	-10,1850	1,2763
	Model salinity	0,7298	0,0791	Model salinity	0,9116	0,1189
	Model salinity^2	-0,0192	0,00207	Model salinity^2	-0,0223	0,00321
	Depth^2	0,00176	0,000477	Depth^2	0,00233	0,00115
	Maxeb	4,3277	1,3017	Maxeb	13,1415	2,3534
	Maxeb^2	-3,0348	1,0775	Maxeb^2	-7,7727	1,9980
	Maxfl	-5,8788	1,0363	Maxfl	-10,7415	1,6378
	Maxfl^2	1,7866	0,8368	Maxfl^2	4,8428	1,3154
				Median	-0,0110	0,00257
				Mud	0,0741	0,0205
				Mud^2	-0,00104	0,000293
	concordance	81,1%		Concordance	86,2%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 88,1 % of the responses correctly (Table 15.4). However, only 41,7% of the modelled (or predicted) presences were also actually observed in the field. When including sediment characteristics in the model, this percentage increased to 60,3%, indicating a better performance of the model including sediment characteristics.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 15.4. Comparative statistics on the predicted and observed occurrence of N. succinea in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model). Fisher exact one-tailed test (observed by model: Po<Ao).

Nereis succinea (p=0,287)
(without sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	120	168	**288**	41,7
Ao	168	2371	**2539**	93,4
Total	**288**	**2539**	**2827**	88,1

Difference between proportions	0,350	
95% CI	-1,000 to 0,399	(normal approximation)

Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)

Nereis succinea (p=0,34)
(with sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	126	83	**209**	60,3
Ao	83	1001	**1084**	92,3
Total	**209**	**1084**	**1293**	79,4

Difference between proportions	0,526	
95% CI	-1,000 to 0,584	(normal approximation)

Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)

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ECOPROFILE OF POLYDORA SPP.

INTRODUCTION

Polydora spec. was, in comparison with *Pygospio elegans*, not a very common spionid species in the Schelde estuary, which was mainly observed in the littoral zone. In general density and biomass values were low and *Polydora spp.* did not contribute much to the total macrobenthic density and biomass in the Schelde estuary.

AUTO-ECOLOGY

POLYDORA SPP.	Annelida, Polychaeta

General

As the genus *Polydora* is a difficult group in terms of determination, and as this genus was not always determined at species level, all individuals belonging to the genus *Polydora* were lumped to *Polydora spp.* Most species were determined as *Polydora ligni*. Other species observed were Polydora ciliata.

The spionid polychaete *Polydora spp.* is a typical euryhaline species, living in a U-shaped, with mucus strengthened burrow (tube). Only the long palps extend out of the sediment surface. *P. ligni* can be found in huge densities, being considered as an indicator for organic pollution (ANGER *et al.*, 1986). REISH (1984) mentions *P. ciliata* as indicator for organic pollution.

Habitat preferences

Salinity: *P. ligni* is a euryhaline species, tolerating a wide range of salinities, with a preference for the brackish zone. In the Delta area *P. ligni* is observed from 1-3 g Cl^-/l to 16.5 Cl^-/l (WOLFF, 1973). *P. ciliata* penetrates the estuary only down to a chlorinity of 10-12 g Cl^-/l (WOLFF, 1973).

Sediment type: *Polydora spp.* can be observed in a wide range of substrates: *P. ligni* prefers, very fine, muddy sediments (WOLFF, 1973) , whereas *P. ciliata* lives (burrows) in hard substrates , like shells (KORRINGA, 1951), sandstone (GUDMUNDSSON, 1985), limestone, wood, etc. (DORSETT, 1961). Seldom *P. liciata* has been observed in loose sediments (WOLFF, 1973).

Feeding

Both *P. ligni* and *P. ciliata* are mainly selective deposit feeders which feed by means of their two lined palps, but they can also behave as suspension feeders (KORRINGA, 1951; BLAKE, 1971; DARO & POLK, 1973; DAUER *et al.*, 1981; TAGHON, 1982). Movement patterns of feeding palps are species-specific, and vary with animal size, types of habitats, presence of suspended particles, and hydrodynamic conditions (DAUER *et al.*, 1981; QIAN & CHIA, 1997).

Population dynamics and life history

P. ligni has a mean life span of 13 months and is already after 1 month sexually mature (ANGER *et al.*, 1986). *Polydora spp.* has separated sexes. The eggs are deposited in a transparent egg capsule in the tube of the female (GUDMUNDSSON, 1985; ZAJAC, 1986). The larvae develop in the tube until a length of three segments, after which they are released in the water column. The larvae settle when they have 15-20 segments (GUDMUNDSSON, 1985; ZAJAC, 1986). ZAJAC (1986) observed negative effects on the growth and reproduction of *P. ligni* with a decreasing food availability and/or an increasing intraspecific density.

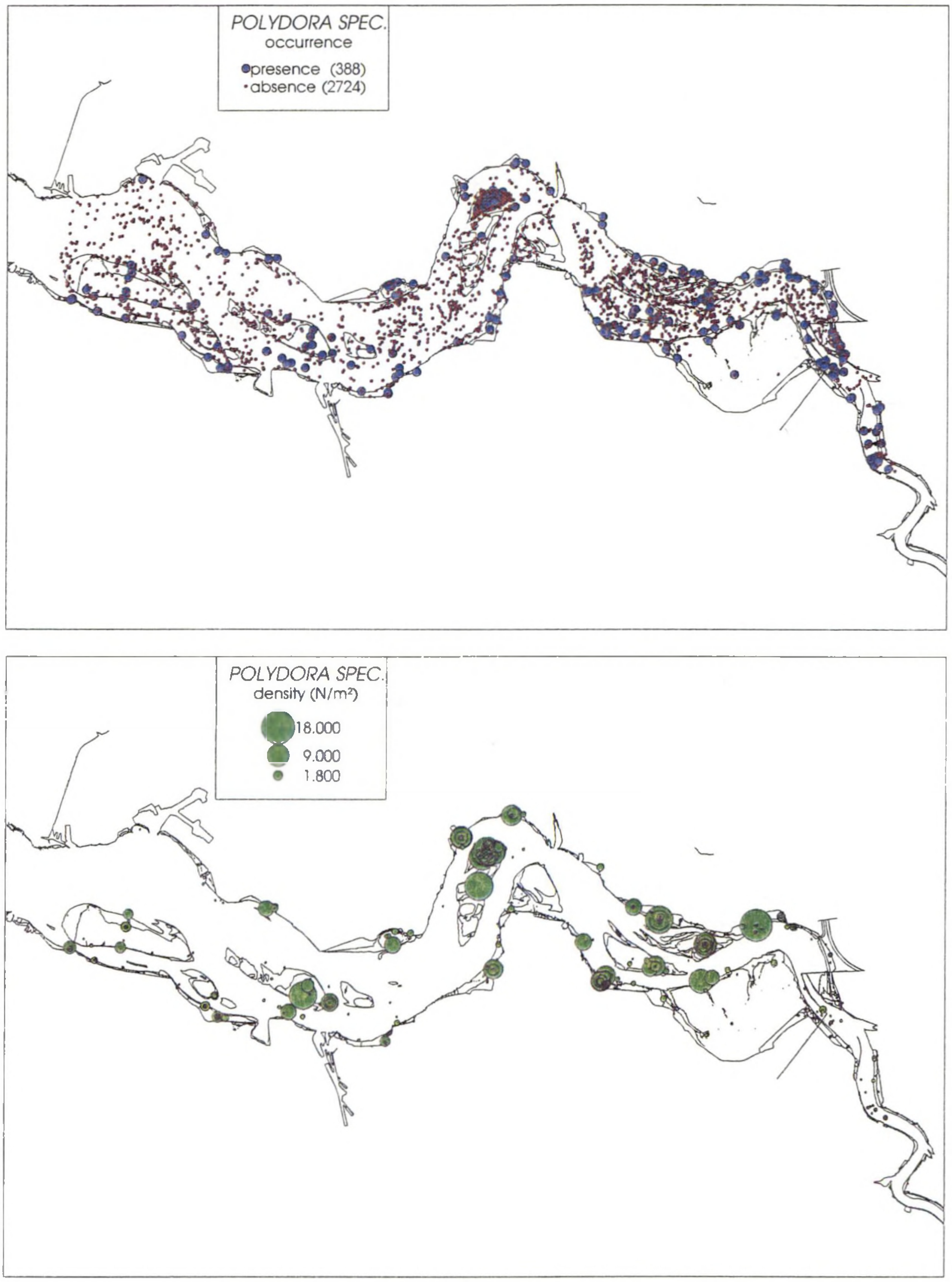


Figure 16.2. Geographical distribution maps of Polydora spp. in the Schelde estuary with presence/absence data (top) and biomass (g AFDW m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

In the polyhaline (salinity region 1 and 2) and the α-mesohaline (salinity region 3) zone *Polydora spp.* was mainly observed in the littoral zone with a presence of 20-23% (Table 16.1); in the subtidal zone the species was observed < 5% of the sampling occasions. In the β-mesohaline zone (salinity region 4) a different pattern was observed, with *Polydora spp.* present in all depth strata, being most observed in the deep subtidal and the channel.

This pattern of occurrence was not reflected in the observed mean biomass and density (Figure 16.1). Only in the littoral zone of salinity regions 2 and 3 relatively high mean values of biomass and density were observed. In all other strata mean biomass and density were very low. *Polydora spp.* does not contribute much to the total macrobenthic density and biomass in the Schelde estuary. The geographical distribution of *Polydora spp.* in the Schelde estuary is shown in Figure 16.2.

Table 16.1. Occurrence (p/a) of Polydora along the salinity and depth gradients of the Schelde estuary. N= number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	21,0 % (n=262)	19,9 % (n= 503)	23,1 % (n=485)	12,2 % (n= 287)
Undeep subtidal	3,3 % 'n=151)	3,9 % (n=153)	2,4 % (n=127)	11,8 % (n=51)
Deep subtidal	0 % (n=123)	2,3 % (n=130)	0,9 % (n=112)	19,4 % (n=67)
Channel	4,8 % (n=186)	4,0 % (n=173)	6,0 % (n=232)	27,1 % (n=70)

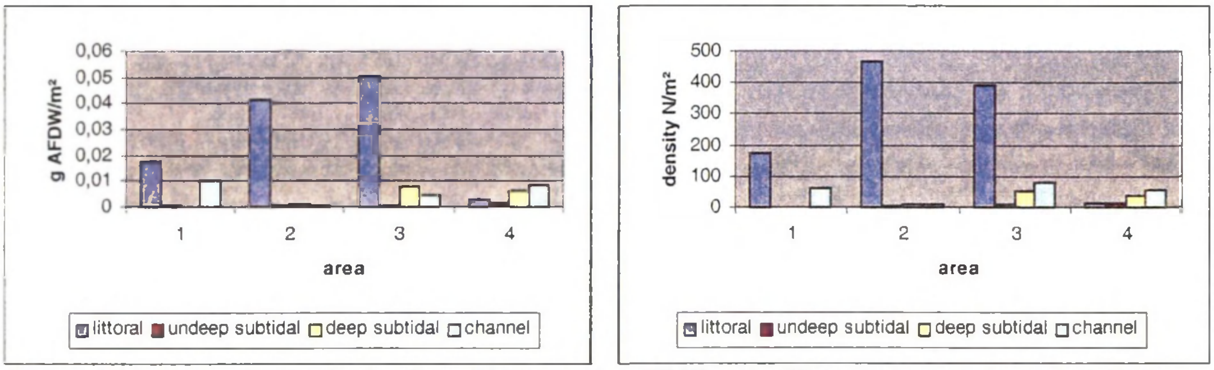


Figure 16.1. Mean density (ind m⁻²) and biomass (g AFDW m⁻²) of Polydora spp. along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

A large difference was observed between spring and autumn occurrence in the littoral zone, with the species being nearly absent in spring, especially in salinity region 4 (Table 16.2). This was clearly reflected in the mean density and biomass.

Table 16.2. Spring (March - May) versus autumn (Augustus - October) occurrence (p/a), density (ind m⁻²) and biomass (g AFDW m⁻²) of Polydora spp. in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

LITTORAL		1	2	3	4
Presence	Spring	5,2 % (n=97)	7,7 % (n= 169)	8,2 % (n=147)	0 % (n= 33)
	Autumn	31,1 % (n=135)	28,0 % (n=218)	30,1 % (n=249)	12,6 % (n= 214)
Density	Spring	3	37	63	0
	Autumn	327	946	637	18
Biomass	Spring	0,0008	0,0093	0,0114	0
	Autumn	0.0298	0,0765	0,0666	0,0026

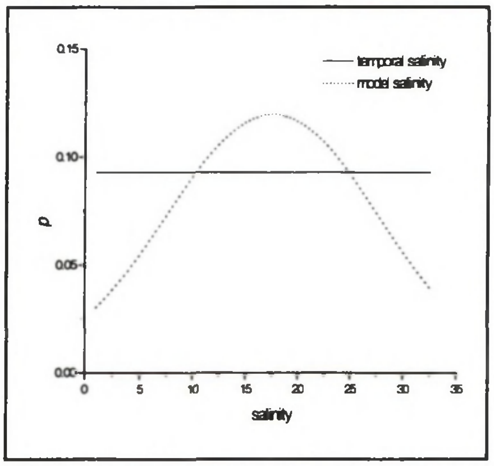
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Both the linear and quadratic term were included in the 'model salinity' model, whereas in the 'temporal salinity' model none of both terms were included. An unimodal response curve for model salinity was observed with an optimum at 17,5 psu. However, *Polydora spp.* showed a broad tolerance, indicating a broad occurrence along the whole estuary, which was already indicated by Table 16.1.

Polydora spp.	*Term*	*Regression coefficient*	*Standard error*
present: 289 absent: 2823			
	Intercept	-2,2791	0,0618
	Temporal salinity	-	-
	Temporal salinity^2	-	-
	Concordance	-	
	Intercept	-3,6535	0,5053
	Model salinity	0,1891	0,0553
	Model salinity^2	-0,00539	0,00142
	Concordance	53,70%	



Depth

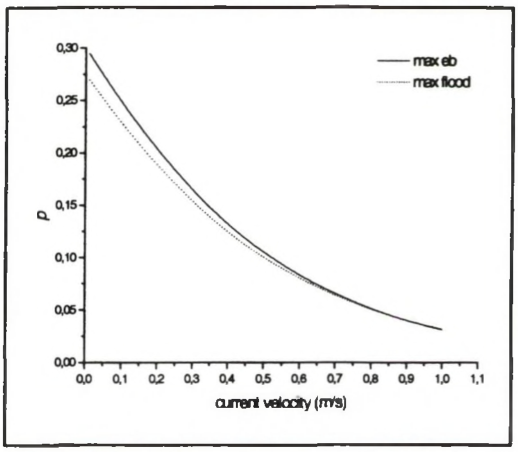
Both the linear and quadratic term of depth were included in the model. The response showed a (shallow) decrease in probability of occurrence with increasing depth, but the slope suggested also the presence of *Polydora spp.* in the subtidal zone, with a small increase in probability of occurrence at a depth > 20m. This is in accordance with Table 16.1, where in the β-mesohaline zone *Polydora spp.* was most observed in the deep subtidal and the channel, but the number of observations here is much less as compared to the other salinity regions, making the response less clear.

