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ScienceDirect

Estuarine, Coastal and Shelf Science xx (2007) 1–12

ESTUARINE COASTAL AND SHELF SCIENCE

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Modelling the migration opportunities of diadromous fish species along a gradient of dissolved oxygen concentration in a European tidal watershed

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Received 15 October 2006; accepted 2 March 2007

Abstract

The relationship between poor water quality and migration opportunities for fish remains poorly documented, although it is an essential research step in implementing EU water legislation. In this paper, we model the environmental constraints that control the movements of anadromous and catadromous fish populations that migrate through the tidal watershed of River Scheldt, a heavily impacted river basin in Western Europe. Local populations of sturgeon, sea lamprey, sea trout, Atlantic salmon, houting and allis shad were essentially extirpated around 1900. For remaining populations (flounder, three-spined stickleback, twaite shad, thinlip mullet, European eel and European smelt), a data driven logistic model was parameterized. The presence or absence of fish species in samples taken between 1995 and 2004 was modelled as a function of temperature, dissolved oxygen concentration, river flow and season. Probabilities to catch individuals from all diadromous species but three-spined stickleback increased as a function of the interaction between temperature and dissolved oxygen. The hypoxic zone situated in the freshwater tidal part of the estuary was an effective barrier for upstream migrating anadromous spawners since it blocked the entrance to historical spawning sites upstream. Similarly, habitat availability for catadromous fish was greatly reduced and restricted to lower brackish water parts of the estuary. The model was applied to infer preliminary dissolved oxygen criteria for diadromous fish, to make qualitative predictions about future changes in fish distribution given anticipated changes in water quality and to suggest necessary measures with respect to watershed management.

Keywords: fish migration; logistic model; dissolved oxygen; water pollution; freshwater tidal reach; anadromy; River Scheldt

1. Introduction

Worldwide, river fragmentation is primarily responsible for the decline of populations of migrating fish (Masters et al., 2006). In particular, many anadromous fish species, which must migrate to fresh water in order to reproduce, are endangered since many are no longer able to reach their natural spawning sites (Masters et al., 2006). Additionally, pollution of rivers effectively prevents upstream or downstream movements and blocks access to spawning grounds. Land use practices, habitat deterioration, or removal and exploitation of commercially interesting populations have contributed to the decline of diadromous populations.

Historically, populations of Acipenseridae, Salmonidae, Osmeridae and Clupeidae migrated into freshwater rivers along the north-eastern board of the Atlantic to spawn. Conversely, European eel *Anguilla anguilla*, as well as a number of species that are considered facultative catadromous, such as the flounder *Platichthys flesus* and the thinlip mullet

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doi:10.1016/j.ecss.2007.03.036

Please cite this article in press as: Maes, J. et al., Modelling the migration opportunities of diadromous fish species along a gradient of dissolved oxygen concentration in a European tidal watershed, Estuar. Coast. Shelf Sci. (2007), doi:10.1016/j.ecss.2007.03.036

Liza ramado, migrated from the freshwaters out to the North Atlantic to spawn. Throughout Europe, many of particularly the anadromous populations are in decline or extirpated (De Groot, 2002; Masters et al., 2006). Human impacts on species that migrate over considerable distances do not stop at borders. Hence, besides national programmes, a number of international initiatives has been established to halt the decline of anadromous fish species. The most important legal framework in Europe with respect to the protection of anadromous species is the European habitats directive 92/43/EEC, which lists the anadromous species under its annex 2 as species of community interest whose conservation requires special areas of conservation. In addition, *Acipenser* species as well as *Coregonus oxyrhynchus* are listed as annex 4 species which need strict protection, while other anadromous species are listed in annex 5 as species, whose taking in the wild and exploitation may be subject to management measures.

The status of the migrating fish fauna of the watershed of River Scheldt basin, a medium-sized lowland river basin in West Europe, is the focus of this study. The River Scheldt, with origin in France, main drainage basin in Belgium and delta in The Netherlands, is characterized by centuries of serious pollution, land claim and habitat quality deterioration. The exponent of the environmental degradation was a virtually anoxic zone during the 1970s situated just above the freshwater saltwater boundary (Van Damme et al., 2005). Since then, and due to efforts to better treat wastewaters, average dissolved oxygen (DO) in the river increased by about 1 mg L^{-1} per decade. Yet, the Scheldt basin still has important nature values and potentials, particularly for migrating fish species. The estuary has a complete salinity gradient including extensive freshwater, brackish and salt marshes to its ecosystem. Tides penetrate much further than salt in the river and influence some of the major tributaries of River Scheldt. It follows that, because of the absence of flow regulating constructions, unique opportunities exist for migratory fish populations in the watershed of River Scheldt.

