Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression

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ABSTRACT: This study aims at contributing to the development of statistical models to predict macrobenthic species response to environmental conditions in estuarine ecosystems. Ecological response surfaces are derived for 10 estuarine macrobenthic species. Logistic regression is applied on a large data set, predicting the probability of occurrence of macrobenthic species in the Schelde estuary as a response to the predictor variables salinity, depth, current velocity and sediment characteristics. Single logistic regression provides good descriptions of the occurrence along 1 environmental variable. The response surfaces obtained by multiple logistic regression provide estimates of the probability of species occurrence across the spatial extent of the Schelde estuary with a relatively high degree of success. Results from subsampling 50% of the original data 10 times indicate that final models were stable. A visual geographical comparison is presented between the mapped probability surfaces and the species occurrence maps. We conclude that where patterns of distribution are strongly and directly coupled to physicochemical processes, as is the case at the estuarine macro- and meso-scale, our modelling approach was capable of predicting macrobenthic species distributions with a relatively high degree of success, although processes controlling estuarine macrobenthic distribution cannot be determined using this method. However, the models and predictions could be used for evaluation of the effects of different management schemes within the Schelde estuary.

KEY WORDS: Benthic macrofauna · Estuarine, spatial gradients · Logistic regression · Response surfaces · Schelde estuary

INTRODUCTION

Estuaries are transitional environments between rivers and the sea, and are characterised by widely varying and often unpredictable hydrological, morphological and chemical conditions (Day et al. 1989). For benthic animals with limited mobility (after settlement) this spatial and temporal variability represents a problem with which they have to cope.

A quantitative prediction of the patterns of occurrence of macrobenthic animals in estuaries is a desirable goal for several reasons. Benthic-pelagic links in estuaries are in general very important (Herman et al. 1999). Understanding the dynamics of the estuarine system requires a quantitative insight into benthic processes, which may be responsible for up to half of the mineralisation of the total system (Heip et al. 1995, Herman et al. 1999). Macrobenthos has a pronounced structuring effect on the sediment properties and mineralisation processes (Rhoads 1974, Aller & Aller 1998), and is an important food resource for epibenthic crustaceans, fishes and birds. Humans harvest many species of shellfish and crustaceans. Rational management of these resources requires predictive capabilities of the dynamics of the populations.

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Nowadays, macrobenthos is often used in monitoring programmes as a bioindicator for possible changes in the system. Within this ecological indicator system approach, a lot of studies have investigated the structure of macrobenthic communities in relation to the abiotic environment, coupling the dominance patterns (e.g. ABC method: Warwick 1986) or functional life-history characteristics (trophic structure: Pearson & Rosenberg 1978, Boesch & Rosenberg 1981, Gaston et al. 1998) of the macrobenthos to human impacts. But within coastal marine and estuarine ecosystems few attempts have been made to statistically model the responses of individual macrobenthic species to environmental variables on a large, e.g. estuarine, scale and to 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.

The aim of this study was to contribute to the development of statistical models to predict macrobenthic species response to environmental conditions in estuarine ecosystems. In this paper, so-called response curves and surfaces are fitted through mathematical relations (Swan 1970, Austin 1987) obtained by logistic regression. The advantage of logistic regression is that the probability of occurrence of an event can be predicted as a function of 1 or more independent variables (Hosmer & Lemeshow 1989, Trexler & Travis 1993). Logistic regression has been applied in many ecological studies, e.g. in vegetation analysis (Huisman et al. 1993, Lenihan 1993, van de Rijt et al. 1996) and bird and wildlife species distributions (Osborne & Tigar 1992, Buckland & Elston 1993, Venier et al. 1999). In the field of marine and estuarine animal ecology, this technique has rarely been used.

Our approach uses physicochemical factors, acting at different spatial scales, as predictors for the occurrence of several macrobenthic species. The realised environmental niches of estuarine macrobenthic species are thus defined and validated. This paper presents a first step in predicting the spatial distribution of macrobenthic populations. The next step will be to extend the models towards prediction of patterns in abundance and biomass and to investigate the possibility of using the models for evaluation of the effects of different management schemes and to investigate the applicability of the models in other estuarine systems.

MATERIALS AND METHODS

Study area. The Schelde estuary, a turbid, nutrient-rich, heterotrophic system, measures 160 km from the mouth near Vlissingen (The Netherlands) to Ghent (Belgium), and is one of the longest estuaries in NW Europe with a still complete salinity gradient. The study area is limited to the Westerschelde (Dutch part) and a small part of the Zeeschelde (Belgian part) near the Dutch-Belgian border (Fig. 1), comprising the complete polyhaline and mesohaline zone of the estuary. The mean tidal range increases from 3.8 m at Vlissingen to 5.0 m near the border. The river discharge varies from 20 m^3 s^{-1} during summer to 600 m^3 s^{-1} during winter, with a mean yearly average of 105 m^3 s^{-1} (Baeyens et al. 1998). The residence time of the water in the estuary is rather high, ranging from 1 to 3 mo, depending on the river discharge (Soetaert & Herman 1995). The most seaward region has a residence time of about 10 to 15 d.

The lower and middle estuary, called the Westerschelde (55 km), is a well-mixed region characterised by a complex morphology with flood and ebb channels surrounding several large intertidal flats and salt marshes. The surface of the Westerschelde amounts to 310 km^2, with the intertidal area covering 35%. The average channel depth is approximately 15 to 20 m. In the lower and middle estuary a multiple channel equilibrium exists, while upstream of the Dutch/Belgian border the estuary is characterised by a single channel. The turbidity maximum is situated in this region of the estuary but moves over a quite large distance, depending among other factors on tidal action and river run-off (Baeyens et al. 1998). Nowadays, dredging activities for shipping as well as pollution are the major anthropogenic stressors. About 8 to 12 million m^3 of sediment is dredged yearly to keep the port of Antwerpen accessible. For more details on the ecological and physicochemical properties of the estuary see Meire & Vincx (1993), Heip & Herman (1995), Baeyens et al. (1998), Herman & Heip (1999) and van Damme et al. (unpubl. data).

Macrobenthos data. An extensive data set on macrobenthos is available for the Schelde estuary. A total of 3112 macrobenthos samples, mainly within the framework of monitoring programmes, were collected in the study area by different institutes in the period 1978 to 1997, but with >90% of the samples collected from 1990 onwards. Qualitatively, no fundamental nor systematic changes in the occurrence of the macrobenthos appeared in the study area. The use of such a large, long-term data set allows us to be more certain of a species being present in a certain environment and to compensate for accidental observations.

By far most of the data were collected and analysed by 2 institutes: the Centre for Estuarine and Coastal

Ecology NIOO-CEMO (e.g. Craeymeersch et al. 1996, Brummelhuis et al. 1997, Craeymeersch 1999), and the Institute of Nature Conservation (e.g. Ysebaert & Meire 1991, Ysebaert 2000, Ysebaert et al. 2000), mainly in co-operation with the National Institute for Marine and Coastal Management (RWS-RIKZ); 54 % were taken in autumn (September and October), 32 % in spring (March, April, May). Most sampling locations (68 %) were sampled only once, but several locations were sampled 2 to 5 times during the sampling period considered, and a few were sampled more frequently within a long-term programme.

In general, multiple sediment cores were used for sampling the intertidal zone, and either a van Veen grab or a Reineck box corer for the subtidal zone. In the intertidal zone most samples (77 %) had a sample size between 0.015 and 0.023 m^2, while another 18 % had a sample size of 0.01 m^2. In the subtidal zone, most samples (76 %) had a sample size of approximately 0.015 m^2, which is comparable to the sample size of the samples in the intertidal zone. A minor percentage of the subtidal samples were much larger (0.10 to 0.12 m^2). As difference in sample size was rather small

between most samples, the effect of sample size on the occurrence of a certain species is expected to be small.

All samples were sieved through 1 mm mesh. For more details on the sampling methods and the design of the monitoring programmes see Meire et al. (1991), Ysebaert et al. (1993) and Craeymeersch (1999).

Abiotic variables. For each sample the following abiotic environmental variables were added to the macrobenthos database: depth/elevation, salinity, current velocities (maximum ebb- and flood-current velocities), sediment characteristics (median grain size and mud content). At subtidal stations depth was recorded at the time of sampling. The elevation of the intertidal stations was measured directly in the field or derived from the RIKZ Geographical Information System, storing all bathymetric data in the area. For 2874 samples (92 %), depth was added in the database. Depth is expressed in m NAP (NAP = Dutch Ordnance level, similar to 'mean sea level').