Polydora spp.	*Term*	*Regression coefficient*	*Standard error*
present: 250 absent: 2624			
	Intercept	-1,3967	0,1075
	Depth	-0,2641	0,0290
	depth^2	0,00753	0,000985
	Concordance	67,80%	

Maximum ebb and flood current velocities (m.s^{-1})

Only the linear term was included in the maximu models. This resulted in more or less similar sigmoidal current velocity, showing a high probability of occurrence with small current velocities and a gradual decreasing probability of occurrence with increasing current velocities.

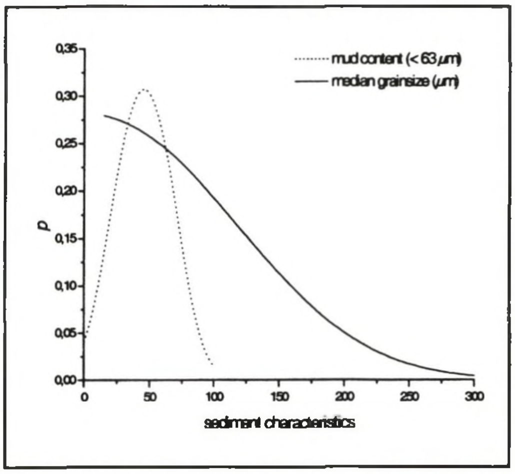
***Polydora* spp.**	*Term*	*Regression coefficient*	*Standard error*
present: 285 absent: 2752			
	Intercept	-0,8481	0,1312
	Maxeb	-2,5872	0,2459
	Maxeb^2	-	-
	Concordance	70,60%	
	Intercept	-0,9719	0,1124
	Maxfl	-2,4457	0,2173
	Maxfl^2	-	-
	Concordance	71,30%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Only the linear term was included in the median grain size model, whereas in the mud content model both the linear and the quadratic term were included. This resulted in a sigmoidal curve for median grain size, showing a high probability of occurrence in muddy and very fine sand sediments (small μm for median grain size), and an unimodal response curve for mud content, with an optimum at 45%., but with a relatively broad tolerance.

***Polydora* spp.**	*Term*	*Regression coefficient*	*Standard error*
present: 172 absent: 1330			
	Intercept	-0,9367	0,1235
	Median	-	-
	median^2	-0,00005	5,742E-6
	Concordance	74,1%	
present: 172 absent: 1214			
	Intercept	-3,1689	0,1772
	Mud	0,1036	0,0130
	mud^2	-0,00114	0,000183
	Concordance	73,90%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, the linear and/or quadratic terms of all abiotic variables were included in the model (Table 16.3), with the linear term of maximum flood current velocity and the quadratic term of depth and temporal salinity adding most to the change in deviance. The model with sediment characteristics performed slightly better, and now the linear term of median grain size and the linear term of model salinity added most to the change of deviance in the model.

Table 16.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

***Polydora* spp.**	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	Without sediment Presence: 250 Absence: 2577			with sediment presence: 155 absence: 1138		
	intercept	-4,4166	0,6060	intercept	-5,7512	0,8993
	Temporal salinity	0,2862	0,0742	Temporal salinity	0,4337	0,1258
	Temporal salinity^2	-0,00521	0,00218	Temporal salinity^2	-0,0107	0,00384
	Model salinity	0,1662	0,0805	Model salinity	0,3275	0,1242
	Model salinity^2	-0,00662	0,00224	Model salinity^2	-0,00758	0,00361
	Depth^2	0,00231	0,000507	Depth^2	0,00260	0,000948
	Maxeb^2	-1,0783	0,3797	Maxfl	-2,5222	0,4731
	Maxfl	-2,4005	0,3726	Median	-0,0172	0,00194
	concordance	77,6%		Concordance	82,7%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 88,3 % of the responses correctly (Table 16.4). However, only 34,0 % of the modelled (or predicted) presences were also actually observed in the field. When including sediment characteristics in the model, this percentage increased to 50,3 %, indicating a better performance of the model including sediment characteristics.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 16.4. Comparative statistics on the predicted and observed occurrence of Polydora spp. in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model). Fisher exact one-tailed test (observed by model: Po<Ao).

Polydora spp.(p=0,226)
(without sediment characteristics)

Response Observed	**Model** Pm	Am	**Total**	**% correct**
Po	85	165	**250**	34
Ao	165	2412	**2577**	93,6
Total	**250**	**2577**	**2827**	88,3

Difference between proportions	0,276	
95% CI	-1,000 to 0,326	(normal approximation)
Fisher exact test: 1-tailed p (observed by model: Po<Ao)	<0.0001	(exact)

Polydora spp. (p=0,281)
(with sediment characteristics)

Response Observed	**Model** Pm	Am	**Total**	**% correct**
Po	78	77	**155**	50,3
Ao	77	1061	**1138**	93,2
Total	**155**	**1138**	**1293**	88,1

Difference between proportions	0,436	
95% CI	-1,000 to 0,503	(normal approximation)
Fisher exact test: 1-tailed p (observed by model: Po<Ao)	<0.0001	(exact)

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ECOPROFILE OF PYGOSPIO ELEGANS

INTRODUCTION

Pygospio elegans is a very common spionid species in the intertidal zone of the Schelde estuary. This species had the highest mean density of all macrobenthic species observed. However, its contribution to the overall macrobenthic biomass is low.

AUTO-ECOLOGY

PYGOSPIE ELEGANS	Annelida, Polychaeta

General

The polychaete *Pygospio elegans* is a typical euryhaline species, which enters the estuaries up to the brackish zones, being very common in the intertidal areas of the Delta area (WOLFF, 1973). *P. elegans* lives in a with mucus strengthened burrow (tube).

Habitat preferences

Salinity: *P. elegans* penetrates the estuary up to the mesohaline zone (WOLFF, 1973). The species has been observed in salinities down to 4,5 g Cl^-/l in the former Zuiderzee (DE VOS, 1936) and salinities down to 3-3,5 g Cl^-/l in Finnish waters (LAAKSO, 1968). GREEN (1968) observed *P. elegans* tolerating salinities down to 1,2 g Cl^-/l for short periods. MUUS (1967) reports that *P. elegans* is still reproducing in mesohaline waters.

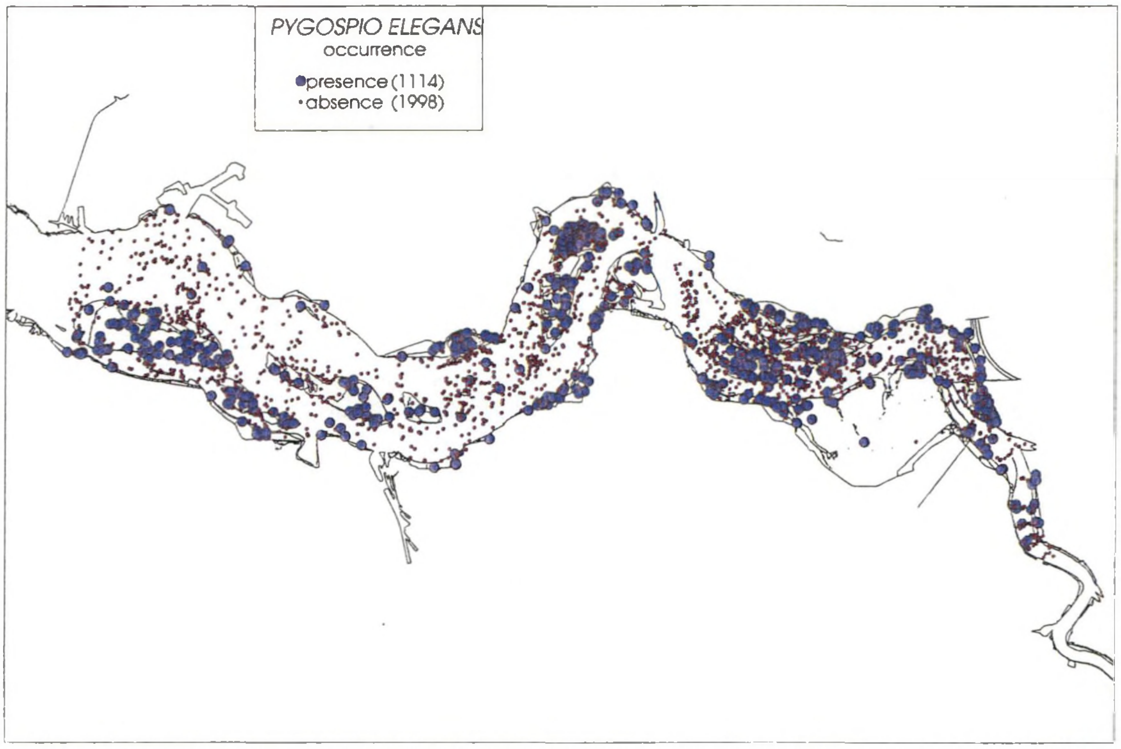
Sediment type and tidal elevation: *P. elegans* prefers fine, muddy sand (WOLFF, 1973). According to MUUS (1967) P. elegans occurs in sandy and mixed sediments, whereas HARTMANN-SCHRÖDER (1971) mentions no certain preference for this species. Also LINKE (1939) states that *P. elegans* does not prefer a certain sediment type, but the presence of diatoms is of importance. DESPREZ *et al.* (1986) observed an increase in *P. elegans* with increasing mud content. The major part of the individuals of *P. elegans* lives in the intertidal zone, which fact is in accordance with the photopositive behaviour of the larvae (WOLFF, 1973).

Feeding

P. elegans is a selective deposit feeder which, like other spionids, scrapes its food with its tentacles into its burrow (TAGHON, 1982). Its food consists of diatoms and small green algae. *P. elegans* also is capable of filter feeding by means of a net of mucus threads (FAUCHALD & JUMARS, 1979).

Population dynamics and life history

The reproduction takes place between February and the end of September, with a peak in June-August. On average there are two generations per year (WOLFF, 1973). The female produces egg chains (up to 16 capsules, each with 50-60 eggs), which are attached to the tube of the adult (SCHMIDT, 1951; RASMUSSEN, 1956; GUDMUNDSSON, 1985). Only a few larvae per egg capsule develop into larvae; the rest of the remaining eggs functions as nourishment for the developing larvae (GUDMUNDSSON, 1985). The larval development varies and both pelagic and demersal larvae can occur (RASMUSSEN, 1973; GUDMUNDSSON, 1985). Their settling is favoured by the presence of a natural sediment; without such a substratum they may prolong their pelagic life for over two months (SMIDT, 1951). Besides sexual reproduction, *P. elegans* also shows asexual reproduction (MUUS, 1967; HOBSON & GREEN, 1968).



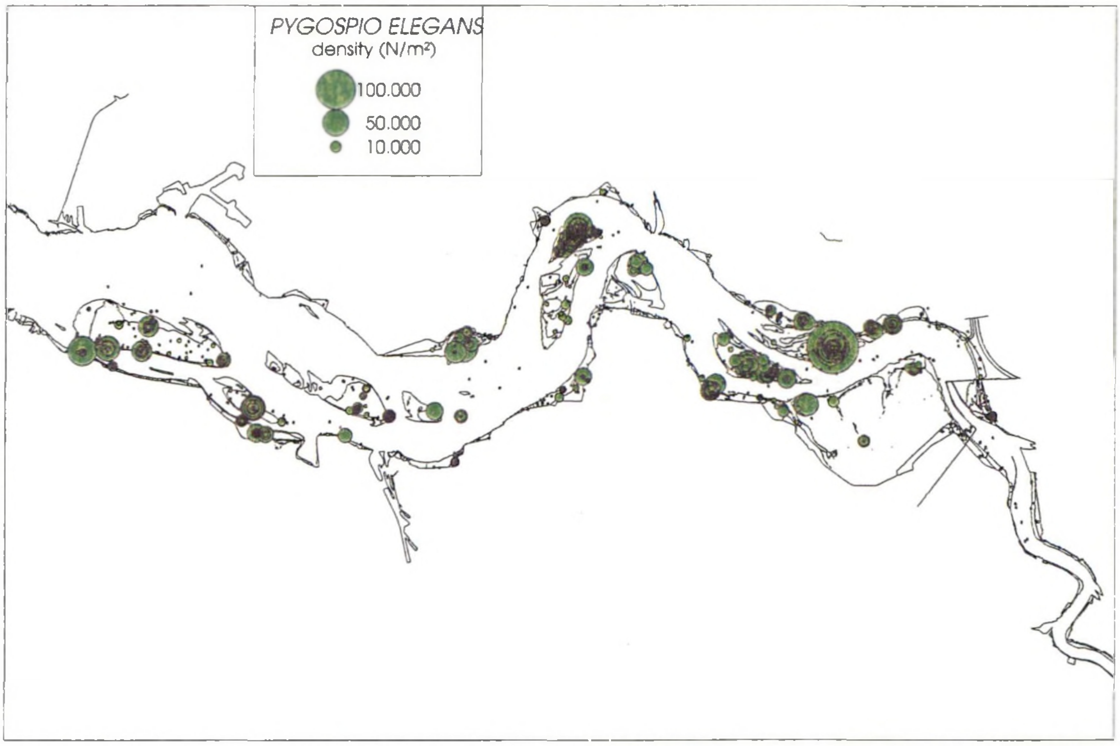


Figure 17.2. Geographical distribution maps of Pygospio elegans in the Schelde estuary with presence/absence data (top) and density (ind m⁻²) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

P. elegans was a typical species of the littoral zone of the Schelde estuary, with an equal presence (± 70%) in salinity regions 1 to 3 (Table 17.1). In the subtidal zone of these salinity regions *P. elegans* showed a decreasing occurrence with increasing depth. In the β-mesohaline zone (salinity region 4) the species was observed less frequently in the littoral zone (35.5%), whereas in the subtidal zone the species was relatively more present as compared to the other salinity regions.

Mean biomass and density showed the same pattern, with highest values in salinity region 3 and very low values both in salinity region 4 and all subtidal strata (Figure 17.1). The geographical distribution of *P. elegans* in the Schelde estuary is shown in Figure 17.2.