At present levels of DO are increasing which has resulted in a recovery of fish populations in the river, particularly in its estuary (Maes et al., 2004, 2005; Van Damme et al., 2005). Moreover diadromous fish populations gradually increase in size. This recovery is well illustrated by the spatiotemporal distribution of the twaite shad *Alosa fallax* in the River Scheldt (Maes et al., in press). The species reoccurred in the river since 1996 and catches gradually increase in upstream direction.

The present situation and the expected improvement of migrant fish populations in the River Scheldt and its basin form the central theme of this paper. Firstly we present up to date information of the present status and distribution of the diadromous fish fauna of the tidal watershed of the River Scheldt. Next, we model water quality constraints that control the distribution and movements of adult anadromous spawners and juvenile catadromous foragers between the North Sea and upstream spawning and nursery grounds using a generalized linear model. The models are subsequently applied to infer preliminary DO criteria for diadromous fish, to make qualitative predictions of the distribution of fish given a further improvement of water quality, and to suggest necessary measures with respect to watershed management.

2. Material and methods

2.1. Study area

The River Scheldt has its origin in the north of France and discharges into the North Sea near Vlissingen (The Netherlands). It is a lowland river with a total length of 355 km and a fall of 100 m at most. The catchment area is approximately 21,000 km^2 with a population of 10 million inhabitants (Van den Bergh et al., 2005). This study focuses on the tidal part of the watershed, presented in Fig. 1. The tidal part of the river is called Western Scheldt (Westerschelde) in The Netherlands and Sea Scheldt (Zeeschelde) in Belgium. The lower estuary (Western Scheldt) is characterized by flood and ebb channels, separated by sandy or muddy intertidal areas. Due to the funnel shape of the lower estuary the maximum vertical tidal range is about 100 km upstream, in the freshwater zone (Van den Bergh et al., 2005). The tidal influence thus extends much further land inward than the freshwater-saltwater boundary (Fig. 1). As a result, an extensive freshwater region under tidal influence is present. The tidal excursion goes as far as Gent, 160 km from the river mouth, where the tide is stopped by sluices (Fig. 1). Also, the tributaries Durme, Rupel, Nete, Kleine Nete, Grote Nete, Dijle and Zenne are under tidal influence and are therefore considered as an integral part of the estuary (Fig. 1).

2.2. Fish sampling

We collected fish samples at four stations along the River Scheldt (Fig. 1) using paired fyke nets. A fyke net is essentially a fish trap consisting of a long bag net distended by hoops, into which fish can pass, without being able to return. Paired fykes nets consist of two 7.7 m fykes between which an 11 m lead net is suspended. The first hoop of each fyke is horse-shoe shaped with a basis of 120 cm and a diameter of 80 cm. Fish can be removed on the other end of the fyke where the mesh size is 8 mm. The fishing gear was placed parallel to the river border on the tidal mudflats during low water. Fish that encounter the leader net during high water are guided into the fykes. Hence, both fish movements as well as mesh size influence the selectivity of fyke nets.

A total of 112 fish samples were collected. The sampling design was spatially and temporally unbalanced, mostly as a result of annual changes in the allocation of research funding to fish monitoring. Spatially, most samples were taken at Zandvliet (51), 26 were taken at Antwerp, 25 at Temse and 10 at Hamme. Samples were taken each year between 1995 and 2004 in the period between March and October. In 2005, 7 samples were taken, two at each site except for the station at Zandvliet, and these were used to validate the statistical models.

All field work was done by trained fish biologists using a standardized working procedure to assure the quality of