Salinity was estimated for each sampling location using a 2Dh-hydrodynamic model SCALDIS400 (Lievense 1994) with a spatial resolution of 400 m. The

Fig. 1. Map of Schelde estuary showing sampling locations
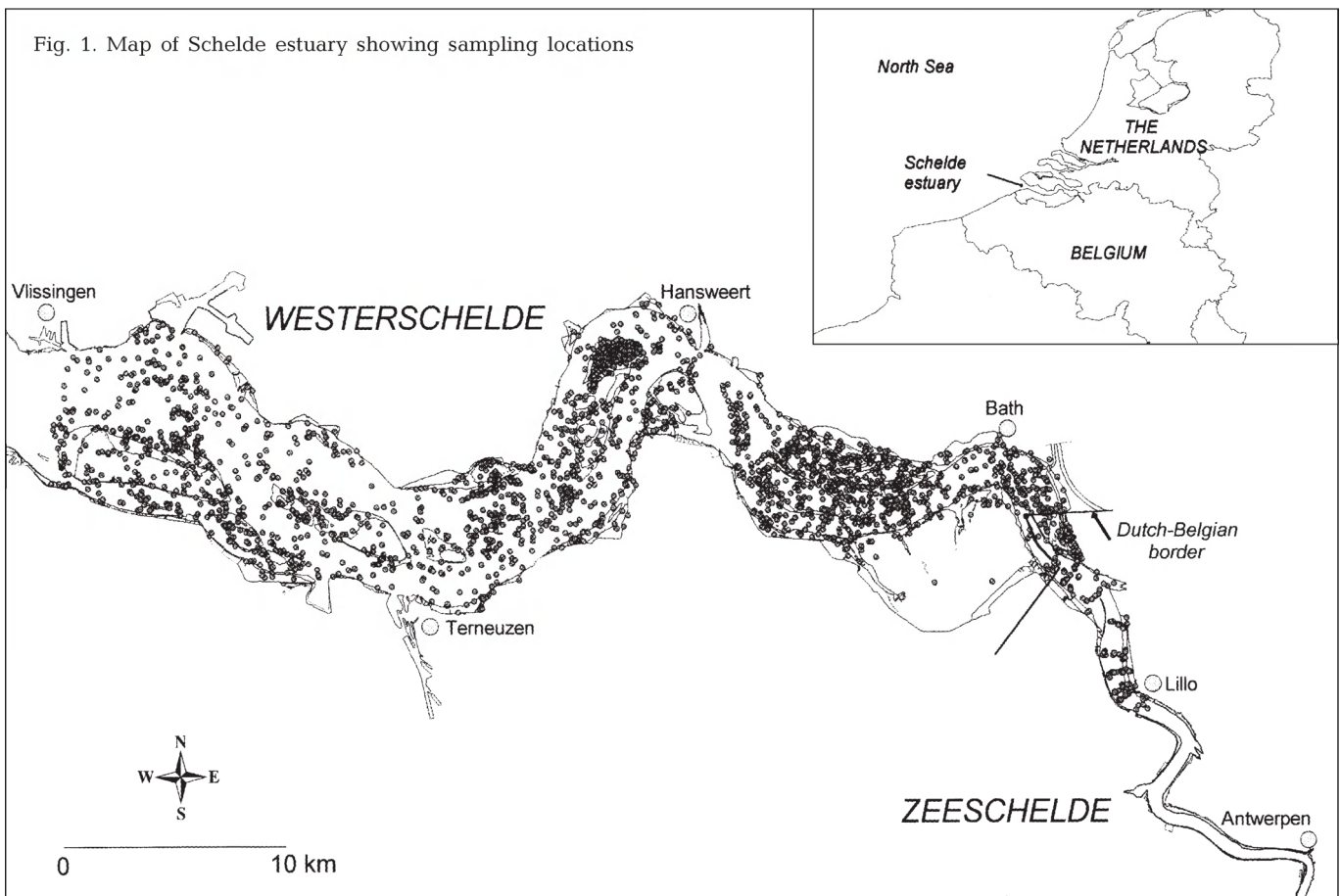
model calculations are based on values for mean tidal conditions with a yearly averaged discharge, giving an average salinity value. The advantage of using the SCALDIS400 model is that a high spatial resolution is obtained but the estimates are not seasonally defined. Therefore, also monthly to fortnightly measurements at 9 stations along the Westerschelde were used to represent the temporal variation in salinity, but at a much coarser spatial resolution than model salinity. For each sample, the temporal salinity was determined as the average salinity of the 3 mo prior to the date of sampling. Estimates obtained from model simulations are called 'model salinities', whereas the values derived from field observations are called 'temporal salinities'.

Current velocities (maximum ebb- and flood-current velocities in m s^{-1}) for each sampling location were estimated with the SCALDIS100 model (Dekker et al. 1994) for mean tidal conditions, with a spatial resolution of 100 m. For 3037 samples (98%), current velocity estimates were added to the database.

Samples for sediment grain-size analysis (by the laser diffraction technique) were collected during several field campaigns. For 1502 and 1386 samples (48 and 45%), median grain size and mud content (vol% <63 µm) values were added to the database respectively.

Statistical analysis. Logistic regression (Cox 1970, Hosmer & Lemeshow 1989, Trexler & Travis 1993, Jongman et al. 1995) falls within the general framework of generalized linear models (GLM) (Nelder & Wedderburn 1972, McCullagh & Nelder 1989) and can be used to analyse the relationship between a binary response variable and 1 or more explanatory variables. Logistic regression is used here to model the response of the occurrence of 20 macrobenthic species to the abiotic environmental predictors. The choice of using binary (presence/absence) data was inspired by the fact that the data could not be considered as homogeneously collected. Especially seasonality (difference in sampling months) and, to a lesser extent, long-term fluctuations and the use of different sampling methods and sample sizes certainly affected the observed variation in density and biomass data. To minimise this variation, presence-absence data were used. Indeed, the presence-absence of most macrobenthic species appeared to be much less seasonally differentiated than density and biomass (Ysebaert 2000). As many species were often found accidentally, we decided to treat densities of <50 ind. m^{-2} as absences (0) for most species (except for *Nephtys cirrosa* and *Arenicola marina*).

In the logistic regression model, a binary response variable is related to 1 or more predictor variables through the logistic link function:

$$\text{logit } \{p(x)\} = \log \{p(x)/1-p(x)\} = b_0 + b_1x + b_2x^2 \quad (1)$$

where p(x) is the probability that the species occurs as a function of an environmental variable x, and b_0, b_1, b_2 are the regression parameters. Eq. (1) can be rewritten to define the estimated probability p(x) as

$$p(x) = \{e^{(b_0 + b_1x + b_2x^2)}\}/\{1 + e^{(b_0 + b_1x + b_2x^2)}\} \quad (2)$$

which is bound between 0 and 1.

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. For second-order polynomials it will approximate a bell-shaped function (Gaussian logit curve), which is an ecologically realistic response (ter Braak and Loonman 1986). Although skewed and more complex response curves can theoretically occur, they cannot be fitted with the GLM approach (see e.g. Bio et al. 1998). In this study, a response surface for each macrobenthic species on each of the independent variables was generated by logistic regression with the statistical package SAS (SAS Institute Inc. 1989). The regression parameters were estimated using the maximum likelihood method, assuming binomially distributed errors. The global model significance, as well as the significance of the different regression parameters, was tested using the $2\ln L$ statistic based on the χ^2-test (p < 0.05), where L is the maximized likelihood. Besides response curves for each single abiotic variable separately, all variables were simultaneously used in a stepwise multiple logistic-regression analysis to derive a multivariate model that would predict the presence or absence of macrobenthic species. Negative depth values, ranging from -56.4 to $+2.2$ m, were replaced by positive values by changing sign (value × -1) and adding 2.5 m. Since sediment characteristics were only available for a limited set of data, the analyses were run separately without (n = 2827) and with (n = 1423) sediment data, hereafter called Data Sets A and B respectively. The significance of the independent variables was tested using the χ^2-test (p < 0.05) on the Wald statistic.

The resulting set of regression equations was validated internally. As a measure of classification accuracy, the percentage of concordant pairs was used (a pair is concordant if the observation with the larger-ordered value of the response has a higher predicted event probability than does the observation with the smaller-ordered value of the response). The predictive success of the response surfaces was further evaluated by cross-tabulating observed and predicted responses (2 × 2 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 of correct predictions, we also examined the sensitivity (the proportion of actual presences that were correctly predicted) and specificity (the proportion of actual absences that were correctly predicted). The probability of the observed contingency table occurring by random chance, given the row and column totals, was calculated with Fisher's exact test, which consists of calculating the actual probability of the observed 2 × 2 contingency table with respect to all other possible 2 × 2 contingency tables with the same column and row totals. The hypothesis was tested if the proportion of presences predicted as present was greater than the proportion of absences predicted as present.

The ability of the final models to predict the probability of occurrence was evaluated by randomly splitting the data (from Data Set A) into 2 equal groups, building the model with the chosen variables using half of the data. We conducted 10 such runs with 10 different splits of the data on each species. Firstly, we tested these 10 model runs, based on the random selections of 50% of the data, for consistency of their prediction. For each species model we generated random sets of abiotic conditions by generating 1000 uniformly distributed random numbers. For each species, ranges for the environmental variables were chosen relative to their observed distribution. For example, for the cockle *Cerastoderma edule*, numbers varied in the ranges 10–30, 7–33, 0–20, 0–1 and 0–1.1 for model salinity, temporal salinity, depth, maximum ebb and maximum flood-current velocity respectively. Temporal salinity was randomly chosen in a range of ±3 of model salinity, and maximum flood-current velocity likewise was selected in the range of ±0.1 m s^{-1} of maximum ebb-current velocity. We then generated predicted p-values for the 10 models, which were compared mutually. Secondly, we tested the predictions with the other half of the data sets by examining the overall percentage correctly predicted, the sensitivity and specificity for each of the 10 data sets. This procedure examines the ability of the model to predict the occurrence of the species for locations that are not included in the model and is therefore a more rigorous test of classification accuracy.