Table 17.1. Occurrence (p/a) of P. elegans along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
littoral	73,3 % (n=262)	71,6 % (n= 503)	70,5 % (n=485)	35,5 % (n= 287)
undeep subtidal	12,6 % 'n=151)	10,5 % (n=153)	10,2 % (n=127)	11,8 % (n=51)
deep subtidal	5,7 % (n=123)	5,4 % (n=130)	3,6 % (n=112)	16,4 % (n=67)
channel	3,8 % (n=186)	3,5 % (n=173)	6,0 % (n=232)	11,4 % (n=70)

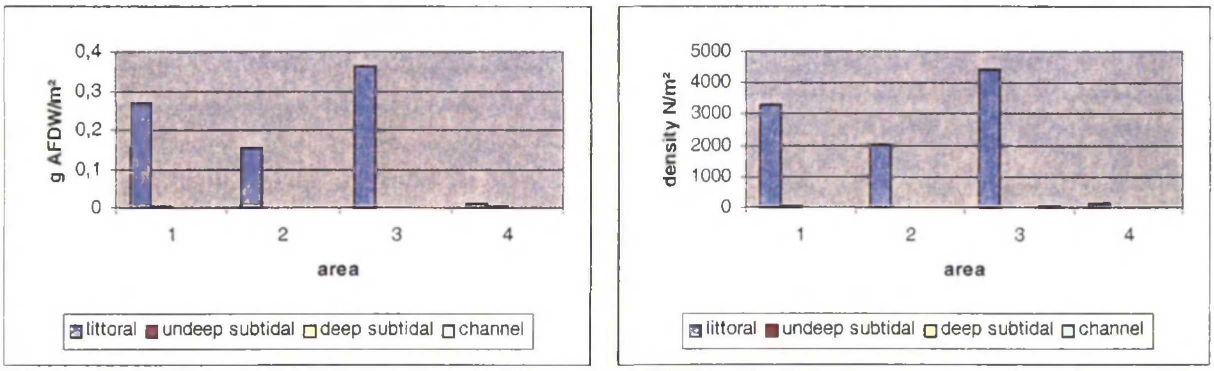


Figure 17.1. Mean density (ind m^{-2}) and biomass (g AFDW m^{-2}) of P. elegans along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

P. elegans was equally present in spring and autumn in all salinity regions (Table 17.2). Mean density was in general 1.5-2x higher in autumn as compared to spring, whereas biomass values were only slightly higher.

Table 17.2. Spring (March - May) versus autumn (Augustus - October) occurrence (p/a), density (ind m^{-2}) and biomass (g AFDW m^{-2}) of P. elegans in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

LITTORAL		1	2	3	4
Presence	Spring	68,0 % (n=97)	76,9 % (n= 169)	61,9 % (n=147)	39,4 % (n= 33)
	Autumn	77,0 % (n=135)	66,1 % (n=218)	71,1 % (n=249)	35,1 % (n= 214)
Density	Spring	2199	1717	2097	146
	Autumn	3894	2438	4745	93
Biomass	Spring	0,2318	0,1424	0,2228	0,0102
	Autumn	0,2567	0,1493	0,3010	0,0088

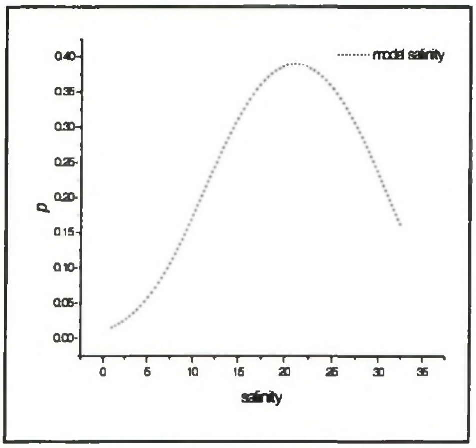
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Both the linear and quadratic term were included in 'model salinity' model, whereas no term was included in the 'temporal salinity' model. A unimodal response curve was observed for model salinity, with an optimum in the polyhaline zone around 21 psu. Towards the oligohaline zone the probability of occurrence became zero.

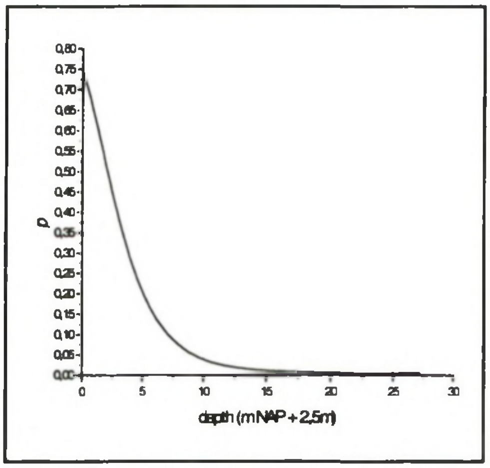
Pygospio elegans	*Term*	*Regression coefficient*	*Standard error*
present: 926 absent: 2166			
	Intercept	-0,8590	0,0392
	Temporal salinity	-	-
	Temporal salinity^2	-	-
	Concordance	-	
	Intercept	-4,5216	0,3745
	Model salinity	0,3878	0,0389
	Model salinity^2	-0,00923	0,000955
	Concordance	61,60%	



Depth

Both the linear and quadratic term of depth were included in the model. The response showed a decrease in chance of occurrence of *P. elegans* with increasing depth, but with still a chance of occurrence in the undeep subtidal.

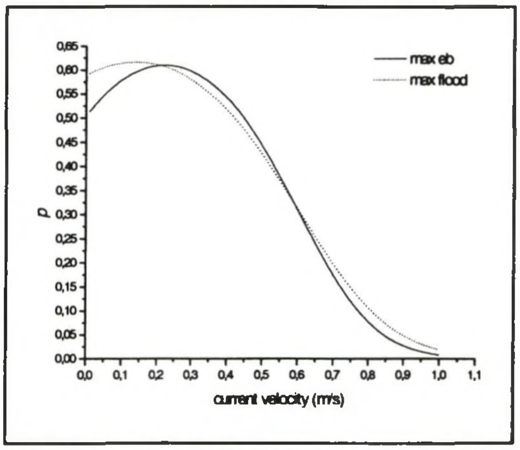
Pygospio elegans	*Term*	*Regression coefficient*	*Standard error*
present: 791 absent: 2083			
	Intercept	1,0818	0,0881
	Depth	-0,5437	0,0282
	depth^2	0,0115	0,00125
	Concordance	83,60%	



Maximum ebb and flood current velocities (m.s^{-1})

Both the linear and quadratic term were included in the maximum ebb (maxeb) and flood (maxfl) current velocity models. The probability of occurrence of *P. elegans* was highest at lower current velocities with an optimum around 0.15-0.25 m.s^{-1}, but with a very broad tolerance, especially in the lower end of the current velocities. From a current velocity of 0.5 m.s^{-1} onwards, a steep decrease in the probability of occurrence was observed in both models.

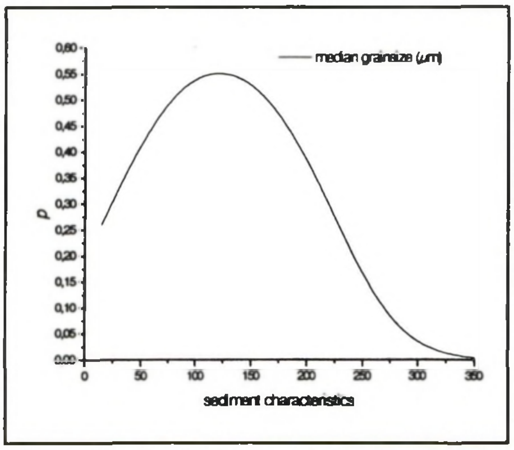
Pygospio elegans	*Term*	*Regression coefficient*	*Standard error*
present: 892 absent: 2145			
	Intercept	0,0158	0,2155
	Maxeb	3,8796	0,9563
	Maxeb^2	-8,7569	0,9913
	Concordance	82,50%	
	Intercept	0,3586	0,1637
	Maxfl	1,6555	0,7689
	Maxfl^2	-5,9637	0,7836
	Concordance	83,60%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Both the linear and quadratic term were included in the median grain size model, whereas no term was included in the mud content model. An unimodal response curve was observed for median grain size, with an optimum at 125 μm. However, *P. elengans* showed a relatively broad tolerance and only in very coarse sediments the chance of observing this species was very small.

Pygospio elegans	*Term*	*Regression coefficient*	*Standard error*
present: 547 absent: 955			
	Intercept	-1,4216	0,2472
	Median	0,0267	0,00374
	median^2	-0,00011	0,000013
	Concordance	74,30%	
present: 744 absent: 642			
	Intercept	-0,4733	0,0552
	Mud	-	-
	mud^2	-	-
	Concordance	-	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, linear and quadratic terms of model salinity and depth and quadratic terms of maximum ebb (maxeb) and flood (maxfl) current velocity were included in the model (Table 17.3), with the linear term of maximum flood current velocity (maxfl), the linear and quadratic term of depth and the linear term of model salinity adding most to the change in deviance. The model with sediment characteristics performed slightly better, with the linear term of maximum flood current velocity (maxfl), the linear and quadratic term of model salinity, and the quadratic term of median grain size adding most to the change of deviance in the model.

Table 17.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Pygospio elegans	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment			With sediment		
	Presence: 773			Presence: 492		
	absence: 2054			Absence: 910		
	Intercept	-5,2640	0,4876	intercept	-7,5609	0,7049
	Model salinity	0,6872	0,0539	Model salinity	0,9682	0,0866
	Model salinity^2	-0,0156	0,00135	Model salinity^2	-0,0213	0,00226
	Depth	-0,3914	0,0393	Depth	-0,4163	0,0609
	Depth^2	0,0103	0,00133	Depth^2	0,0125	0,00198
	Maxeb^2	-1,0291	0,3782	Maxfl	-3,1578	0,4176
	Maxfl^2	-2,3810	0,2974	Median	0,0102	0,00513
				Median^2	-0,00006	0,000015
	Concordance	90,3%		concordance	91,5%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 85,6 % of the responses correctly (Table 17.4). The model performed very well with 75,7 % of the modelled (or predicted) presences which were also actually observed in the field. When including sediment characteristics in the model, this percentage was 71,1%, indicating an equal performance of both models.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 17.4. Comparative statistics on the predicted and observed occurrence of P. elegans in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model). Fisher exact one-tailed test (observed by model: Po<Ao).

Pygospio elegans (p=0,50)
(without sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	585	188	**773**	75,7
Ao	188	1866	**2054**	90,8
Total	**773**	**2054**	**2827**	85,6

Difference between proportions	0,665	
95% CI	-1,000 to 0,693	(normal approximation)
Fisher exact test: 1-tailed p (observed by model: Po<Ao)	<0.0001 (exact)	

Pygospio elegans (p=0,353)
(with sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	350	142	**492**	71,1
Ao	142	768	**910**	84,4
Total	**492**	**910**	**1402**	79,7

Difference between proportions	0,555	
95% CI	-1,000 to 0,594	(normal approximation)
Fisher exact test: 1-tailed p (observed by model: Po<Ao)	<0.0001 (exact)	

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ECOPROFILE OF SCROBICULARIA PLANA

INTRODUCTION

Scrobicularia plana occurred only in the littoral, polyhaline and α-mesohaline zone of the Schelde estuary. Although not frequently observed, the mean biomass of *S. plana* contributes substantially to the overall macrobenthic biomass in the estuary.

AUTO-ECOLOGY

SCROBICULARIA PLANA (Da Costa, 1778)	Mollusca, Bivalva

General

S. plana is a common, euryhaline bivalve species. Severe winters can cause huge mortality in the populations. After severe winters there is however in general a large recruitment (ESSINK *et al.*, 1991).

S. plana is living in a vertical position in the substrate, to a maximal depth of 20 cm (HUGHES, 1969) to 30 cm (GREEN, 1968) for adults. Smaller individuals live less deep as compared to larger ones (Zwarts & Wanink, 1989). An inhalating siphon is held vertically and reaches the surface, whereas the exhalating one is much shorter and curved (HUGHES, 1969). Burrowing capacity is dependent on sedimenttype (GUÉRIN, 1961) and favoured by its big foot. According to HODGSON (1982), vertical migration occurs during winter. Horizontal migration is very rare, unlike the other Tellinids.

Habitat preferences

Salinity: *Scrobicularia plana* is a euryhaline species (GUERIN, 1961). With large fresh water influx shells are closed. In the Delta area *S. plana* inhabits a large range of salinities. It has been found at salinities permanently over 16,5 g Cl^-/l, as well as at about 11 g Cl^-/l at high tide in the Westerschelde (WOLFF, 1973).

Sediment: *S. plana* is most abundant in fine sediments (muddy sand / soft mud) high in the intertidal area (DANKERS & BEUKEMA, 1981; SPOONER & MORE, 1940; WOLFF, 1973); subtidally the species is confined to the upper part (RASMUSSEN, 1973; WOLFF, 1973). More important than sediment type and height as distribution determining factors is the presence of a waterfilm on the flat during low tide (GUÉRIN, 1961; REICHERT & DÖRJES, 1980).

Feeding

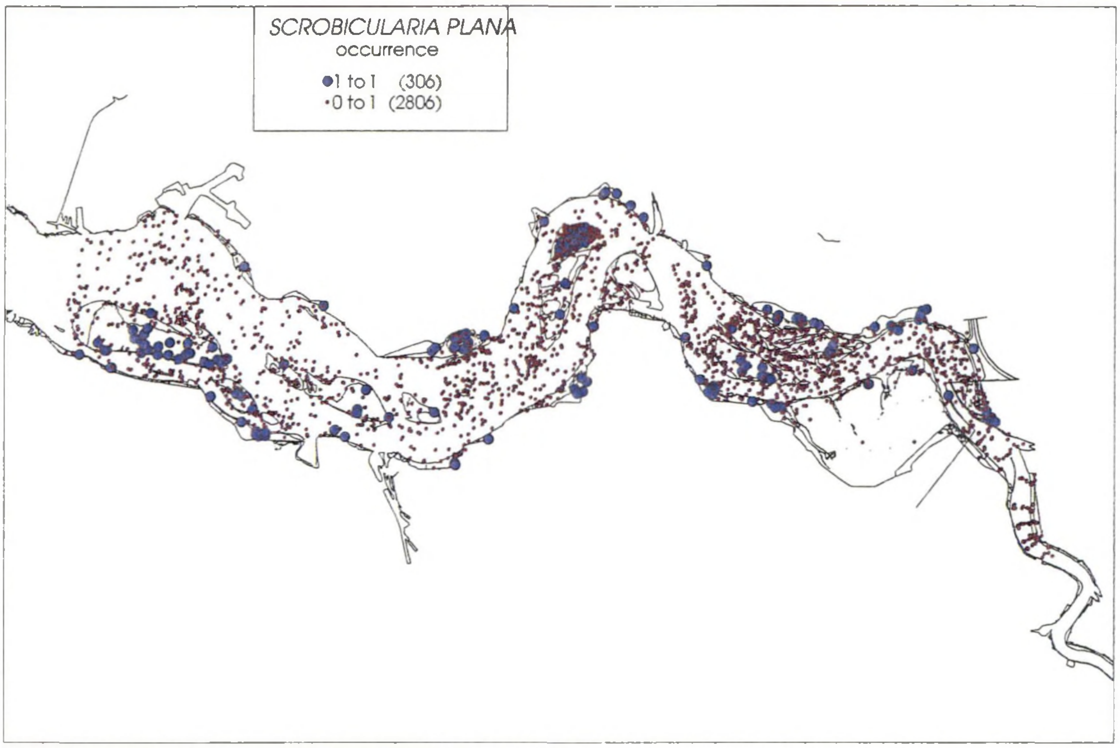
S. plana is primarily a non-selective deposit feeder during the whole low water period. However, the presence of a waterfilm is necessary for the intake of food particles (HUGHES 1969; REICHERT & DÖRJES 1980). The inhalating siphon is held 5-8 cm out of the sediment, where it moves round and round (ZWARTS *et al.* 1994). Since *S. plana* is most abundant in anaerobic sediments, sulphur bacteria (4-40 μm) are an important food source. The availability of food is an important factor that determines growth in a significant way (WORRALL & WIDOWS 1983; WORRALL *et al.* 1983). Besides deposit feeding, *S. plana* can also behave as a filter feeder: when the sediment is inundated, the siphon is retracted to protect it against predators and to take up particles from the water column. Deposit feeding activity decreases in November and remains low until bottom temperatures rises above 7° C.

Population dynamics and life history

S. plana is a gonochoristic species with comparable numbers of male and females (HUGHES, 1971). Hermaphrodites are scarce (PAES-DA-FRANCA, 1956). *S. plana* becomes sexually mature in its second summer, at a size of approximately 20 mm. Maturation of gametes starts in April when bottom temperature exceeds 10 °C, and ends up in the second half of June. Spawning takes place in July-August. In bays and estuaries along the English Channel and North Sea recruitment is irregular and has only one cohort per year. In the latter areas, especially in the Wadden Sea, recruitment may be absent for several years (ESSINK *et al.*, 1990). In southern populations along the Atlantic ocean (south of Brittany), ripe gametes are found the whole year round, resulting in two or three distinct spawning periods (PAES-DA FRANCA, 1956; ESSINK *et al.*, 1990). Sperma-tozoids are released through the exhalating siphon, to disperse into the watercolumn. Spawning in males is synchronised and takes about 15 minutes. It does not induce egg deposition by females. After spawning, there is a resting period of several months. *S. plana* can become old (18 years) and as big as 54 mm (GREEN, 1968).

Biotic interactions

S. plana is an important prey-item for several birds. HUGHES (1971) found a mortality rate of 5-6 % due to predation by Oystercatchers (*Haematopus ostralegus*). Siphon retraction – after changes in pressure on the substrate - forms the visual stimulus for these birds (HUGHES, 1970). Other predators of *S. plana* are fishes (*Pleuronectes platessa*, *Gadus morhua*, *Anguilla anguilla*, ...) and crabs. Very often, they can only take parts of the siphon ('cropping') which regenerates quickly (HODGSON, 1981). However, siphon predation has several negative consequences (HODGSON, 1982; ZWARTS, 1986).



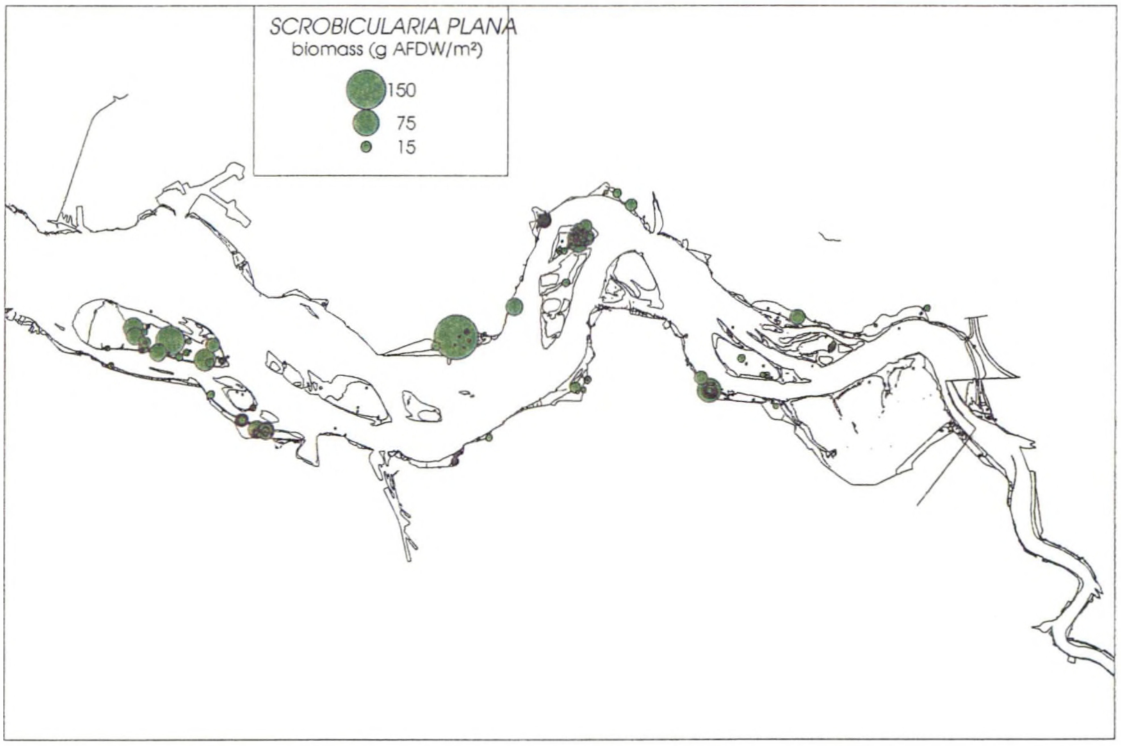


Figure 18.2. Geographical distribution maps of Scrobicularia plana in the Schelde estuary with presence/absence data (top) and biomass (g AFDW m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

S. plana occurred only in the polyhaline (salinity regions 1 and 2) and α-mesohaline (salinity region 3) zone, with the highest occurrence in salinity region 1 (Table 18.1). In the β-mesohaline zone (salinity region 4) the species was nearly completely absent. *S. plana* was only observed in the littoral zone, being almost completely absent in the subtidal zone.

Both mean biomass and density was highest in salinity region 1, and decreased towards salinity region 4 (Figure 18.1). Although not frequently observed, the mean biomass of *S. plana* contributes substantially to the overall macrobenthic biomass in the estuary. The geographical distribution of *S. plana* in the Schelde estuary is shown in Figure 18.2.

Table 18.1. Occurrence (p/a) of S. plana along the salinity and depth gradients of the Schelde estuary. N= number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
Littoral	34,4 % (n=262)	20,7 % (n= 503)	20,0 % (n=485)	2,4 % (n= 287)
undeep subtidal	1,3 % 'n=151)	0,7 % (n=153)	0,8 % (n=127)	0 % (n=51)
deep subtidal	0 % (n=123)	0 % (n=130)	0,9 % (n=112)	0 % (n=67)
channel	0,5 % (n=186)	0 % (n=173)	0,4 % (n=232)	1,4 % (n=70)

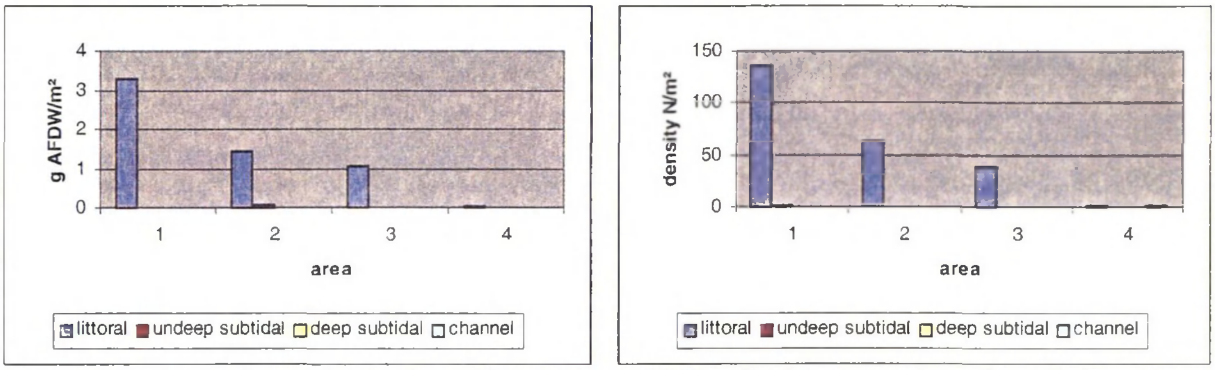


Figure 18.1. Mean density (ind m⁻²) and biomass (g AFDW m⁻²) of S. plana along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

The littoral occurrence and density of *S. plana* were comparable between spring and autumn in all salinity regions, except for somewhat higher values in autumn in salinity region 2 (Table 18.2). Mean biomass was higher in autumn in all salinity regions.

Table 18.2. Spring (March - May) versus autumn (Augustus - October) occurrence (presence/absence), density (ind m⁻²) and biomass (g AFDW m⁻²) of Scrobicularia plana in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

LITTORAL		1	2	3	4
Presence	Spring	30,9 % (n=97)	14,8 % (n= 169)	17,0 % (n=147)	0 % (n= 33)
	Autumn	31,9 % (n=135)	23,9 % (n=218)	19,7 % (n=249)	3,3 % (n= 214)
Density	Spring	170	15	25	0
	Autumn	112	110	35	2
Biomass	Spring	2,91	1,01	0,55	0
	Autumn	3,28	1,96	1,15	0,04

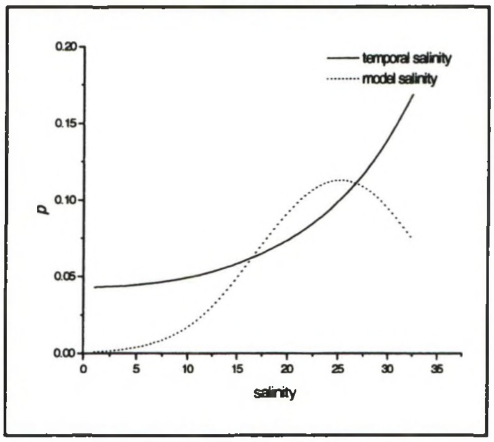
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Only the quadratic term was included in the 'temporal salinity' model, whereas both the linear and quadratic term were included in the 'model salinity' model. This resulted in two different response curves. The response curve for temporal salinity showed a sigmoidal increase in probability of occurrence with increasing salinity, whereas for model salinity a unimodal curve was observed, with an optimum at 25 psu.

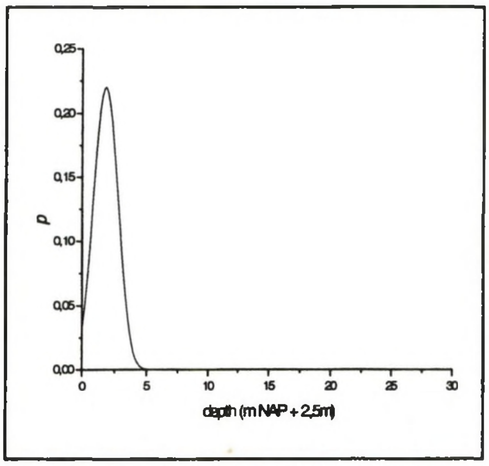
Scrobicularia plana	*Term*	*Regression coefficient*	*Standard error*
present: 243 absent: 2869			
	Intercept	-3,1038	0,1361
	Temporal salinity	-	-
	Temporal salinity²	-0,00143	0,000242
	Concordance	60,50%	
	Intercept	-7,5441	0,9343
	Model salinity	0,4355	0,0878
	Model salinity²	-0,00865	0,00200
	Concordance	57,80%	



Depth

Both the linear and quadratic term were included in the depth model, resulting in an unimodal response curve for *S. plana.* An optimum as observed at 0.7m above NAP (1.8 m NAP on the figure) with a very narrow tolerance. This indicated not only a steep decrease in probability of occurrence with increasing depth, but also in the higher intertidal zone the probability of occurrence of *S. plana* was small.

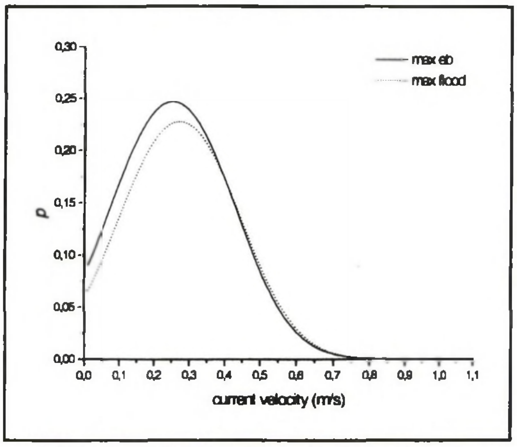
Scrobicularia plana	*Term*	*Regression coefficient*	*Standard error*
present: 188 absent: 2686			
	Intercept	-3,3876	0,3577
	Depth	2,3558	0,3900
	depth²	-0,6535	0,1011
	Concordance	86,40%	



Maximum ebb and flood current velocities (m.s^{-1})

Both the linear and quadratic terms were included in the maximum ebb and flood current velocity models. This resulted in similar unimodal response curves for maximum ebb and flood current velocity with an optimum around 0.25 and 0.275 m.s^{-1} respectively.

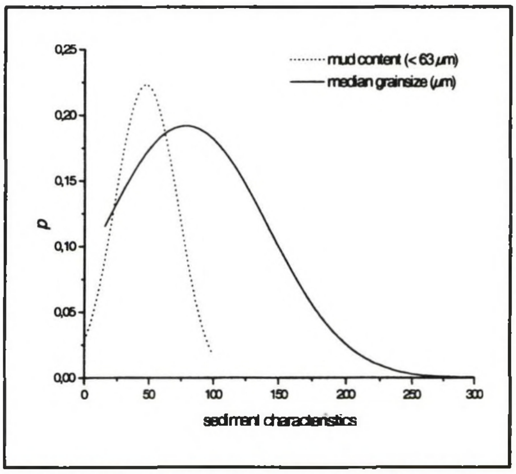
Scrobicularia plana	*Term*	*Regression coefficient*	*Standard error*
present: 237 absent: 2800			
	Intercept	-2,4124	0,3952
	Maxeb	10,3366	2,3785
	Maxeb^2	-20,5947	3,3339
	Concordance	83,30%	
	Intercept	-2,7641	0,3202
	Maxfl	11,3836	1,9979
	Maxfl^2	-21,0065	2,8975
	Concordance	82,70%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Both the linear and quadratic term were included in the median grain size model and the mud content model. *S. plana* clearly prefered very fine sandy, muddy sediments, showing unimodal response curves for median grain size with an optimum at ± 80 μm and for mud content with an optimum at 47 %. Especially in coarser sediments the probability of observing *S. plana* became very small.

Scrobicularia plana	*Term*	*Regression coefficient*	*Standard error*
present: 131 absent: 1371			
	intercept	-2,3574	0,4123
	median	0,0235	0,00792
	median^2	-0,00015	0,000034
	concordance	77,40%	
present: 124 absent: 1262			
	intercept	-3,5404	0,2092
	mud	0,0967	0,0147
	mud^2	-0,00102	0,000202
	concordance	74,10%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, linear and quadratic terms of depth and maximum flood (maxfl) current velocity, the quadratic term of temporal salinity and the linear term of maximum ebb (maxeb) current velocity were included in the model (Table 18.3), with the linear term of maximum ebb current velocity (maxeb), the linear term of temporal salinity and the quadratic term of maximum flood (maxfl) current velocity adding most to the change in deviance. The model with sediment characteristics performed slightly less well, with the linear term of maximum flood current velocity (maxfl), the quadratic term of temporal salinity, and the linear term of median grain size adding most to the change of deviance in the model.