For 10 contrasting macrobenthic species, results are presented in detail: the polychaetes *Heteromastus filiformis*, *Pygospio elegans*, *Nephtys cirrosa*, *Nereis diversicolor*, *Spio* sp. and *Arenicola marina*, the molluscs (bivalves) *Macoma balthica* and *Cerastoderma edule*, and the crustaceans (amphipods) *Bathyporeia* sp. and *Coro-phium volutator*. 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 (Ysebaert et al. 1993, 1998, Ysebaert & Meire 1999, Ysebaert 2000).

For *Macoma balthica*, *Cerastoderma edule*, *Nephtys cirrosa* and *Corophium volutator* a visual geographical comparison between the mapped probability surfaces and the species occurrence maps is also presented.

RESULTS

Characterization of the abiotic environment

Average model salinity, based on model calculations, varied between 5.7 and 31.6 for the whole study area (Table 1). Most samples (60%) were situated in the polyhaline zone (salinity >18), 31% in the α-meso-haline zone (salinity 10 to 18) and 15% in the β-meso-haline zone (salinity 5 to 10). Depth ranged between –56.4 and +2.2 m NAP. About 50% of the sampling took place in the intertidal zone (above –2 m NAP). Most of the subtidal samples (68%) were situated above –10 m NAP. Maximum ebb- and flood-current velocities varied between 0.01 and 1.64 m s^{-1}, with a mean of 0.64 m s^{-1}; 11% of the samples had current velocities <0.25 m s^{-1}, 27% between 0.25 and 0.5 m s^{-1}, 24% between 0.50 to 0.75 m s^{-1}, 22% between 0.75 and 1.00 m s^{-1} and 16% >1.00 m s^{-1}. Median grain size varied between 16 and 664 μm, with a mean of 165 μm. Mud content varied between 0 and 95%, with a mean of 19%; 13% of the samples were characterised as muddy (median grain size in the range 2 to 63 μm), 19% as very fine sand (63 to 125 μm), 54% as fine sand (125 to 250 μm) and 15% as medium sand (250 to 500 μm). More details on the abiotic environment of the same data set as used in this paper can be found in Ysebaert & Meire (1999) and Ysebaert (2000).

Table 1. Environmental variables with numbers of observations (n), median, minimum and maximum values. NAP: Dutch Ordnance level

Variable		n	Median	Min.	Max.
Model salinity	(psu)	3112	22.3	5.69	31.61
Temporal salinity	(psu)	3112	19.1	1.15	32.39
Depth	(NAP)	2874	–2.9	–56.4	+2.2
Maximum ebb-current velocity	(m s^{-1})	3037	0.60	0.01	1.64
Maximum flood-current velocity	(m s^{-1})	3037	0.64	0.01	1.61
Median grain size	(μm)	1502	162	16	664
Mud content (<63 μm)	(%)	1386	7.0	0	95.45

Observed distributions of macrobenthic species along environmental variables

Fig. 2 presents the observed distribution of 10 macrobenthic species along the environmental variables salinity, depth, maximum ebb-current velocity and median grain size as box-and-whisker plots. Characteristic polyhaline species, such as *Arenicola marina*, *Cerastoderma edule*, *Nephtys cirrosa* and *Spio* sp. were clearly distinguished from mesohaline species such as *Corophium volutator and Nereis diversicolor*, although the latter had a very wide range of occurrence. Species like *Bathyporeia* sp., *Heteromastus filiformis*, *Macoma balthica* and *Pygospio elegans* took intermediate positions. With respect to depth, most species were observed mainly in the intertidal zone. Only *N. cirrosa* and *Spio* sp. were typically subtidal species, and *Bathyporeia* sp. and *H. filiformis* appeared to be present both in the intertidal and the subtidal zones.

Most species had a median of occurrence between 0.3 and 0.5 m s^{-1} for maximum ebb-current velocity, with lowest values observed for *Corophium volutator*

and *Nereis diversicolor*. Only *Nephtys cirrosa* and *Spio* sp. had a median occurrence at much higher current velocities. For maximum flood-current velocity similar results were obtained. *C. volutator* and *N. diversicolor* were observed mainly in very fine sand sediments, whereas *Spio* sp. and especially *N. cirrosa* were observed in coarser sediments.

Response curves for a single environmental (explanatory) variable

As an example of the obtained response curves for a single abiotic variable, Figs 3 to 6 show the fitted Gaussian logit curves for the 10 macrobenthic species in relation to model salinity, depth, maximum ebb-current velocity and median grain size. For all species, at least 1 regression parameter was significantly entered in the different models by forward selection. The obtained response curves were in general agreement with the observed distributions from Fig. 2.

Species such as *Corophium volutator* and, to a lesser extent, *Nereis diversicolor*, showed a high probability of occurrence at low salinity (Fig. 3). For *C. volutator*, a steep decrease in the curve was observed with increasing salinity, whereas for *N. diversicolor* the decrease in the curve was much smoother, indicating that this species could also occur at higher salinity. *Bathyporeia* sp. showed a bell-shaped curve with an optimum at intermediate salinities; the probability of occurrence of this species decreased both at the lower end and at the upper end of the salinity range. Several species, such as *Cerastoderma edule*, *N. cirrosa*, *Spio* sp. and *Arenicola marina*, showed a clear optimum towards the higher end of the salinity range. These species differed in the position of their optimum, and in their tolerance towards the lower end of the salinity range. *Macoma balthica* had an almost horizontal curve, indicating a very broad tolerance for salinity. Another species showing a broad tolerance for salinity was *Heteromastus filiformis*. In general results for 'temporal salinity' were similar to those for results as 'spatial salinity'.

For most macrobenthic species (e.g. *Pygospio elegans*, *Cerastoderma edule*, *Nereis diversicolor*, *Corophium volutator*) the response curves in relation to
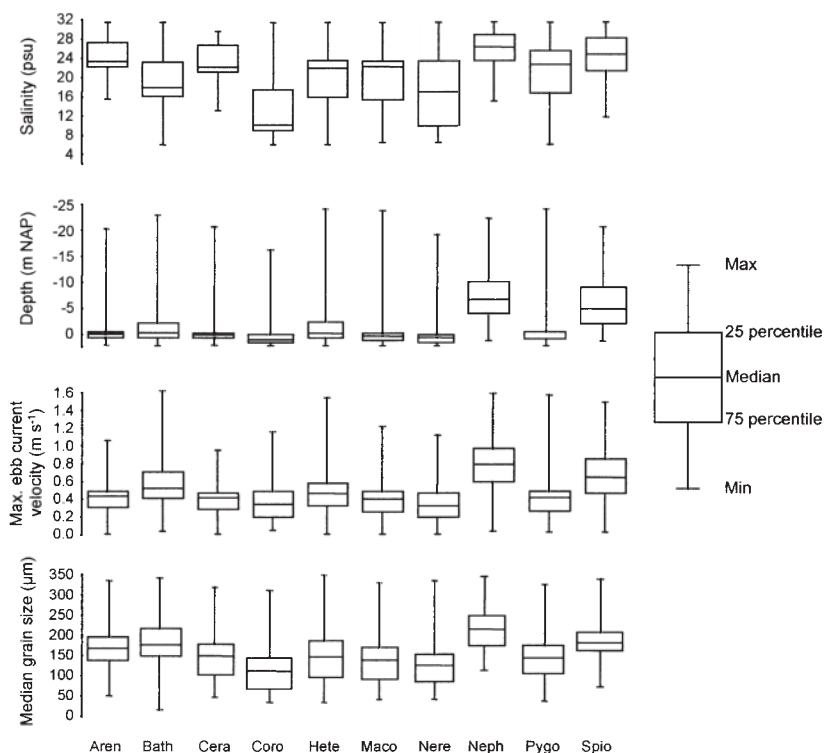
Fig. 2. Box-and-whisker plots for 10 macrobenthic species with respect to (model) salinity, depth, maximum ebb-current velocity and median grain size in the Schelde estuary. Species are ordered alphabetically. Aren: *Arenicola marina*; Bath: *Bathyporeia* sp.; Cera: *Cerastoderma edule*; Coro: *Corophium volutator*; Hete: *Heteromastus filiformis*; Maco: *Macoma balthica*; Nere: *Nereis diversicolor*; Neph: *Nephtys cirrosa*; Pygo: *Pygospio elegans*; Spio: *Spio* sp.
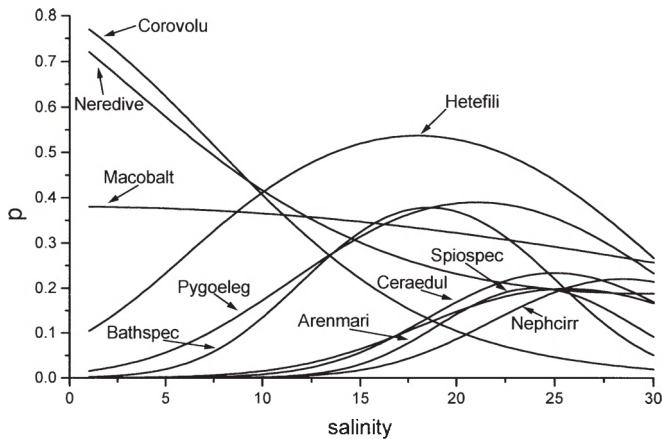
Fig. 3. Probability of occurrence (p) of 10 macrobenthic species in relation to (model) salinity (psu) in the Schelde estuary, fitted with logistic regression. Hetefili: *Heteromastus filiformis*; Macobalt: *Macoma balthica*; Pygoeleg: *Pygospio elegans*; Bathspec: *Bathyporeia* sp.; Ceraedul: *Cerastoderma edule*; Nephcirr: *Nephtys cirrosa*; Neredive: *Nereis diversicolor*; Corovolu: *Corophium volutator*; Spiospec: *Spio* sp.; Arenmari: *Arenicola marina*