Table 18.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Scrobicularia plana	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment			With sediment		
	presence: 186			Presence: 108		
	absence: 2641			Absence: 1185		
	intercept	-4,5367	0,5469	Intercept	-4,6465	0,8574
	Temporal salinity^2	0,00266	0,000371	Temporal salinity^2	0,00296	0,000561
	Depth	1,6149	0,4132	Maxeb^2	-3,0796	1,3788
	Depth^2	-0,4312	0,1004	Maxfl	28,6043	5,5262
	Maxeb	-2,7782	0,7596	Maxfl^2	-45,3814	8,6444
	Maxfl	13,5840	3,1460	Median	-0,0112	0,00217
	Maxfl^2	-21,0666	4,3857			
	concordance	91,9%		Concordance	89,4%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 92,6 % of the responses correctly (Table 18.4). The model performed only 44,1 % of the modelled (or predicted) presences which were also actually observed in the field. When including sediment characteristics in the model, this percentage was 51,9 %, indicating a slightly better performance including sediment characteristics into the model.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 18.4. Comparative statistics on the predicted and observed occurrence of S. plana in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model). Fisher exact one-tailed test (observed by model: Po<Ao).

Scrobicularia plana (p=0,283)
(without sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	82	104	**186**	44,1
Ao	104	2537	**2641**	96,1
Total	**186**	**2641**	**2827**	92,6

Difference between proportions	0,401	
95% CI	-1,000 to 0,462	(normal approximation)
Fisher exact test: 1-tailed p (observed by model: Po<Ao)	-<0.0001	(exact)

Scrobicularia plana (p=0,231)
(with sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	56	52	**108**	51,9
Ao	52	1133	**1185**	95,6
Total	**108**	**1185**	**1293**	92,0

Difference between proportions	0,475	
95% CI	-1,000 to 0,554	(normal approximation)
Fisher exact test: 1-tailed p (observed by model: Po<Ao)	<0.0001	(exact)

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ECOPROFILE OF SPIO SPP.

INTRODUCTION

The distinction between the different species of the genus *Spio* is very difficult. Most species were determined as *Spio filicornis* and *Spio martinensis* but several individuals were not determined at species level. Therefore, all individuals belonging to the genus *Spio* were lumped to *Spio spp.*

Spio spp. was present in the polyhaline zone (salinity region 1 and 2) and the α-mesohaline zone (salinity region 3), but was completely absent in the β-mesohaline zone (salinity region 4) of the Schelde estuary. *Spio spp.* was observed both in the littoral zone as in all depth strata of the subtidal zone, with the subtidal zone becoming relatively more important in salinity region 3. Mean biomass and density were very low and did not show clear patterns.

AUTO-ECOLOGY

SPIO SPP.	Annelida, Polychaeta

General

The distinction between the different species of the genus *Spio* is very difficult. Most species were determined as *Spio filicornis* and *Spio martinensis* but several individuals were not always determined at species level. Therefore, all individuals belonging to the genus *Spio* were lumped to *Spio spp.*

Spio is a very opportunistic species. The worms build tubes, protruding above the surface of the sediment.

Habitat preferences

Salinity: *S. martinensis* is abundant in the offshore parts of the North Sea and it penetrates far into the estuaries (WOLFF, 1973). The limit of its occurrence is formed by the isohaline of 10 g Cl^-/l at high tide during average river discharge (WOLFF, 1973). However, WOLFF (1973) mentions this species being nearly absent in the Westerschelde.

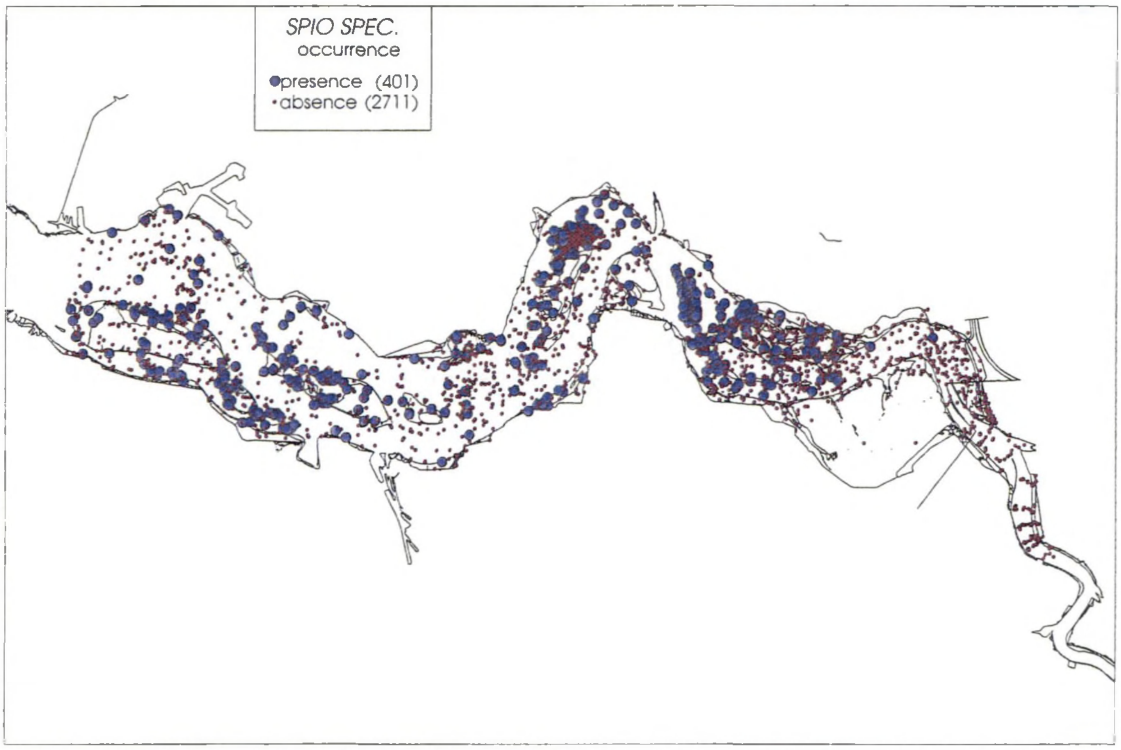
Sediment type: *Spio spp.* Prefers medium to fine sandy, well sorted sediments (WOLFF, 1973). The species is well adapted to unstable sediments. For *S. setosa*, an American species, a preference for medium to coarse sand, often mixed with shell, large cobbles, and small boulders was observed (DAUER *et al.*, 1981).

Feeding

S. martinensis is a suspension-feeder as well as a selective deposit-feeder (WOLFF, 1973). *S. setosa*, an American species, fed on both suspended (including resuspended) and deposited particles and increased their feeding rate in the presence of a current transporting suspended particles (DAUER *et al.*, 1981). Most of the polychaetous annelids of the family Spionidae feed at the sediment-water interface with a single pair of tentaculate palps. They are mostly classified as both deposit- and suspension-feeders (e.g. FAUCHALD & JUMARS, 1979, TAGHON *et al.*, 1980).

Population dynamics and life history

As an opportunistic species, *Spio spp.* reproduces already after 2 to 8 months, has a short life span of ± 1 year, and a high productivity (2-4x per year with ± 2000 eggs per female per laying period) (GUDMUNDSSON, 1985).



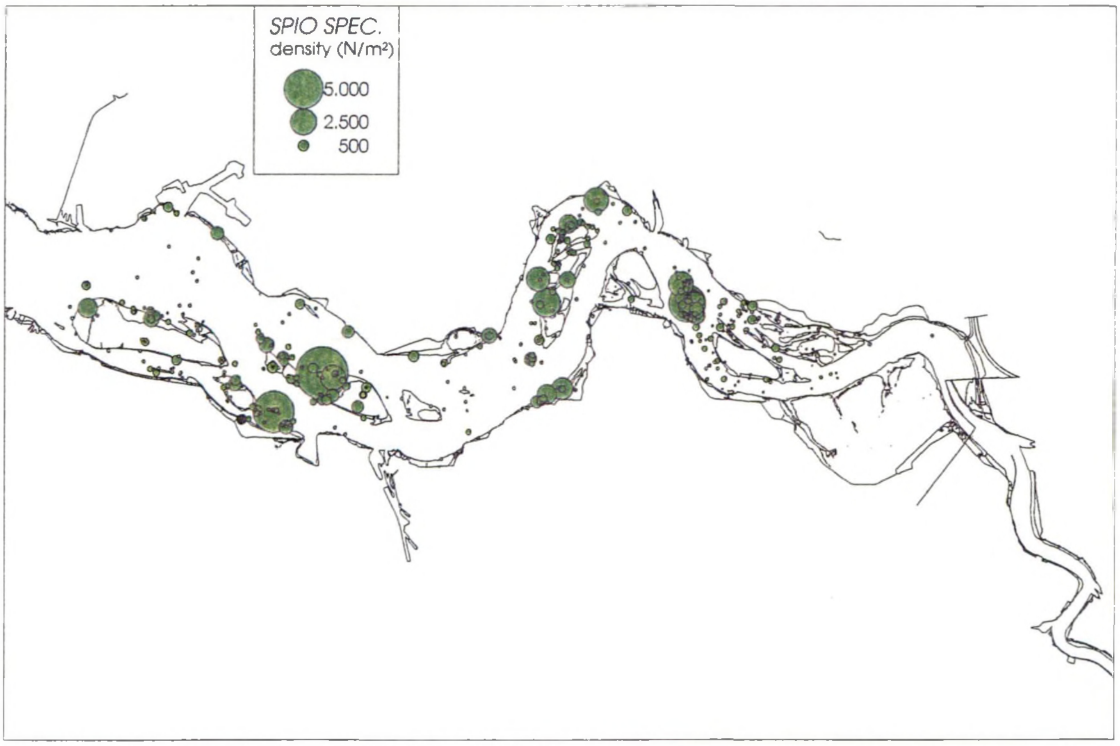


Figure 19.2. Geographical distribution maps of Spio spp. in the Schelde estuary with presence/absence data (top) and density (ind m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

Spio spp. was present in the polyhaline zone (salinity region 1 and 2) and the α-mesohaline zone (salinity region 3), but was completely absent in the β-mesohaline zone (salinity region 4) (Table 19.1). *Spio spp.* was observed both in the littoral zone as in all depth strata of the subtidal zone, with the subtidal zone becoming relatively more important in salinity region 3.

Mean biomass and density were very low and did not show clear patterns (Figure 19.1). In salinity region 1 the undeep subtidal had the highest biomass and density, whereas in salinity region 2 and 3 the deep subtidal and the channel had relatively the highest density and biomass. The geographical distribution of *Spio spp.* in the Schelde estuary is shown in Figure 19.2.

Table 19.1. Occurrence (p/a) of Spio spp. along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
littoral	20,2 % (n=262)	8,5 % (n= 503)	3,5 % (n=485)	0 % (n= 287)
undeep subtidal	33,1 % 'n=151)	16,3 % (n=153)	15,0 % (n=127)	0 % (n=51)
deep subtidal	26,0 % (n=123)	20,0 % (n=130)	17,0 % (n=112)	0 % (n=67)
channel	12,9 % (n=186)	11,6 % (n=173)	31,5 % (n=232)	0 % (n=70)

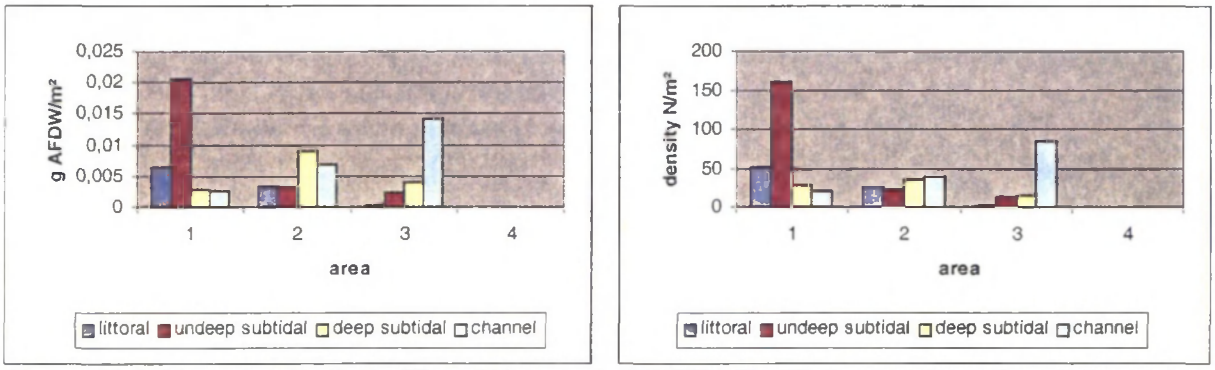


Figure 19.1. Mean density (ind m⁻²) and biomass (g AFDW m⁻²) of Spio spp. along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

A large difference was observed between spring and autumn occurrence, with the species being nearly absent in spring, especially in salinity region 3 (Table 19.2). This was clearly reflected in the mean density and biomass.

Table 19.2. Spring (March - May) versus autumn (Augustus - October) occurrence (presence/absence), density (ind m⁻²) and biomass (g AFDW m⁻²) of Spio spp. in the subtidal zone of the Schelde estuary (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

SUBTIDAL		1	2	3	4
Presence	Spring	9,6 % (n=187)	4,4 % (n= 203)	0,7 % (n=140)	0 % (n= 33)
	Autumn	32,5 % (n=268)	25,5 % (n=243)	33,2 % (n=331)	0 % (n= 155)
Density	Spring	10	5	0,5	0
	Autumn	110	57	69	0
Biomass	Spring	0,002	0,0034	0,00007	0
	Autumn	0,013	0,0088	0,012	0

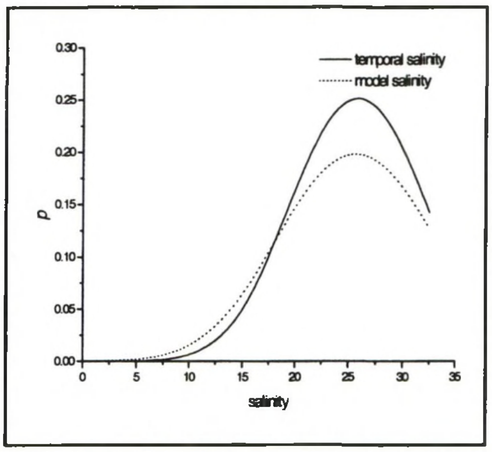
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed.

Model salinity and temporal salinity

Both the linear and quadratic term were included in both salinity models, giving unimodal similar response curves for both models. Both models showed an optimum in the polyhaline zone at a salinity of 26 psu. Downwards a salinity of 20 psu, a steep decline in the probability of occurrence was observed.

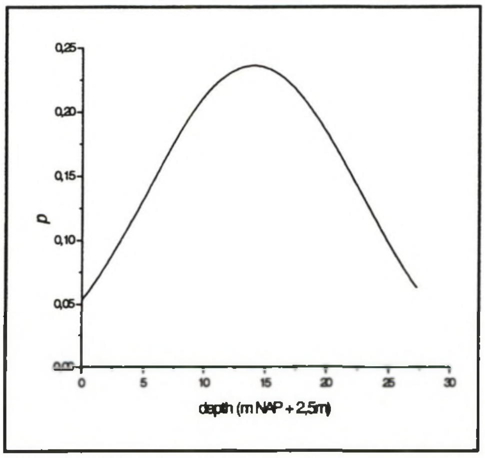
Spio spp.	*Term*	*Regression coefficient*	*Standard error*
present: 401 absent: 2711			
	Intercept	-11,6328	1,0660
	Temporal salinity	0,8162	0,0958
	Temporal salinity²	-0,0158	0,00211
	Concordance	72,10%	
	Intercept	-8,8219	0,9056
	Model salinity	0,5793	0,0826
	Model salinity²	-0,0113	0,00183
	concordance	61,80%	



Depth

Both the linear and quadratic term were included in the depth model, resulting in a unimodal response curve for *Spio spp.* An optimum was observed at 11.5 m NAP (14 m NAP on the figure). However, *Spio spp.* showed a relatively broad tolerance for depth, as was already indicated by Table 19.1.

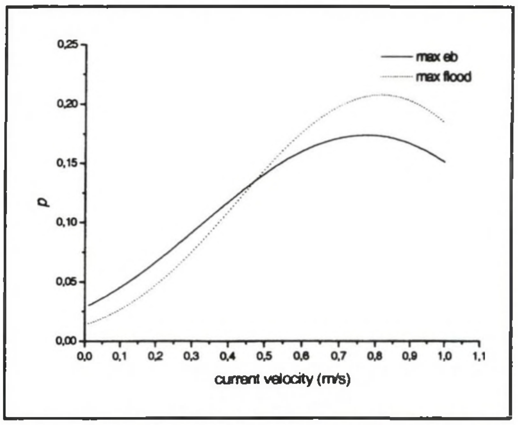
Spio spp.	*Term*	*Regression coefficient*	*Standard error*
present: 390 absent: 2484			
	intercept	-2,8752	0,1369
	depth	0,2436	0,0295
	depth²	-0,00872	0,00131
	concordance	64,20%	



Maximum ebb and flood current velocities (m.s^{-1})

Both the linear and quadratic terms were included in the maximum flood and ebb current velocity models. The response curves were similar for both models, showing a sigmoidal response with an increase in probability of occurrence with increasing current velocity. Only at the highest current velocities there was a small drop in probability of occurrence of *Spio spp.* Of all common spionid species in the Schelde estuary, *Spio spp.* clearly preferred the highest current velocities.

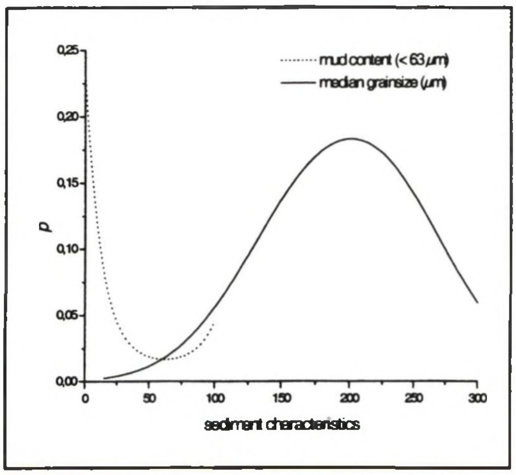
Spio spp.	*Term*	*Regression coefficient*	*Standard error*
Present: 399 absent: 2638			
	Intercept	-3,5240	0,2894
	Maxeb	5,0769	0,8758
	Maxeb^2	-3,2829	0,6114
	Concordance	58,70%	
	Intercept	-4,2677	0,2748
	Maxfl	7,1850	0,7985
	Maxfl^2	-4,4092	0,5388
	Concordance	63,80%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Both the linear and quadratic term were included in the median grain size model and the mud content model. *Spio spp.* clearly prefered more coarse sediments, showing a unimodal response curves for median grain size with an optimum at ± 200 μm. For mud content the probability of occurrence decreased gradually with increasing mud content.

Spio spp.	*Term*	*Regression coefficient*	*Standard error*
present: 170 absent: 1332			
	intercept	-6,7564	0,7407
	median	0,0523	0,00798
	median^2	-0,00013	0,000021
	concordance	70,10%	
present: 169 absent: 1217			
	intercept	-1,1985	0,1183
	mud	-0,0925	0,0187
	mud^2	0,00074	0,000296
	concordance	69,70%	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, only the linear and quadratic terms of both temporal and model salinity were included in the model (Table 19.3), with the linear term of temporal salinity and the quadratic term of model salinity adding most to the change in deviance. The model with sediment characteristics performed much better (concordance 91%), with the linear term of temporal salinity, the quadratic term of model salinity and the linear term of maximum flood current velocity (maxfl) adding most to the change of deviance in the model.

Table 19.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Spio spp.	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment presence: 388 absence: 2439			with sediment Presence: 169 Absence: 1124		
	intercept	-12,8212	1,2161	Intercept	-17,1183	2,8417
	Temporal salinity	0,6477	0,1445	Temporal salinity	1,1932	0,2422
	Temporal salinity^2	-0,00738	0,00317	Temporal salinity^2	-0,0151	0,00535
	Model salinity	0,3082	0,1246	Model salinity^2	-0,00635	0,00114
	Model salinity^2	-0,0115	0,00281	Maxfl	6,0268	1,4107
				Maxfl^2	-2,7218	0,8959
				Median^2	-0,00003	6,254E-6
				Mud	-0,1292	0,0274
				Mud^2	0,00146	0,000423
	concordance	79,5%		concordance	91,0%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 83,2 % of the responses correctly (Table 19.4). However, only 38,2% of the modelled (or predicted) presences were also actually observed in the field. When including sediment characteristics in the model, this percentage increased to 60,9%, indicating a better performance of the model including sediment characteristics.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 19.4. Comparative statistics on the predicted and observed occurrence of Spio spp. in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model). Fisher exact one-tailed test (observed by model: Po<Ao).

Spio spp. (p=0,281)
(without sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	151	237	**388**	38,9
Ao	237	2202	**2439**	90,3
Total	**388**	**2439**	**2827**	83,2

Difference between proportions	0,292	
95% CI	-1,000 to 0,334	(normal approximation)
Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)	

Spio spp. (p=0,411)
(with sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	103	66	**169**	60,9
Ao	66	1058	**1124**	94,1
Total	**169**	**1124**	**1293**	89,8

Difference between proportions	0,551	
95% CI	-1,000 to 0,614	(normal approximation)
Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)	

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ECOPROFILE OF THARYX MARIONI

INTRODUCTION

Tharyx marioni was a relatively common spionid species in the Schelde estuary, showing a decrease in occurrence with decreasing salinity and increasing depth. *T. marioni* was only regularly observed in the littoral, polyhaline zone. However, the species was not completely absent in the subtidal zone, being situated between the other spionids *P. elegans* (a more littoral species) *and Spio spec.* (a more subtidal species). In the mesohaline zone *T. marioni* was nearly completely absent. Mean biomass and density were by far highest in the littoral zone of salinity region 1.

AUTO-ECOLOGY

THARYX MARIONI (SAINT-JOSEPH, 1894)	Annelida, Polychaeta

General

Tharyx marioni is a small, euryhaline polychaete which can be observed from the eulittoral zone to a depth of 5000 m (HARTMANN-SCHRÖDER, 1971). *T. marioni* lives in the upper 5 cm of the sediment in non permanent burrows and can perform a high intensity of digging.

Habitat preferences

Salinity: *T. marioni* is categorised as an euryhaline species (WOLFF, 1973). In the Westerschelde the species is found at a salinity of 7-8 g Cl^-/l (WOLFF, 1973).

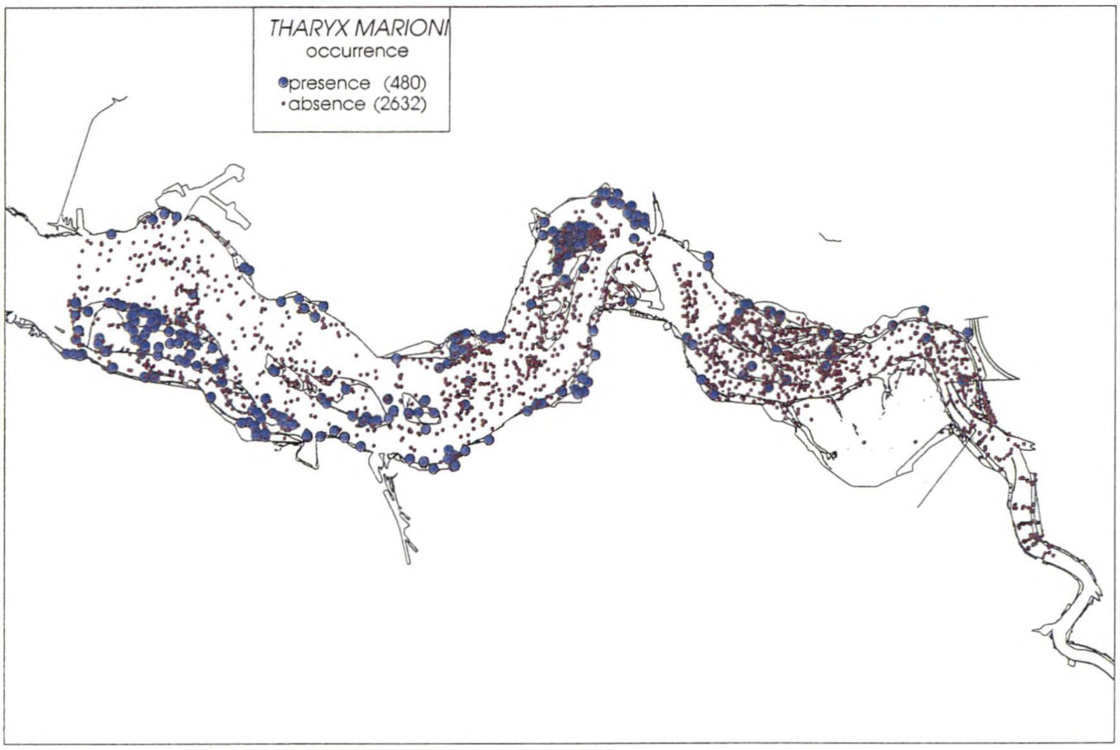
Sediment type and vertical distribution: *T. marioni* prefers less well sorted, muddy sediments (WOLFF, 1973). Also SOUTHWARD (1957) and GIBBS (1969) describes the sediment preference of *T. marioni* as mud and muddy sand. On the other hand, HARTMANN-SCHRÖDER (1971) recorded the species alsof from coarse sands with pebbles and stones. The vertical distribution of T. marioni ranges from the upper part of the intertidal zone down to a depth of 25 m (WOLFF, 1973).

Feeding

T. marioni is a non selective deposit feeder (WOLFF, 1973).

Population dynamics and life history

T. marioni is capable of reproducing several times per year, but the first reproduction takes place at the end of the second year of its life (GIBBS, 1971; FARKE, 1979). DALES (1951a) mentions egg deposition in the sand, after which the hatched larvae immediately burrow themselves and therefore do not know any pelagic life cycle (GIBBS, 1971; FARKE, 1979). However, according to HARTMANN-SCHRÖDER (1971) the larvae are indeed pelagic.



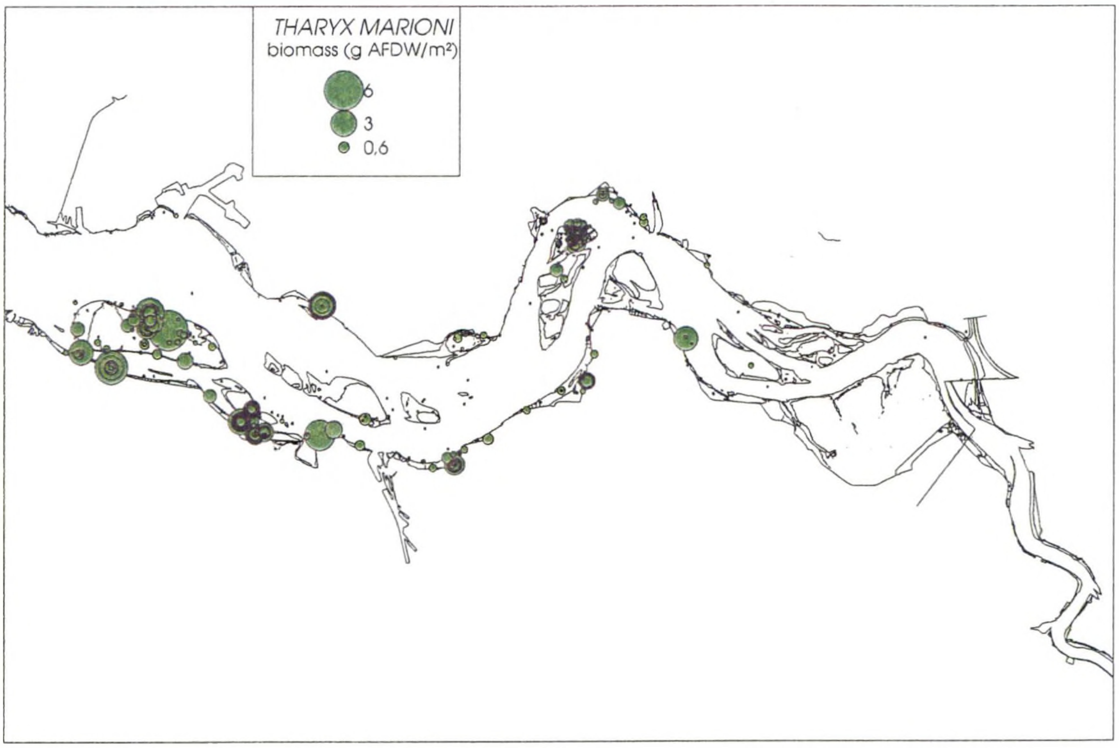


Figure 20.2. Geographical distribution maps of Tharyx marioni in the Schelde estuary with presence/absence data (top) and biomass (g AFDW m^{-2}) data (bottom).

OCCURRENCE IN THE SCHELDE ESTUARY

General occurrence in relation to salinity and depth

Tharyx marioni showed a typical decrease in occurrence with decreasing salinity and increasing depth (Table 20.1). *T. marioni* was only regularly observed in the littoral, polyhaline zone (salinity region 1-2). However, the species was not completely absent in the subtidal zone, being situated between the other spionids *P. elegans* (a more littoral species) *and Spio spp.* (a more subtidal species). In the mesohaline zone *T. marioni* was nearly completely absent. Mean biomass and density were by far highest in the littoral zone of salinity region 1 (Figure 20.1). The undeep subtidal zone of salinity region 1 and the littoral zone of salinity region 2 had comparable values for both biomass and density. In the other zones biomass and density were very low. The geographical distribution of *T. marioni* in the Schelde estuary is shown in Figure 20.2.