Fig. 4. Probability of occurrence (p) of 10 macrobenthic species in relation to depth (m NAP = Dutch Ordnance level) in the Schelde estuary, fitted with logistic regression. Species abbreviations as in Fig. 3

depth were similar, with high probabilities of occurrence above NAP, and decreasing probabilities of occurrence with increasing depth (Fig. 4). These species differed in their tolerance towards the deeper end of the depth range. *Heteromastus filiformis*, for instance, showed a relatively high tolerance, with a still relatively high probability of occurrence in the subtidal zone. *Bathyporeia* sp. showed only a slightly higher probability of occurrence in the intertidal zone, indicating a very broad depth tolerance. Species showing an optimum in the subtidal zone of the estuary were *Nephtys cirrosa* and *Spio* sp.

Species such as *Nereis diversicolor* and *Corophium volutator* displayed the highest probability of occurrence at the lowest ebb-current velocities (Fig. 5). Other species such as *Macoma balthica* and *Pygospio elegans* showed a broad tolerance in the range 0 to 0.5 m s^{-1}, after which a steep decline was observed in the probability of occurrence with increasing current velocities. This broad tolerance was even more pronounced for *Heteromastus filiformis*, which showed a decrease in probability of occurrence only at the highest current velocities. *Bathyporeia* sp. on the other hand displayed an almost horizontal curve, indicating that current velocity did not discriminate well 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. Similar results were obtained for maximum flood-current velocity.

The response curves in relation to median grain size clearly revealed different responses for the different macrobenthic species (Fig. 6). *Nereis diversicolor* showed the highest probability of occurrence in very muddy sediments with a low median grain size, with a 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 *Heteromastus filiformis* and *Macoma balthica*. *Pygospio elegans* and *Cerastoderma edule* showed a bell-shaped curve with an optimum between 100 and 150 μm. This optimum shifted more towards a higher median grain size for *Arenicola marina* (approx. 155 μm), *Spio* sp. (approx. 200 μm) and *Bathyporeia* sp.

Fig. 5. Probability of occurrence (p) of 10 macrobenthic species in relation to maximum ebb-current velocity in the Schelde estuary, fitted with logistic regression. Species abbreviations as in Fig. 3
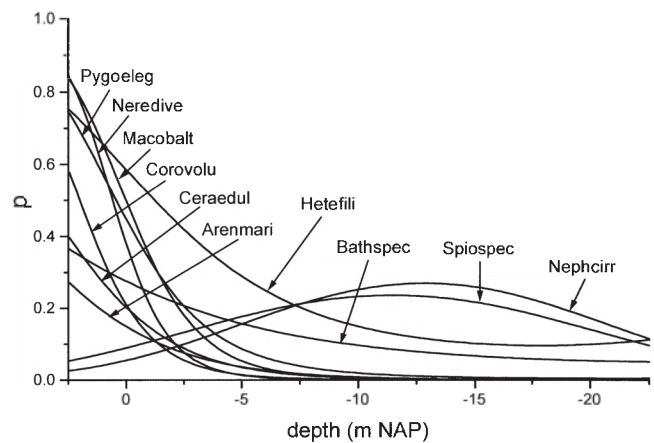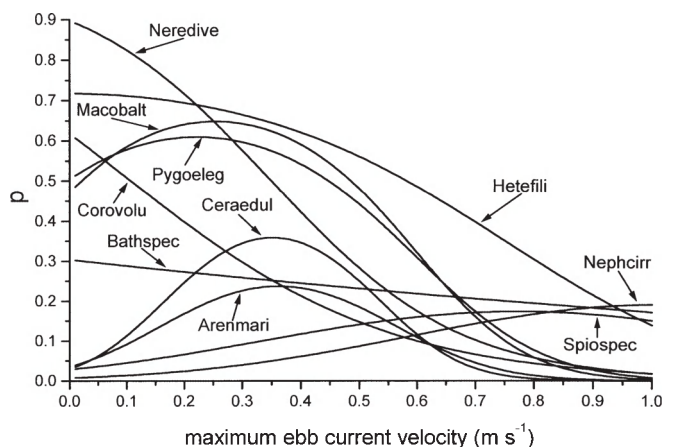
Fig. 6. Probability of occurrence (p) of 10 macrobenthic species in relation to median grain size in the Schelde estuary, as fitted with logistic regression. Species abbreviations as in Fig. 3

(approx. 225 μm). *Nephtys cirrosa* showed an optimum towards the higher end of the median grain size range.

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.

Appendix 1 indicates the order in which the environmental variables were entered into the stepwise selection models. In all models, salinity (either model salinity, temporal salinity or both), depth, current velocity and sediment characteristics (for the models based on Data Set B) were entered into the models. Only for *Macoma balthica* was salinity not entered in the model based on Data Set A, which corresponds with the univariate model for salinity in which *M. balthica* showed a large tolerance.

Table 2. Diagnostics for final multiple logistic regression models for each of 10 macrobenthic species for data set without sediment data (Data Set A) and data set with sediment data (Data Set B). See Appendix 1 for variables included in each model. Species abbreviations as in Fig. 3

Diagnostics	Hetefili	Macobalt	Pygoeleg	Bathspec	Ceraedul	Nephcirr	Neredive	Corovolu	Spiospec	Arenmari
Data Set A										
No. present	1164	820	773	583	352	339	660	394	304	269
No. absent	1663	2007	2054	2244	2475	2488	2167	2433	2523	2558
Intercept only (-2ln L)	3831	3405	3317	2877	2125	2074	3072	2283	1930	1777
Intercept + covariates (-2ln L)	2897	1915	1965	2356	1176	1623	1581	1210	1485	1214
Chi-square	952	1490	1352	521	949	451	1491	1074	445	563
df	8	6	7	7	9	6	6	5	6	8
Probability	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Concordant pairs	92.9%	91.1%	90.3%	79.1%	93.0%	82.2%	82.3%	92.5%	83.6%	88.8%
p-threshold	0.51	0.61	0.50	0.38	0.42	0.32	0.47	0.33	0.29	0.35
% correctly predicted	75.2%	85.5%	85.6%	78.1%	90.0%	84.0%	88.3%	90.2%	87.8%	89.5%
Sensitivity	69.9%	75.0%	75.7%	46.8%	59.9%	33.3%	75.0%	64.7%	43.1%	44.6%
Specificity	80.0%	89.8%	90.8%	86.2%	94.3%	90.9%	92.4%	94.3%	93.1%	94.2%
Fisher exact test: 1-tailed p	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Data Set B										
No. present	686	562	492	331	232	102	454	313	169	172
No. absent	607	731	910	962	1061	1191	839	1089	1124	1121
Intercept only (-2ln L)	1788	1770	1817	1471	1217	714	1676	1489	1003	1014
Intercept + covariates (-2ln L)	1091	770	990	1044	679	449	896	750	604	620
Chi-square	696	1000	827	427	538	264	780	739	399	394
df	12	8	7	7	7	6	8	5	8	8
Probability	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Concordant pairs	89.2%	91.7%	91.5%	85.3%	92.0%	91.1%	94.0%	92.7%	91.0%	90.8%
p-threshold	0.56	0.61	0.35	0.46	0.42	0.19	0.50	0.36	0.42	0.36
% correctly predicted	81.4%	87.3%	79.7%	80.8%	87.5%	91.8%	75.9%	88.9%	89.8%	86.9%
Sensitivity	82.5%	85.4%	71.1%	62.5%	65.1%	48.0%	65.6%	75.1%	60.9%	50.6%
Specificity	80.2%	88.8%	84.4%	87.1%	92.4%	95.6%	81.4%	92.8%	94.1%	92.4%
Fisher exact test: 1-tailed p	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

The final model for each species contained between 5 and 9 variables with concordant pairs of 79.1 to 93% for Data Set A, and between 5 and 12 variables with concordant pairs of 85.3 to 94.0% for Data Set B (Table 2). The explained deviance between the intercept-only model and the intercept+covariates model varied between 18.2 and 48.5% and between 29.0 and 52.5% for Data Sets A and B respectively. All final models were highly significant, with p-values at 0.0001 for both data sets. The sensitivity and specificity were moderate to high for most species, the sensitivity being higher in most cases for the data set with sediment characteristics.

Final models for each species appeared quite stable, as 10 model runs (based on the random selections of 50% of the data) on randomly generated sets of abiotic conditions generated highly correlated predictions (Table 3). All linear correlation coefficients between pairs of models were in the range of 0.89 to 0.99 for each species. Also the percentage of concordant pairs, percentage correctly predicted, sensitivity and specificity did not change much as a function of which random set of 50% of the data was used to build the model (Table 3a) and test the model (Table 3b). The standard deviations of these diagnostics were low, suggesting that the models were not very dependent on any particular set of observations.

Maps of the probability of occurrence of the macrobenthic species appeared to be fairly consistent with the observations of presence and absence in the Schelde estuary, as shown in Figs 7 to 10 for *Macoma balthica*, *Cerastoderma edule*, *Corophium volutator* and *Nephtys cirrosa* respectively. *M. balthica* was observed along the complete salinity gradient, mainly in the intertidal zone, and the highest probabilities of occurrence coincided with this distribution. This was also observed *for C. edule* and *C. volutator*, 2 species with a mainly polyhaline, intertidal distribution and a mainly mesohaline, intertidal distribution respectively. *C. edule* showed a low probability of occurrence in the α-mesohaline zone, and *C. volutator* a low probability of occurrence in the polyhaline zone of the estuary. *N. cirrosa* was a relatively common species in the subtidal polyhaline zone of the Schelde estuary, penetrating the estuary up to the α-mesohaline zone. The model predicted a much broader distribution for this species, as was observed from the high probabilities of occurrence at almost all sampling locations in the subtidal polyhaline zone. Upstream of the polyhaline zone the model indicated a decreasing probability of occurrence.

Table 3. Summary of classification diagnostics for 50% of data (based on Data Set A, n = 2827) used to build models; 50% of data was resampled 10 times to create 10 sets of data to build models (a) and 10 sets of data to test models (b). Standard deviation is in parentheses. Consistency of the 10 model runs (a) for each species was tested on random sets of abiotic conditions, by generating 1000 uniformly distributed random numbers. The generated predicted p-values for the 10 model runs were compared mutually and the range of the linear correlation coefficients between all pairs is presented

| Species	Correlation between 10 model runs	Mean concordance	Threshold p	% correctly predicted	Sensitivity	Specificity
(a) Model-fitting data						
Heteromastus filiformis	0.976–0.999	82.4 (0.75)	0.50 (0.015)	75.5 (0.69)	70.0 (1.28)	79.3 (0.68)
Macoma balthica	0.968–0.998	91.2 (0.56)	0.59 (0.014)	85.9 (0.54)	75.4 (1.55)	90.1 (0.42)
Pygospio elegans	0.889–0.998	90.5 (0.78)	0.50 (0.010)	86.3 (0.76)	74.9 (1.77)	90.6 (0.56)
Bathyporeia sp.	0.979–0.999	79.2 (0.91)	0.38 (0.011)	77.7 (0.97)	47.2 (2.53)	85.9 (0.66)
Cerastoderma edule	0.895–0.991	92.8 (0.41)	0.41 (0.020)	89.9 (0.90)	59.1 (2.73)	94.2 (0.54)
Nephtys cirrosa	0.889–0.996	82.4 (0.70)	0.32 (0.018)	84.1 (0.80)	34.3 (2.11)	91.0 (0.51)
Nereis diversicolor	0.958–0.998	93.0 (0.43)	0.43 (0.012)	87.7 (0.88)	66.0 (4.63)	92.7 (0.49)
Corophium volutator	0.963–0.999	92.3 (0.76)	0.33 (0.012)	90.3 (1.18)	64.5 (2.08)	94.2 (1.32)
Spio sp.	0.973–0.999	83.5 (1.08)	0.29 (0.015)	87.4 (0.90)	42.1 (3.10)	93.0 (0.53)
Arenicola marina	0.889–0.994	88.6 (0.35)	0.35 (0.017)	89.2 (0.77)	43.1 (3.91)	94.1 (0.49)
(b) Model-testing data						
Heteromastus filiformis			0.50 (0.022)	75.3 (1.48)	70.2 (1.86)	78.9 (1.38)
Macoma balthica			0.61 (0.022)	95.0 (0.41)	74.4 (1.15)	89.4 (0.42)
Pygospio elegans			0.52 (0.024)	86.4 (0.64)	74.9 (1.69)	90.6 (0.45)
Bathyporeia sp.			0.39 (0.020)	78.6 (0.83)	46.8 (2.58)	86.6 (0.56)
Cerastoderma edule			0.41 (0.020)	89.9 (0.87)	59.7 (2.74)	94.3 (0.53)
Nephtys cirrosa			0.33 (0.026)	85.1 (0.73)	30.2 (2.02)	91.6 (0.46)
Nereis diversicolor			0.42 (0.024)	87.9 (0.86)	69.6 (2.01)	92.5 (0.72)
Corophium volutator			0.34 (0.032)	90.4 (0.57)	67.2 (2.43)	94.4 (0.34)
Spio sp.			0.29 (0.024)	88.7 (0.69)	42.3 (2.44)	93.7 (0.41)
Arenicola marina			0.35 (0.030)	89.1 (0.78)	42.4 (4.84)	94.0 (0.45)
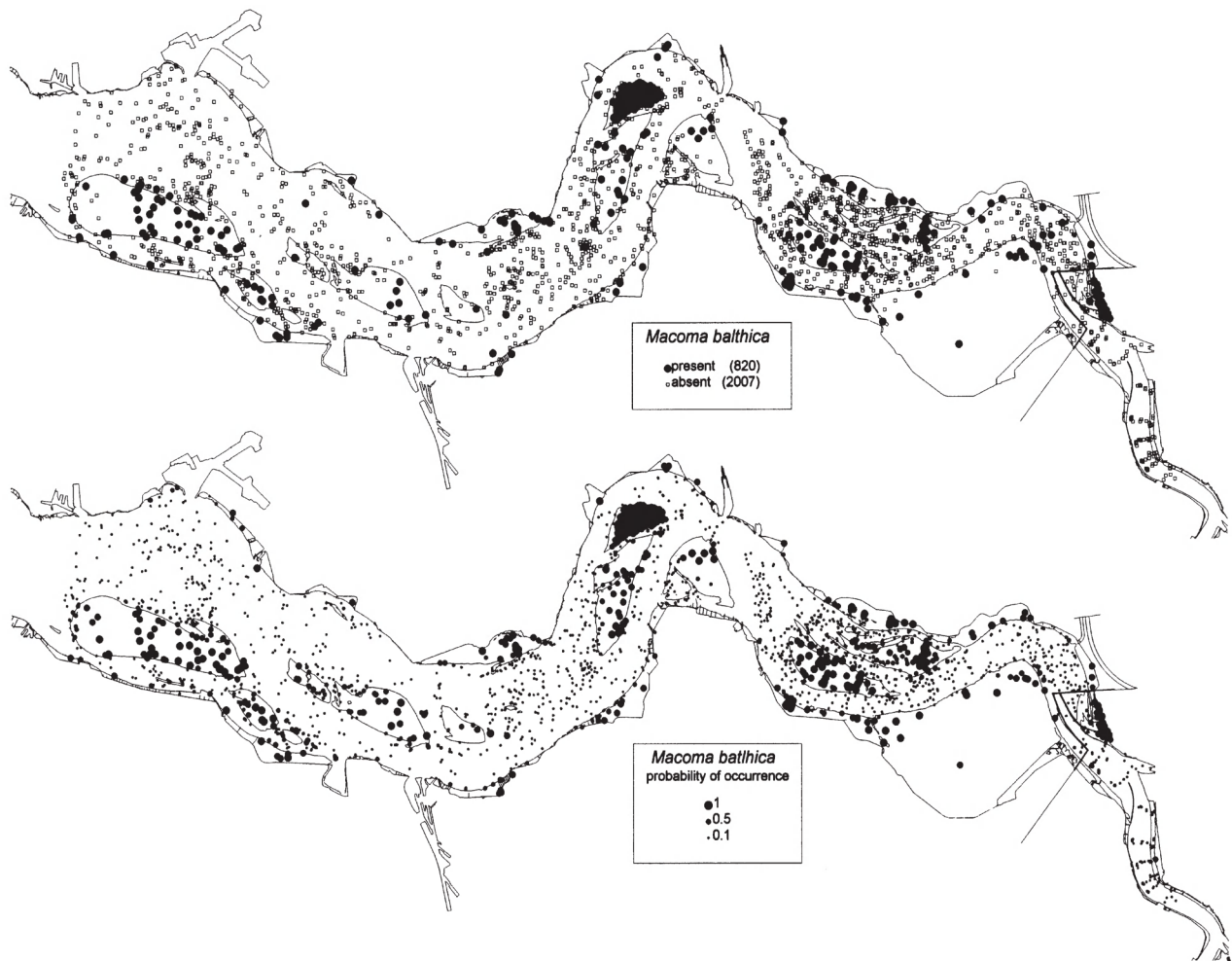
Fig. 7. Observed distribution (presence/absence) of *Macoma balthica* (top graph) and distribution of the determined probabilities of species occurrence based on multiple logistic regression model without sediment data (bottom graph). Probabilities of occurrence (p) are shown on a graduated scale

DISCUSSION

In a review on the ecology of benthic macro-invertebrates in soft-sediment environment, Constable (1999) stated that the established need for developing statistical models and rigorous experimental designs has not penetrated far into the soft-substratum ecological literature. In this study, we statistically modelled and predicted the distribution (presence/absence) of individual macrobenthic species at scales relevant to management, based on small-scale core-sample information and environmental habitat variables including salinity, depth, currents (flow) and sediment composition.