Table 20.1. Occurrence (p/a) of T. marioni along the salinity and depth gradients of the Schelde estuary. N = number of observations (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

	1	2	3	4
littoral	50,8 % (n=262)	42,0 % (n= 503)	5,0 % (n=485)	0,4 % (n= 287)
undeep subtidal	21,2 % 'n=151)	9,8 % (n=153)	4,7 % (n=127)	1,9 % (n=51)
deep subtidal	13,0 % (n=123)	6,9 % (n=130)	0,9 % (n=112)	0,0 % (n=67)
channel	5,4 % (n=186)	9,8 % (n=173)	1,7 % (n=232)	0,0 % (n=70)

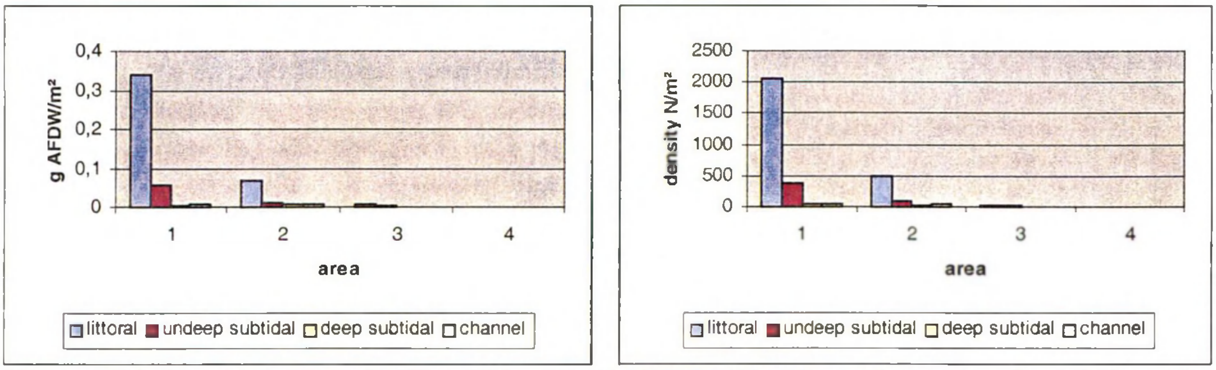


Figure 20.1. Mean density (ind m^{-2}) and biomass (g AFDW m^{-2}) of T. marioni along the salinity and depth gradient in the Schelde estuary (areas: 1&2: polyhaline; 3&4: mesohaline).

Seasonal variations: spring versus autumn occurrence

T. marioni was equally present in spring and autumn in all salinity regions (Table 20.2). In salinity region 1 mean density doubled in autumn, whereas in salinity region 2 only a slight increase was noticed. Biomass values were comparable.

Table 20.2. Spring (March - May) versus autumn (Augustus - October) occurrence (p/a), density (ind m^{-2}) and biomass (g AFDW m^{-2}) of T. marioni in the littoral zone of the Schelde estuary (salinity regions: 1&2: polyhaline; 3&4: mesohaline).

LITTORAL		1	2	3	4
Presence	Spring	46,4 % (n=97)	40,8 % (n= 169)	5,4 % (n=147)	3,0 % (n= 33)
	Autumn	51,1 % (n=135)	42,2 % (n=218)	5,2 % (n=249)	0,0 % (n= 214)
Density	Spring	1271	454	46	2
	Autumn	2414	569	7	0
Biomass	Spring	0,2664	0,0775	0,0230	0,000025
	Autumn	0,3095	0,0669	0,0014	0

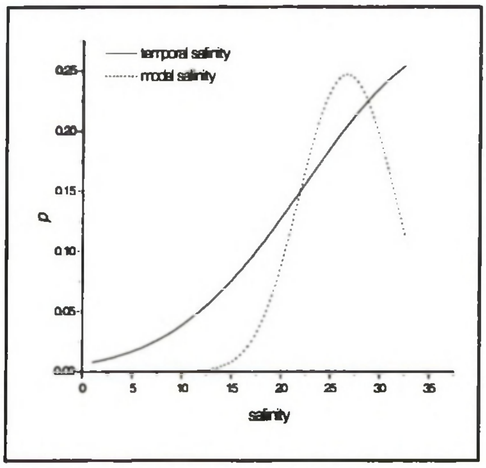
RESPONSE CURVES FOR A SINGLE ABIOTIC (EXPLANATORY) VARIABLE

A logistic regression model for binary (presence/absence) data was performed. Only at densities > 50 ind m^{-2} or sampling occassions with more than one individual found, the species was considered as being present.

Model salinity and temporal salinity

Both the linear and quadratic term were included in both salinity models. However, two different response curves were obtained. The response curve for temporal salinity showed a sigmoidal increase in probability of occurrence with increasing salinity, whereas for model salinity a unimodal curve was observed, with an optimum at 26,5 psu.

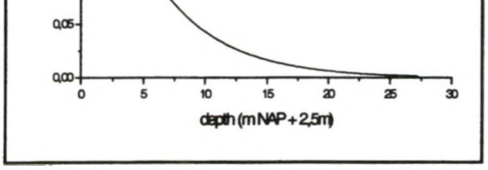
Tharyx marioni	*Term*	*Regression coefficient*	*Standard error*
present: 377 absent: 2735			
	Intercept	-5,0642	0,5397
	Temporal salinity	0,2131	0,0542
	Temporal salinity^2	-0,00278	0,00131
	Concordance	68,4	
	Intercept	-20,4502	2,0632
	Model salinity	1,4531	0,1688
	Model salinity^2	-0,0273	0,00341
	Concordance	70,10%	



Depth

Only the linear term of depth was included in the model, giving a linear logit curve for depth. The relatively shallow slope of the curve indicated also the presence of *T. marioni* in the subtidal zone (see also Table 20.1).

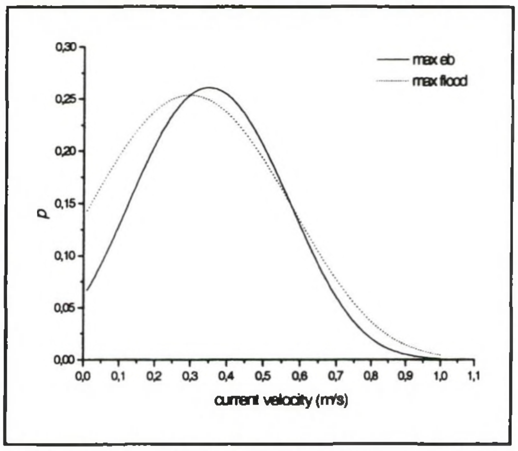
Tharyx marioni	*Term*	*Regression coefficient*	*Standard error*
present: 320 absent: 2554			
	Intercept	-1,1171	0,0895
	Depth	-0,1985	0,0190
	depth^2	-	-
	Concordance	69,20%	



Maximum ebb and flood current velocities (m.s^{-1})

Both the linear and quadratic terms were included in the maximum ebb and flood current velocity models. This resulted in unimodal response curves for maximum ebb and flood current velocity with an optimum around 0.35 and 0.30 m.s^{-1} respectively.

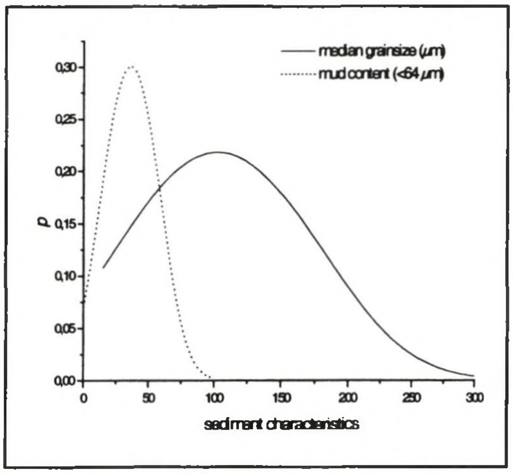
Tharyx marioni	*Term*	*Regression coefficient*	*Standard error*
present: 360 absent: 2677			
	Intercept	-2,7354	0,3166
	Maxeb	9,7184	1,5009
	Maxeb²	-13,9420	1,6792
	Concordance	78,50%	
	Intercept	-1,8410	0,2164
	Maxfl	5,1387	1,0834
	Maxfl²	-8,6742	1,1839
	Concordance	77,30%	



Sediment characteristics: median grainsize (μm) and mud content (%)

Both the linear and quadratic term were included in the median grain size model and the mud content model. *T. marioni* clearly prefered very fine sandy sediments, showing unimodal response curves for median grain size with an optimum at ± 100 μm and for mud content with an optimum of 35%. However, *T. marioni* showed a relatively broad tolerance and only in very coarse sediments or sediments with a very high mud content the probability of observing this species was very small.

Tharyx marioni	*Term*	*Regression coefficient*	*Standard error*
present: 208 absent: 1294			
	Intercept	-2,4274	0,3442
	Median	0,0225	0,00546
	median²	-0,00011	0,00002
	Concordance	68,90%	
present: 199 absent: 1187			
	Intercept	-2,5818	0,1467
	Mud	0,0961	0,0129
	mud²	-0,00133	0,000202
	Concordance	69,80 %	



MULTIPLE STEPWISE LOGISTIC REGRESSION

Binary logistic regression model

A multiple stepwise logistic regression was run with all abiotic variables together. Since sediment characteristics were only available for a limited set of data, the analysis was run seperately with and without sediment data.

In the regression model without sediment characteristics, the linear and quadratic terms of model salinity and of maximum ebb (maxeb) current velocity, and the linear term of maximum flood (maxfl) current velocity were included in the model (Table 20.3), with the linear term of maximum flood current velocity and the linear term of model salinity adding most to the change in deviance. The model with sediment characteristics performed slightly better, and now the linear term of model salinity, of maximum ebb current velocity (maxeb) and of median grain size added most to the change of deviance in the model.

Table 20.3. Results for the binary multiple logistic regression model, without and with sediment characteristics included, respectively.

Tharyx marioni	*Term*	*Regression coefficient*	*Standard error*	*Term*	*Regression coefficient*	*Standard error*
	without sediment presence: 311 absence: 2516			with sediment Presence: 175 Absence: 1118		
	Intercept	-19,0210	2,5408	Intercept	-25,8280	4,3270
	Model salinity	1,3346	0,2147	Temporal salinity	-0,0561	0,0258
	Model salinity^2	-0,0238	0,00439	Model salinity	2,2086	0,3668
	Maxeb	7,4817	1,9223	Model salinity^2	-0,0395	0,00768
	Maxeb^2	-9,9597	1,9936	Maxfl	-3,0273	0,5573
	Maxfl	-3,0372	0,3964	Median	-0,0157	0,00190
	Concordance	90,2%		concordance	93,1%	

Percent correct predictions

The logistic regression model, without sediment characteristics, included, predicts overall 89,5 % of the responses correctly (Table 20.4). The model performed well with 52,1% of the modelled (or predicted) presences which were also actually observed in the field. When including sediment characteristics in the model, this percentage increased to 68%, indicating a better performance of the model including sediment characteristics.

The Fisher exact test was for both models highly significant, indicating that the model and the observations performed better than by random chance. In other words, the proportion of actually observed presences in the class where the model also predicted presences was significantly higher than by random chance (one-tailed test).

Table 20.4. Comparative statistics on the predicted and observed occurrence of T. marioni in the Schelde estuary based on the regression models without and with sediment characteristics included, respectively. (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model). Fisher exact one-tailed test (observed by model: Po<Ao).

Tharyx marioni (p=0,397)
(without sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	162	149	**311**	52,1
Ao	149	2367	**2516**	94,1
Total	**311**	**2516**	**2827**	89,5

Difference between proportions	0,462	
95% CI	-1,000 to 0,509	(normal approximation)
Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)	

Tharyx marioni (p=0,378)
(with sediment characteristics)

Response	**Model**			**%**
Observed	Pm	Am	**Total**	**correct**
Po	119	56	**175**	68
Ao	56	1062	**1118**	95
Total	**175**	**1118**	**1293**	91,3

Difference between proportions	0,630	
95% CI	-1,000 to 0,689	(normal approximation)
Fisher exact test: 1-tailed p **(observed by model: Po<Ao)**	<0.0001 (exact)	

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PART THREE

External validation of the 'response curve' regression models from the Schelde estuary in another coastal area, the Oosterschelde

External validation of the 'response curve' regression models from the Schelde estuary in another coastal area, the Oosterschelde

INTRODUCTION

In order to examine the suitability or the predictive power of the obtained 'response curve' models in other estuarine or coastal areas, a preliminary validation was performed on macrobenthos data of the Oosterschelde. As the Oosterschelde is a quite different ecosystem, being more a 'coastal basin' then a 'true estuary', this comparison can indicate to what extent the response models obtained in the Schelde estuary are applicable in other systems.

MATERIAL & METHODS

The abiotic environment of the Oosterschelde

A large scale coastal engineering project has been carried out in the southwest of the Netherlands to protect the Delta area of the Rhine and Meuse from flooding. It has resulted in several former estuaries being closed off from the North Sea and the Oosterschelde being partially closed by a storm-surge barrier. These engineering works were completed in 1987. The construction of the storm-surge barrier and the compartment dams on the northern and eastern boundaries of the estuary changed some of the abiotic characteristics. As a result, the Oosterschelde can not be considered anymore as a 'true' estuary, but rather a coastal basin, characterised by a stable high salinity (very low freshwater load) in the whole area and small nutrient loads with very low concentrations of suspended matter. Sediments in the Oosterschelde are overall relatively sandy with a low silt content.

Therefore, it can be concluded that the Oosterschelde 'coastal basin' ecosystem is quite different from that of the Schelde 'estuarine' ecosystem.

Macrobenthos data on the the Oosterschelde

Data on macrozoobenthos were available from two different datasets. A first dataset, the Interecos campaign of 1989, contained 300 sampling locations, sampled on three different intertidal flats of the Oosterschelde in August 1989 (MEIRE *et al.*, 1994). The 305 sampling locations were distributed over different, predefined strata according to a stratified random sampling strategy (VAN DER MEER *et al.*, 1989).

A second macrobenthos database was obtained from the BIOMON project, which is the Dutch national monitoring programme of the Delta area, which started in spring 1990. In this monitoring programme, the different salt water systems of the Delta area (Westerschelde, Oosterschelde, Veerse Meer, and Grevelingen) are being surveyed twice a year, in spring (March-April-May) and autumn (August-September-October). In the Oosterschelde, three different areas were chosen, one near the storm surge barrier (mouth) of the estuary, one in the northern branch of the estuary and one in the southern branch of the estuary (CRAEYMEERSCH, 1999). In each subarea, four depth strata were defined (see Material & Methods for the Westerschelde data), in which randomly 10 sampling locations were selected in autumn 1994. These stations were revisited at each sampling campaign. This gave 120 sampling locations at each survey. Data used in this study deal with the period autumn 1994 – autumn 1997, thus comprising seven surveys, with a total of 840 sampling occassions.

In total 1140 sampling occassions were used for the purpose of the validation. In general, similar sampling strategies and laboratory methodologies were used, as the analyses were performed by the same institutes as for the Schelde estuary.