Our model approach gave environmental response surfaces for individual macrobenthic species based on several known deterministic abiotic environmental variables (salinity, depth/elevation, tidal currents and sediment characteristics) which act at different spatial scales. Salinity obviously is a major determining factor of species distributions in estuaries (Boesch 1977, Dittmer 1983, Michaelis 1983, Wolff 1983, Mannino & Montagna 1997, Ysebaert et al. 1998), and will determine the large-scale, longitudinal distributions. By including 'temporal salinity', we also built in the possible role of seasonal variation in salinity in explaining species distribution (e.g. Holland et al. 1987). Depth/elevation, especially when considering the full range from the deep subtidal zone to the high intertidal zone, has a pronounced effect on the macrofauna species distribution along the vertical gradient within estuaries (Craeymeersch 1999, Ysebaert & Meire 1999, Ysebaert 2000). Related to depth are tidal currents, which are generally stronger in the subtidal than in the intertidal
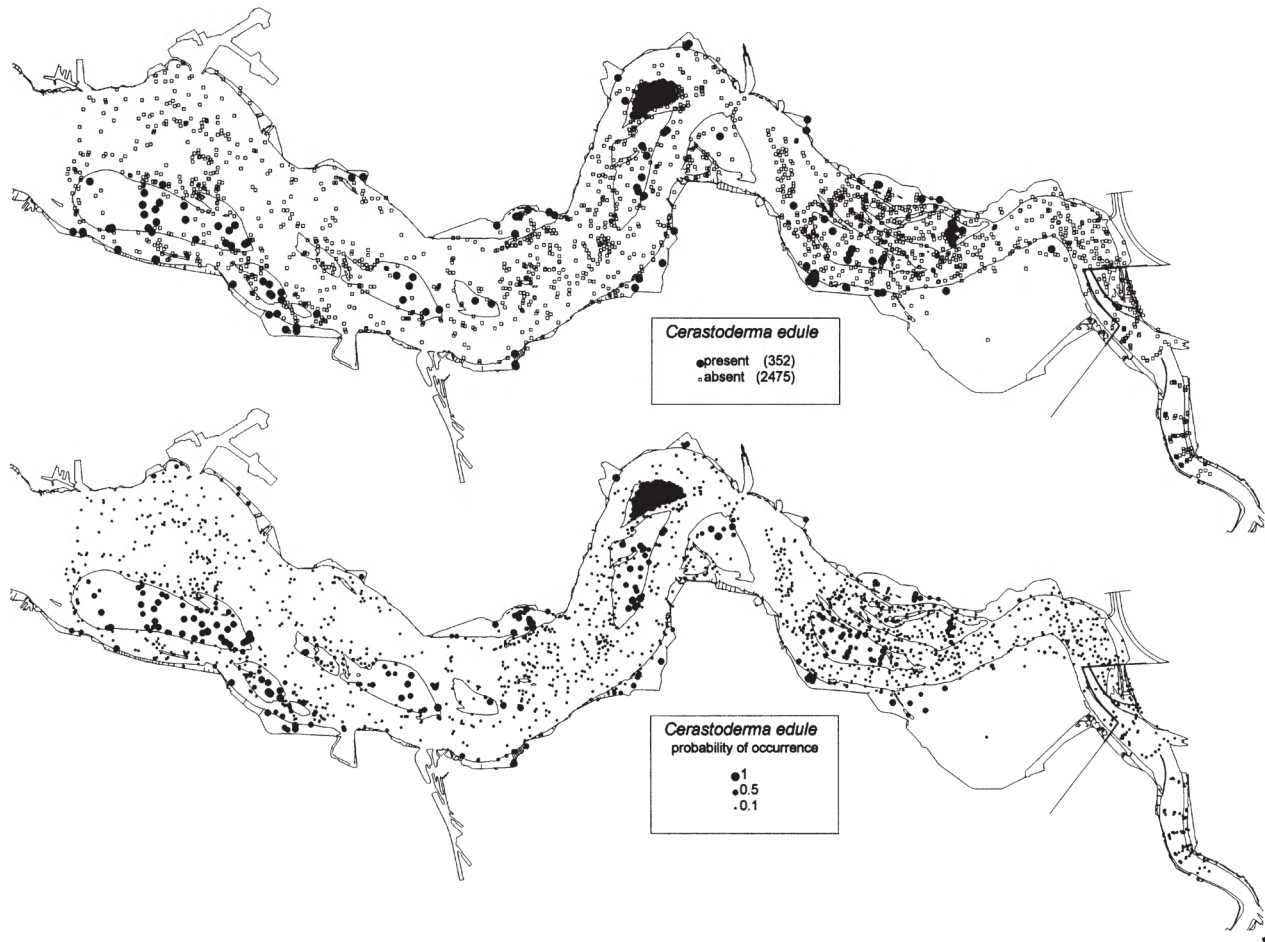
Fig. 8. The observed distribution (presence/absence) of *Cerastoderma edule* (top graph) and the distribution of the determined probabilities of species occurrence based on the multiple logistic regression model without sediment data (bottom graph). Probabilities of occurrence (p) are shown on a graduated scale

zone. Interactions of macrobenthic communities with their environment have traditionally been considered in the context of 'static' physical factors such as sediment characteristics and tidal inundation or exposure time, which are in turn determined largely by hydrodynamic processes (Warwick & Uncles 1980, Nowell & Jumars 1984, Warwick et al. 1991, Hall 1994). The importance of hydrodynamic variables such as current velocity, bed shear stress and wind-wave activity have also been recognised as influencing larval settlement and post-settlement transport (Grant 1983, Butman 1987, Commito et al. 1995), availability of particulate food resources (Miller et al. 1992, Wildish & Kristmanson 1997) and the stability of the substratum (Warwick et al. 1991, Bell et al. 1997, Grant et al. 1997). At the local (smaller) spatial scale, sediment composition has been shown to influence estuarine benthic assemblage structure and species distribution (Gray 1974, Beu-

kema 1976, Junoy & Viétez 1990, Warwick et al. 1991, Meire et al. 1994).

These abiotic environmental variables (salinity, depth, maximum ebb- and flood-current velocities, median grain size and mud content) were used to statistically model and predict, through logistic regression, the distribution (presence/absence) of individual estuarine macrobenthic species at the estuarine macro- and meso-scale. Logistic regression has been applied in many ecological studies, but in the field of marine and estuarine animal ecology this technique has barely been used. On a univariate level, the obtained response curves as a function of the different abiotic environmental variables were in general agreement with the descriptive statistics on the occurrence of the different species along these gradients and are in general agreement with findings in the literature (see also Ysebaert & Meire 1999).
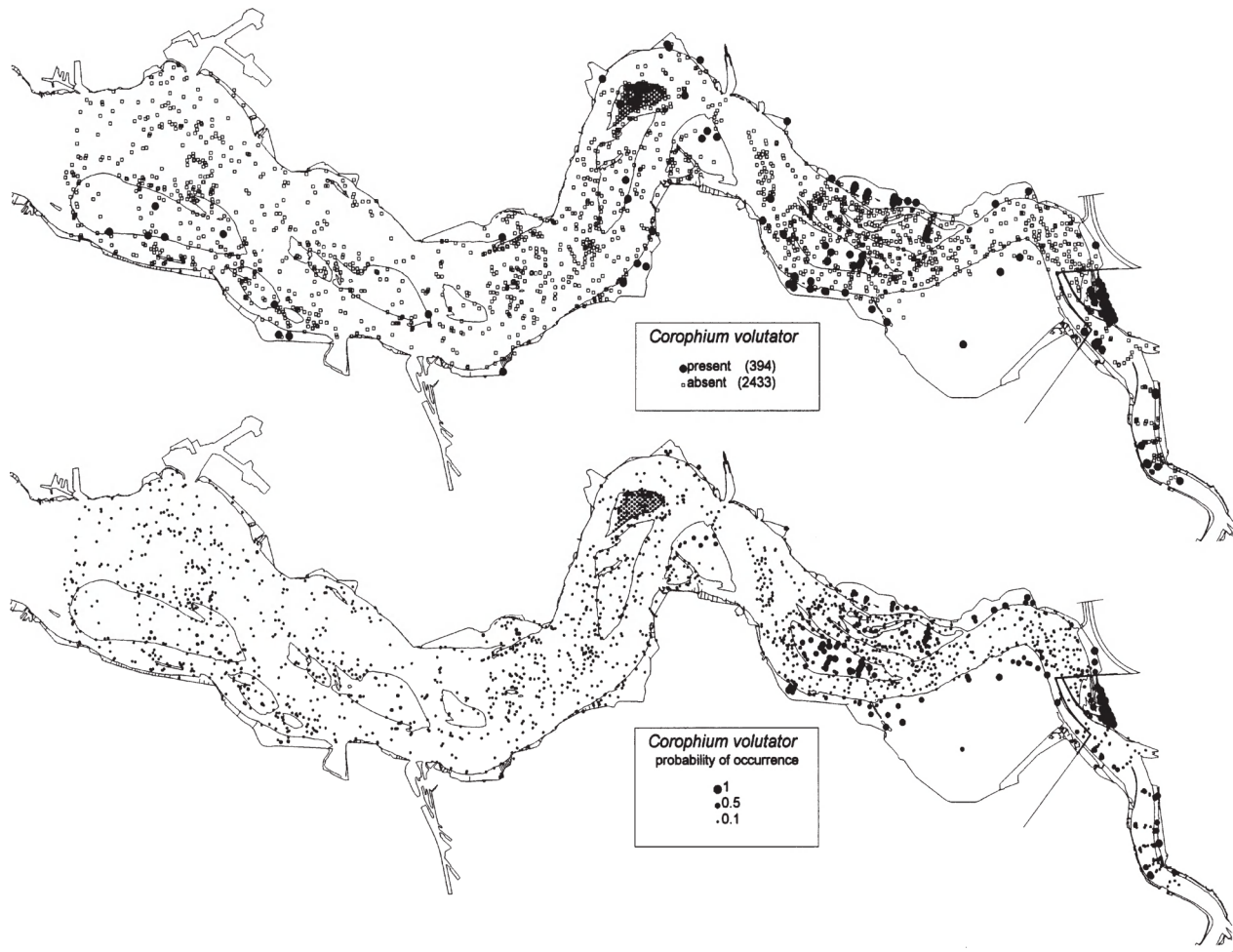
Fig. 9. Observed distribution (presence/absence) of *Corophium volutator* (top graph) and the distribution of the determined probabilities of occurrence based on the multiple logistic regression model without sediment data (bottom graph). Probabilities of occurrence (p) are shown on a graduated scale

In most of our multivariate models, 1 or more estimates of salinity, depth, current velocity and sediment characteristics (for the models with sediment data) are entered into the models. This multivariate modelling approach allows incorporation of heterogeneity both within and across scales. Several of the environmental variables included in this analysis are correlated (see also Ysebaert 2000). As an example, depth is highly correlated with current velocities and, to a lesser extent, with sediment characteristics. Many pairs of mutually correlated variables were nevertheless included in the stepwise procedure in the same model. This is probably due to the fact that these correlations were not spatially consistent. When examined at different scales, the correlation between 2 variables may change. Therefore, when 1 variable is entered into the model, a second variable that is on average correlated

with the first may still explain variation in the probability of occurrence.

In our model approach we used environmental variables as predictors for the distribution of macrobenthic species. An alternative, but not mutually exclusive viewpoint is that distributions are controlled more directly by biotic interactions, such as predation and inter- and intraspecific competition (Wilson 1991, Olafsson et al. 1994). The relative importance of processes determining the spatial distribution of macrofaunal species may depend on the scale considered. Biologically-generated patterns tend to be more important at the micro-scale (<1 m) but are less likely to appear at the macro- or meso-scale (Legendre et al. 1997, Thrush et al. 1997). However, relatively large-scale patterns generated by biological interactions have also been described. The lugworm *Arenicola marina* influences
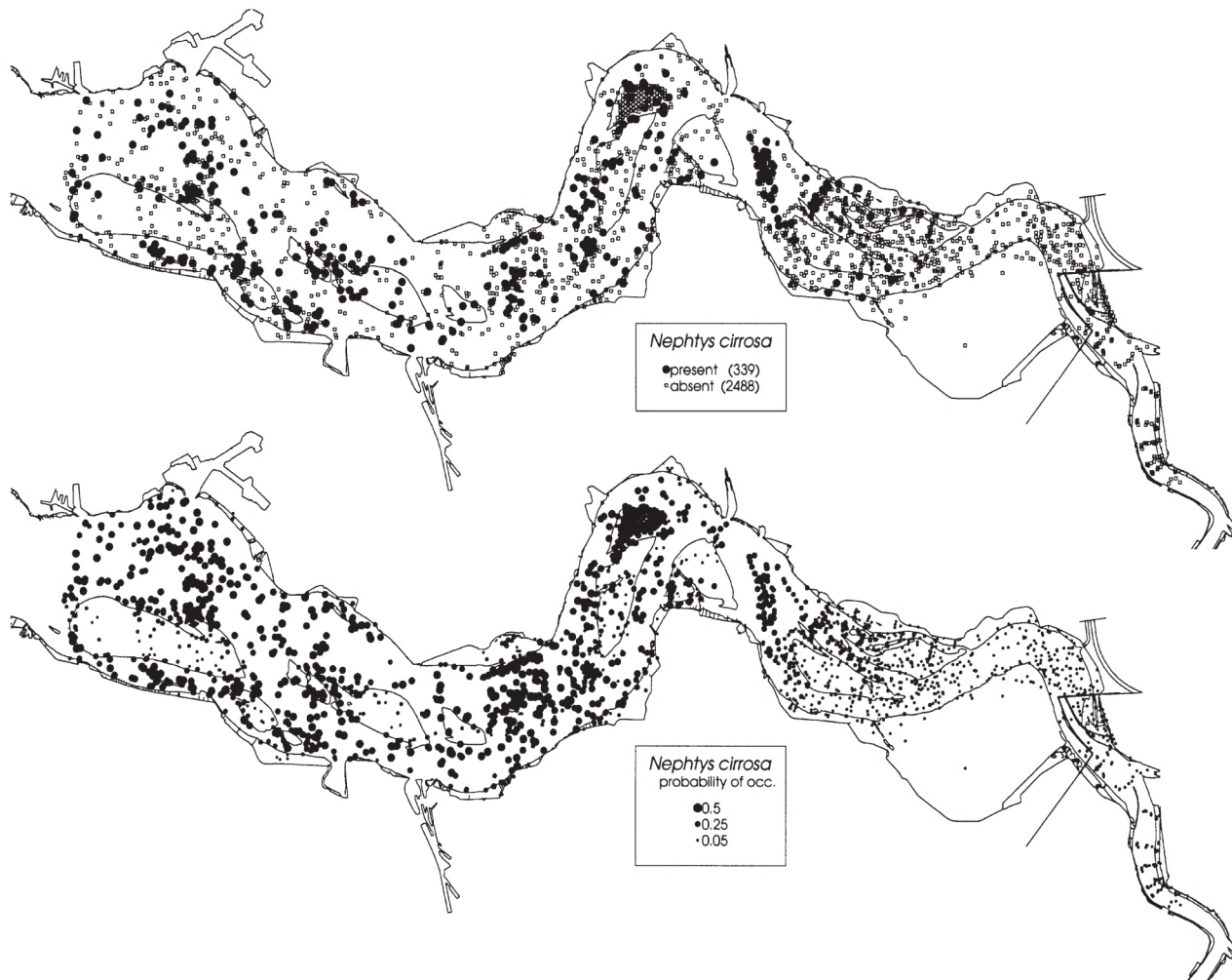
Fig. 10. Observed distribution (presence/absence) of *Nephtys cirrosa* (top graph) and distribution of the determined probabilities of occurrence based on the multiple logistic regression model without sediment data (bottom graph). Probabilities of occurrence (p) are shown on a graduated scale

the distribution of many other species by its bioturbating activities, e.g. the polychaete *Pygospio elegans* (Reise 1985), the amphipod *Corophium volutator* (Flach 1992), the seagrass *Zoltera noltii* (Philippart 1994). It is likely, in such cases, that the environmental factors determining the distribution of the superior competitor will be indirectly reflected in the response functions for the expelled species, falsely suggesting a direct dependence on abiotic factors where in fact a biologically-mediated dependence may be the case. Similar arguments may be valid with respect to the possibilities for settlement of some species. If the abiotic conditions at a particular place are within the tolerance limits of the adults, but conditions are adverse for settlement of juveniles, this may lead to absence of the species. In addition, different abiotic factors control the spatial distribution of adults and juveniles of sev-

eral species (e.g. Legendre et al. 1997). In the Schelde estuary too there is evidence of such a difference. For instance, in the eastern (mesohaline) part of the estuary juvenile *Cerastoderma edule* was able to settle during summer but did not survive winter (and therefore did not mature) because of low salinity at that time (Ysebaert 2000). It would therefore be useful to analyse adult and juvenile stages separately, but unfortunately data on life stages were not always available in our data set.

In summary, therefore, the patterns described by the response curves should not be interpreted as descriptions of the physiological limits of the species or of the adults in the species, but as descriptions of actual distribution patterns as a function of abiotic variables, whatever the direct or indirect dependence on these variables may be.

Quantifying the associations between the probability of occurrence of estuarine macrobenthic species and abiotic environmental variables allows us to generate predictions of distribution, which may be robust even if the mechanisms or processes are not known. Indeed, the type of pattern analysis conducted in this study does not allow any direct conclusions to be drawn on the processes that determine macrobenthic species distribution. Nevertheless, pattern analysis and modelling are critical steps in ecological research and resource management (Thrush et al. 1999). Where patterns of distribution are strongly and directly coupled to physicochemical processes, as is the case at the estuarine macro- and meso-scales, our modelling approach was capable of predicting macrobenthic species distributions with a relatively high degree of success.