As for the Schelde estuary, salinity and current velocity (both maximum ebb and maximum flood current velocities) estimates were obtained from model calculations. Because the Oosterschelde was characterised by a very stable salinity, with no clear seasonal differences, 'temporal salinity' was set equal to 'model salinity'. At all subtidal stations, depth was recorded at the time of sampling. The height of the intertidal stations was for some stations measured directly in the field, but for far the most the height was obtained from a Geographical Information System (GIS), storing all bathymetric data in the area.

Data on sediment characteristics were only available for the Interecos campaign (n= 300) and one Biomon campaign (spring 1996, n=106).

Statistical analysis

The regression model obtained for each macrobenthic species from the Schelde estuary data was used to calculate predictions for the Oosterschelde sampling occasions. As only a very limited dataset on sediments were available, only the regression models without sediment characteristics were used.

Predictions of species responses on these sampling occassions were compared to the really observed presence/absence data analogous to the procedure followed for the Schelde estuary. Also these pairs of values were sorted on the basis of predicted responses and divided into four classes with increasing p-value ($p < 0.25$; $0.25<p<0.50$; $0.50<p<0.75$; >0.75).

RESULTS

Abiotic characterisation of the Oosterschelde sampling occassions

The Oosterschelde was characterised by a very high salinity in the whole area, resulting in a mean salinity of 29.98 (Table 1). Only in the most upper regions of the two branches of the estuary a somewhat lower salinity was observed, but the whole Oosterschelde was situated in the polyhaline zone, and therefore resembles the salinity region 1 of the Schelde estuary. As the river runoff to the Oosterschelde is neglictable, only slight seasonal differences in salinity were observed, resulting in an almost stable salinity throughout the year. Therefore, no 'temporal salinity' was estimated for the Oosterschelde, as it was for the Schelde estuary.

Mean maximum ebb and flood current velocities were lower as compared to the Schelde estuary, with higher mean values under flood conditions. Current velocities were lower in the intertidal zone as compared to the subtidal zone, with 0.16/0.26 (ebb/flood) and 0.28/0.43 (ebb/flood) respectively. Based on the median grain size, the Oosterschelde sediments were in general fine sand sediments, but with a very low mud content, especially in comparison to mud contents observed in the Schelde estuary.

Table 1. Mean, minimum and maximum of some abiotic variables in the Oosterschelde (current velocities in m.s^{-1}, median grain size in µm, and mud content in volume %).

Parameter	*N*	*Mean*	*Min.*	*Max.*
Salinity	n = 1140	29.98	27	32
Maximum ebb current velocity	n = 1011	0.233	0.02	0.8
Maximum flood current velocity	n = 1085	0.356	0.02	0.9
Median grain size	n = 406	159.6	91.9	559
Mud content	n = 406	3.5	0	48.6

Characterisation of the Oosterschelde macrobenthos

The Oosterschelde macrobenthos was different from that of the Schelde estuary, in the first place because no salinity gradient was present in the Schelde estuary, resulting in a typical polyhaline macrobenthic community. Therefore, species composition was most similar with that of salinity region 1 (polyhaline zone) of the Schelde estuary.

In the intertidal zone of the Oosterschelde most common species observed were *Scoloplos armiger* and *Arenicola marina* (Table 2). Despite the low mud content, *Oligochaeta* were very common. Spionids like *Pygospio elegans*, *Spio spp.* and *Tharyx marioni* were also very common. Most frequently observed molluscs were the bivalves *Cerastoderma edule* and *Macoma balthica* and the gastropod *Hydrobia ulvae*. In terms of density, the intertidal macrobenthic community was dominated by Oligochaeta, *Hydrobia ulvae*, *Pygospio elegans*, *Tharyx marioni* and *Scoloplos armiger*. In terms of biomass, *Cerastoderme edule* was by far the most important species. Besides this species, *Arenicola marina*, *Macoma balthica*, *Hydrobia ulvae*, *Nereis spp./diversicolor*, and *Scoloplos armiger* were the most important species. Some clear differences were observed between the Interecos intertidal campaign of 1989 and the intertidal Biomon data of the period 1994-1997. Several species showed a clear decrease in presence, density and biomass (e.g. *Scoloplos armiger*, *Macoma balthica*, *Cerastoderma edule*, *Heteromastus filiformis*). The occurrence of the dominant spionids *Pygospio elegans* and *Tharyx marioni* did not change, whereas the less dominant spionids *Spio spp.* and *Spiophanes bombyx* did decrease between the two periods. Only a few species increased between both periods, with the most pronounced being *H. ulvae*.

The intertidal macrobenthic community of the Oosterschelde showed a similar dominance in biomass of *Cerastoderma edule* as the polyhaline zone of the Schelde estuary (salinity region 1) and a similar dominance in density of several spionid species (*Pygospio elegans, Tharyx marioni*) and Oligochaeta, but mean densities of these species were much lower in the Oosterschelde. *Heteromastus filiformis* was much less dominant in the Oosterschelde, whereas *Arenicola marina* and *Scoloplos armiger* showed the opposite, being a very important part of the macrobenthic community in the Oosterschelde. Probably these patterns reflected the more sandy habitats in the Oosterschelde as compared to the more muddy sediments of the Schelde estuary.

In the subtidal zone of the Oosterschelde most common species were *Scoloplos armiger*, *Nephtys hombergii* and *Spiophanes bombyx* (Table 2). In terms of density, dominant species were Oligochaeta, *Lanice conchilega*, *Tharyx marioni* and *Scoloplos armiger*. Because of the sampling in some musselbeds, *Mytilus edulis* was the dominant species in terms of biomass. Besides this species, *Lanice conchilega*, *Scoloplos armiger* and *Cerastoderma edule* were the most important species.

Table 2. Occurrence (%), density (ind m^{-2}) and biomass (g AFDW m^{-2}) of the most important macrobenthic species in the Oosterschelde for the Interecos intertidal dataset (autumn 1989), the Biomon intertidal dataset (spring/autumn 1994-1997) and the Biomon subtidal dataset (spring/autumn 1994-1997).

	Interecos intertidal dataset autumn 1989 (n=300)			Biomon intertidal dataset spring/autumn 1994-1997 (n= 210)			Biomon subtidal dataset spring/autumn 1994-1997 (n=630)		
	Occurrence	Density	Biomass	Occurrence	Density	Biomass	Occurrence	Density	Biomass
Anai muco	42.7	60	0.066	20.0	27	0.032	11.3	14	0.013
Aren mari	81.3	27	6.839	58.6	75	2.942	6.3	17	0.115
Bath spp.	23.0	513	0.075	16.7	164	0.039	2.5	2	0.0006
Capi capi	56.7	226	0.033	51.0	141	0.032	32.7	129	0.043
Cera edul	66.8	260	77.117	54.3	154	16.132	3.5	7	0.543
Coro volu	-	-	-	0	0	0	0.2	0.1	0.00002
Coro aren	-	-	-	29.5	174	0.040	0	0	0
Coro spp.	35.7	172	0.037	-	-	-	-	-	-
Eteo spp	37.0	37	0.020	21.9	19	0.013	4.8	4	0.001
Hete fili	43.3	132	0.383	14.3	20	0.033	6.2	9	0.011
Hydr ulva	32.7	1058	0.844	61.4	7685	3.371	7.0	16	0.003
Lani conc	25.7	71	0.548	10.0	24	0.278	26.7	178	2.443
Maco balt	65.0	120	2.224	31.0	32	0.361	2.2	1.5	0.009
Myse bide	5.0	5	0.004	7.1	8	0.003	18.9	57	0.012
Myti edul	5.7	6	7.258	0.5	0.3	0.00001	8.4	78	20.644
Nemertini	4.3	5	0.0080	4.3	4	0.0024	7.5	6	0.0080
Neph cirr	-	-	-	2.4	2	0.006	15.9	19	0.079
Neph homb	-	-	-	33.8	28	0.237	56.2	116	0.470
Neph spp.	56.7	58	0.633	-	-	-	-	-	-
Nere dive	-	-	-	41.9	131	1.294	0.8	0.5	0.005
Nere succ	-	-	-	2.9	2	0.025	3.8	9	0.080
Nere spp.	57.3	236	0.828	-	-	-	-	-	-
Oligochaeta	69.7	2791	0.223	65.2	1038	0.096	37.1	227	0.011
Poly spp.	19.3	36	0.014	14.8	21	0.005	12.5	107	0.019
Pygo eleg	64.7	725	0.093	66.2	1009	0.067	10.2	29	0.002
Scol armi	87.3	1357	0.886	53.8	248	0.358	58.3	140	0.429
Scro plan	12.4	12	0.258	13.3	18	0.387	1.0	0.2	0.00003
Spio bomb	16.7	31	0.021	1.9	1.3	0.0009	39.0	73	0.070
Spio spp.	57.3	662	0.089	28.6	62	0.005	28.9	69	0.008
Thar mari	47.0	818	0.151	49.0	832	0.117	29.7	174	0.018
Urot spp.	17.3	44	0.013	34.8	222	0.074	13.5	62	0.020

Validation of the model

Figure 1 and Table 3 summarizes the comparative statistics on the predicted (based on Schelde estuary models) and actual observed occurrence of ten macrobenthic species in the Oosterschelde.

Figure 1 gives an idea on the p-values obtained for each species at each sampling location. The higher p-classes in general had also relatively the highest proportion of actually observed presences, which was very well demonstrated by *Macoma balthica* and *Pygospio elegans*. This indicated a good performance of the models.

The overall prediction, including both the prediction of the presences and absences, performed for most species very well (Table 3) and also for the % predicted observed versus actually observed in the field, only slightly lower estimates were obtained as for the internal validation. For *Arenicola marina* even a better ratio was obtained in the Oosterschelde. For some species, like e.g. *Heteromastus filiformis*, a rather low ratio was obtained in comparison to the internal validation.

Despite the fact that the Oosterschelde could be considered as a different system, being more a ‘coastal basin’ then a ‘true estuary’, the regression models from the Schelde estuary seemed to be applicable in the Oosterschelde.

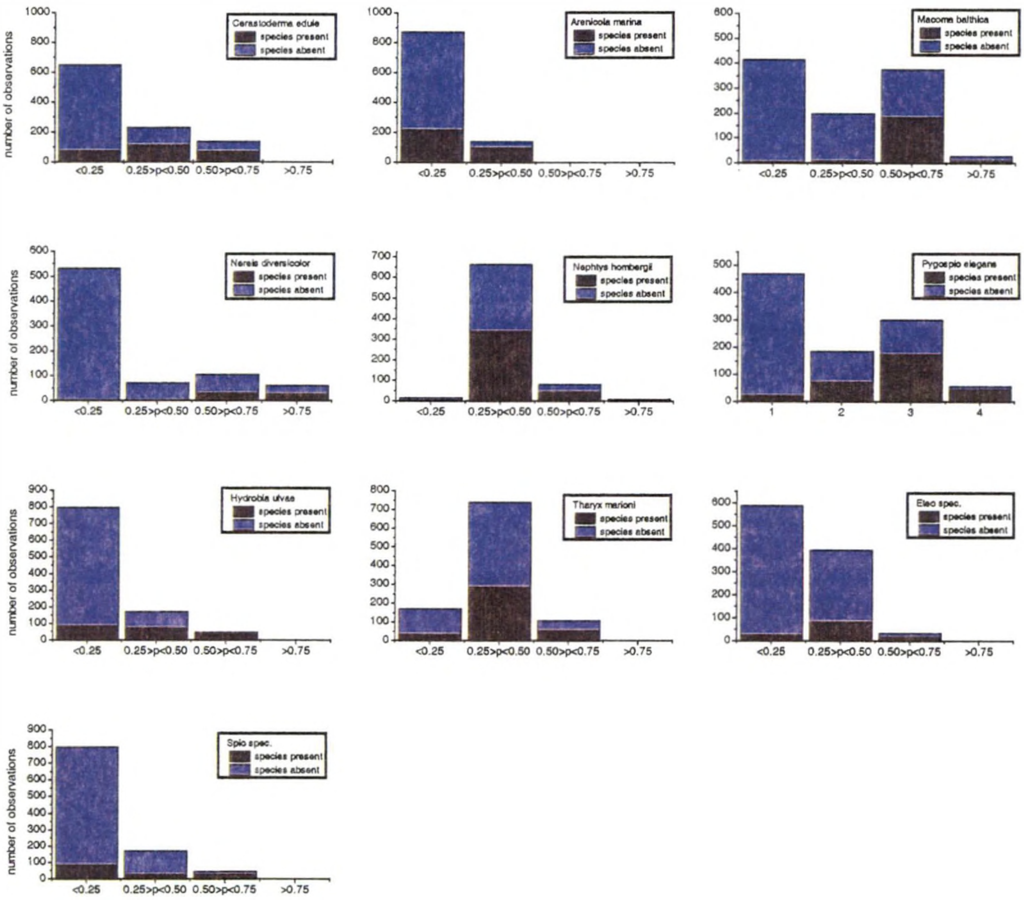

Figure 1. P-values (predicted probability of occurrence), divided into four classes (p<0.25, 0.25<p<0.50, 0.50<p<0.72, p>0.75), for ten macrobenthic species in the Oosterschelde, based on the regression models obtained from the Schelde estuary. In each class the observed presence/absence in the field is indicated.

Table 3. Comparative statistics on the predicted and observed occurrence of ten macrobenthic species in the Oosterschelde based on the regression models (without sediment characteristics) obtained from the Westerschelde data (Po = Present observed; Ao = Absent observed; Pm = Present predicted by the model; Am = Absent predicted by the model).

Cerastoderma edule (p=0,336)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	*153*	115	268	57,1
Ao	115	*630*	745	84,6
Total	268	745	1013	77,3

Macoma balthica (p=0,656)

Response	Model			%
Observed	Pm	Am	Total	**Correct**
Po	*101*	116	217	46,5
Ao	116	*680*	796	85,4
Total	217	796	1013	77,1

Arenicola marina (p=0,172)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	*215*	110	315	68,3
Ao	110	*578*	688	84,0
Total	325	688	1013	78,3

Heteromastus fili.(p=0,474)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	*54*	115	169	32,0
Ao	115	*729*	844	86,4
Total	169	844	1013	72,0

Pygospio elegans (p=0,536)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	*201*	121	322	62,4
Ao	121	*570*	691	82,5
Total	169	922	1013	76,1

Hydrobia ulvae (p=0,256)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	*116*	93	209	55,5
Ao	93	*711*	804	88,4
Total	209	804	1013	81,6

Tharyx marioni (p=0,318)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	*161*	223	384	41,9
Ao	223	*406*	629	64,5
Total	384	629	1013	56,0

Eteone longa (p=0,437)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	*58*	76	134	43,3
Ao	76	*803*	879	91,4
Total	134	879	1013	85,0

Nephtys hombergii (p=0,36)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	*239*	164	403	59,3
Ao	164	*201*	365	55,1
Total	403	365	768	57,3

Nereis diversicolor (p=0,255)

Response	Model			%
Observed	Pm	Am	Total	**correct**
Po	*64*	3	67	95,5
Ao	3	*698*	701	99,6
Total	67	701	768	99,2

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