We are able to predict the probability of occurrence for some species better than for others. This variability in success may have different causes. It is difficult to ascertain that all (or most) of the relevant factors for the distribution of a species have been taken into account. Statistical approaches such as that followed here depend on the ability to assemble sufficient environmental information at all sampling points. Potentially important factors related to food availability (e.g. biomass and productivity of microphytobenthos [Herman et al. 2000] and productivity of the phytoplankton [Herman et al. 1999]) have not been taken into account. Likewise, we have restricted our analyses here to single species, excluding possible strong interactions between different macrobenthic populations. The spatial resolution for most abiotic variables used was very high, but may still have been insufficient, especially at the edges of the intertidal flats. Strong gradients in height, current velocities and sediment composition may occur at these edges, and this may be a reason for the relatively high percentage of prediction failures at these edges. Moreover, intertidal flats are mobile over time, and we have imposed a fixed bathymetry and current patterns onto a biological data set gathered over a 10 yr period. From sampling practice, we know that some edges of tidal flats may move tens or even hundreds of meters in a few years. Although preliminary trend-analyses did not reveal strong evolutions of the biological communities over the past 10 yr, some trends could also have gone unnoticed and caused additional unexplained variation. Finally, our analysis has not taken into account the small-scale spatial structure of macrobenthic populations. Due to patchiness of the populations, and the size of the sampling units, a zero observation (species absent) can have quite different meanings: either the species is really absent from the zone sampled, or is immediately adjacent but missed by the sampling.

Such effects are predictably variable between species. Rare, large or very clumped populations are expected to have more 'false zeros' then abundant, small and homogeneously distributed populations. Correction of the estimation methods for these effects would require a thorough investigation of small-scale distributions of the different species, which could potentially lead to an improvement of the prediction success. Identifying patterns at various spatial scales may also provide a clue as to the kinds of processes that operate at that particular scale (Thrush et al. 1999).

The next step will be to investigate the possibility of using the models and predictions for evaluation of the effects of different management schemes (e.g. a further deepening of the shipping channel) within the Schelde estuary. This requires an evaluation of the robustness of the models to different states of the system. The most appropriate test for this robustness is to investigate the applicability of the models to other estuarine systems. Inclusion of process information (especially on the feeding habits of the macrobenthic species) and natural history information will certainly improve the quality and generality of the models by making the predictions more robust to changes in physico-chemical forcing of the system and, in the long-term, will allow the development of models describing the action and interaction of processes operating at different scales (Allen & Starr 1982, Wiens 1982, Thrush 1991, Schneider 1994, Thrush et al. 1999).

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Appendix 1.

Maximum-likelihood estimates of logistic regression parameters for species response surfaces, showing order in which environmental variables (variable^2 = quadratic term of the variable) were entered into models. Probability of occurrence is calculated as $p = e^{-x} / (1 + e^{-x})$, where x is the solution to the regression function. Parameters derived both from the model without sediment data (n = 2827 samples) and the model with sediment data (n = 1293 samples) are presented. Negative depth values, ranging from −56.4 to +2.2 m, were replaced by positive values by changing sign (value × −1) and adding 2.5 m. Temp. sal.: temporal salinity; Model sal.: model salinity; Max. ebb: Maximum ebb-current velocity; Max. flood: maximum flood-current velocity; Median: median grain size; Mud: mud content

Heteromastus filiformis

Without sediment data		With sediment data	
Intercept	−2.2298	Intercept	−7.5618
Max. flood	removed	Max. flood	−2.9286
Max. ebb^2	−0.7335	Depth	−0.2340
Temp. sal.^{2}	−0.00426	Median	−0.00552
Temp. sal.	0.1147	Model sal.	0.4851
Model sal.	0.3433	Model sal.^{2}	−0.00845
Model sal.^{2}	−0.00845	Mud	0.1073
Max. flood^2	−1.7250	Mud^2	−0.00114
Depth^2	0.00448	Max. flood^2	removed
Depth	−0.1261	Temp. sal^2	−0.0129
		Temp. sal	0.3599
		Depth^2	0.00732
		Max. ebb	7.7127
		Max. ebb^2	−4.9373

Nereis diversicolor

Without sediment data		With sediment data	
Intercept	7.3822	Intercept	9.0758
Max. flood	−1.1788	Max. ebb	−3.8073
Depth	−0.6146	Median	−0.00954
Depth^2	0.0106	Depth	−0.6606
Model sal.	−0.4199	Depth^2	0.0197
Max. ebb	−2.8955	Model sal.	−0.0878
Model sal.^{2}	0.00871	Model sal.^{2}	removed
		Mud^2	−0.00024
		Temp. sal	−0.3703
		Temp. sal^2	0.0105

Corophium volutator

Without sediment data		With sediment data	
Intercept	6.6438	Intercept	6.2743
Model sal.	−0.4245	Median	−0.0111
Max. ebb	−3.2311	Max. ebb	−3.3653
Depth	−0.4134	Model sal.	−0.1884
Depth^2	0.00755	Depth	−0.4738
Model sal.^{2}	0.00582	Depth^2	0.0145

Nepthys cirrosa

Without sediment data		With sediment data	
Intercept	−19.6625	Intercept	−13.8353
Temp. sal	0.7573	Depth	0.5568
Max. ebb	7.4088	Temp. sal.	0.8223
Temp. sal.^{2}	−0.0151	Depth^2	−0.0181
Max. ebb^2	−3.6803	Temp. sal^2	−0.0154
Model sal.	0.4195	Mud	−0.1074
Model sal.^{2}	−0.00728	Max. ebb^2	−0.8913

Cerastoderma edule

Without sediment data		With sediment data	
Intercept	−13.2667	Intercept	−11.5229
Max. flood	removed	Max. flood	−4.0737
Model sal.	0.6427	Model sal.	0.6943
Depth	−0.3871	Median^2	−0.00004
Model sal.^{2}	−0.0129	Model sal.^{2}	−0.0114
Temp. sal.	0.2972	Temp. sal	0.4338
Max. flood^2	−4.0479	Depth	−0.1868
Depth^2	0.00696	Temp. sal.^{2}	−0.0103
Max. ebb^2	−18.4287		
Max. ebb	14.7480		
Temp. sal.^{2}	−0.00503		

Macoma balthica

Without sediment data		With sediment data	
Intercept	0.4229	Intercept	0.6798
Max. flood	3.5401	Median^2	−0.00006
Depth	−0.4422	Depth	removed
Depth^2	0.00823	Model sal.	−0.3009
Max. flood^2	−5.8467	Max. flood^2	−10.5546
Max. ebb^2	−4.7585	Temp. sal^2	−0.0159
Max. ebb	3.6948	Temp. sal	0.3963
		Model sal.^{2}	0.0140
		Depth^2	−0.0980

Pygospio elegans

Without sediment data		With sediment data	
Intercept	−5.2640	Intercept	−7.5609
Max. flood	removed	Max. flood	−3.1578
Depth	−0.3914	Model sal.	0.9682
Depth^2	0.0103	Model sal.^{2}	−0.0213
Model sal.	0.6872	Median^2	−0.00006
Model sal.^{2}	−0.0156	Depth	−0.4163
Max. ebb^2	−1.0291	Depth^2	0.0125
Max. flood^2	−2.3810	Median	0.0102

Bathyporeia sp.

Without sediment data		With sediment data	
Intercept	−7.2309	Intercept	−2.6535
Depth	−0.2882	Mud	−0.0978
Temp. sal.^{2}	−0.00626	Depth	−0.4620
Temp. sal.	0.1585	Depth^2	0.0126
Max. ebb^2	1.1721	Max. ebb	4.1235
Depth^2	0.00571	Temp. sal^2	−0.0125
Model sal.	0.6689	Temp. sal	0.3857
Model sal.^{2}	−0.0169	Max. ebb^2	−1.7495

Spio sp.

Without sediment data		With sediment data	
Intercept	−16.9542	Intercept	−17.1183
Temp. sal.^{2}	removed	Temp. sal.	1.1932
Temp. sal.	0.3402	Model sal.^{2}	−0.00635
Model sal.^{2}	−0.0204	Max. flood	6.0268
Model sal.	0.7173	Max. flood^2	−2.7218
Max. ebb^2	−0.5283	Temp. sal^2	−0.0151
Max. ebb	removed	Median^2	−0.00003
Max. flood	8.0842	Mud	−0.1292
Max. flood^2	−5.1461	Mud^2	0.00146

Arenicola marina

Without sediment data		With sediment data	
Intercept	−13.4934	Intercept	−9.3460
Max. flood	−1.9627	Model sal.	0.2921
Model sal.	1.0284	Max. flood	−3.3583
Model sal.^{2}	−0.0194	Temp. sal.^{2}	−0.00260
Depth	−0.2633	Depth	1.4338
Max. ebb^2	−6.6295	Depth^2	−0.3155
Max. ebb	5.4847	Max. ebb	3.0047
Depth^2	0.00438	Median^2	−0.00007
Temp. sal.^{2}	−0.00099	Median	0.0208

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