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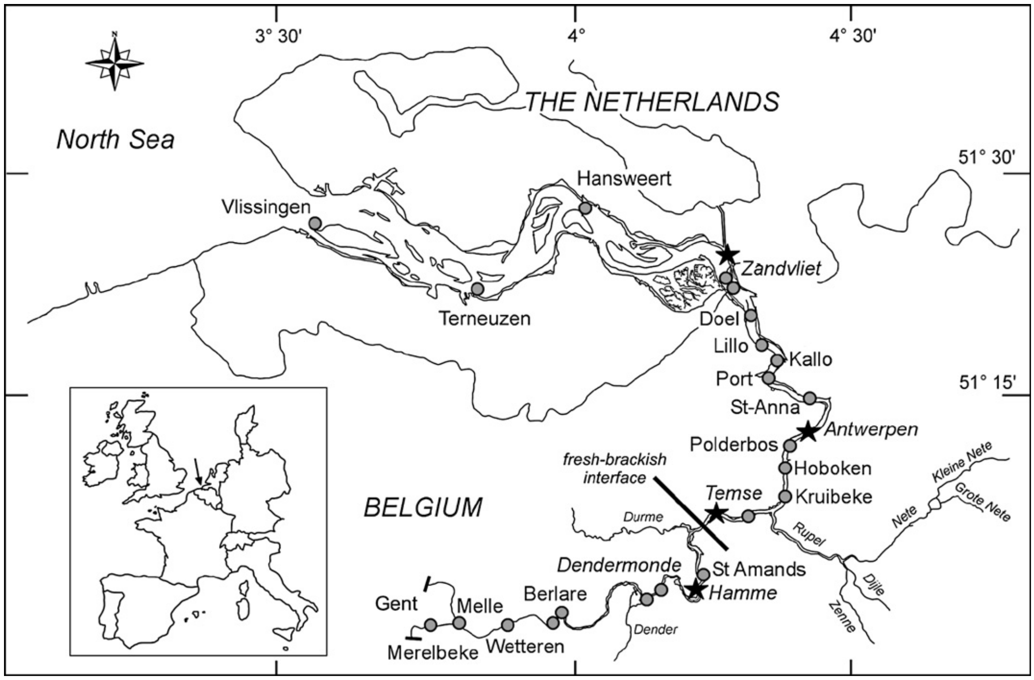

Fig. 1. Map of the tidal part of the Scheldt basin indicating the River Scheldt and tributary rivers (Rupel, Nete, Dijle, Zenne, Dender, Durme). End point of the rivers represent the tidal limit. The map shows the fish sampling stations (stars) and the water quality sampling stations (circles). A flow gauge is operated by Rijkswaterstaat at station Lillo. Water quality sites and fish sites are spatially not matched. To feed the statistical model, we used water quality data of the water quality stations that were most close to the fish sampling station.

the work. Fish captured were identified on site using a single field guide (Nijssen and De Groot, 1987), but quality assurance of the fish identifications was performed by occasional cross-examination in the laboratory, especially of small sized specimens. Fish data recorded included species-specific fish frequencies, individual total lengths (±1 mm) and wet weights (±1 g).

2.3. Environmental data

Temperature, dissolved oxygen and freshwater flow were used as predictor variables in the statistic models as well as to infer spatio-temporal distribution plots of fish species. Water temperature (°C) and oxygen concentration (mg L^{-1}), both measured at the surface of the river, were derived from two different water quality databases. Data for the Western Scheldt, situated in The Netherlands, was derived from Waterbase, a publicly available internet resource of the Dutch traffic and waterways ministry (Rijkswaterstaat, 2006). Data for the Sea Scheldt, situated in Belgium, was downloaded from the Flemish Environmental Agency internet site (Flemish Environmental Agency, 2006). Freshwater flow rate data ($m^3\ s^{-1}$) was obtained from the Dutch Rijkswaterstaat database (Rijkswaterstaat, 2006), based on a flow gauge situated in Lillo (Fig. 1). Flow and oxygen concentrations were measured monthly. Temperature was measured daily in The Netherlands and monthly in Belgium. Temperature and DO data was acquired for three sampling stations in the Western Scheldt and for 19 stations in the Sea Scheldt, while a flow gauge, operated by Rijkswaterstaat, is situated in Belgium. As a result, data of temperature and DO vary both monthly and spatially while for flow, only monthly data are available for the entire river gradient. All stations are shown in Fig. 1. Both agencies assure the quality of their data and QA documents can be obtained upon request.

It is important to note that fish samples and water quality samples were not matched in time and space. But, in order to construct statistical models, we used environmental data from stations that were sampled both spatially and temporally as close as possible to the fish sampling stations. The distance between fish sampling stations and water sampling stations averaged 2.5 km and varied between 0.9 km for the fish sampling station at Hamme and 3.3 km for the station at Antwerp. These distances are considerably lower than the tidal excursion which is between 10 and 15 km.

2.4. Statistical models

The presence or absence of anadromous spawners and catadromous foragers was modelled using logistic regression (Hosmer and Lemeshow, 2000). Only species that occurred with sufficient frequency in the samples were retained in this analysis (Table 1). In the model, a binary response variable (presence/absence) was expressed as a linear combination of a set of candidate predictor variables through a logit link function. The set of continuous predictor variables included dissolved oxygen concentration, temperature, flow, the product between temperature and dissolved oxygen and the square of temperature. Temperature was entered as a second order polynomial model in order to account for a bell shaped response.

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Table 1
Frequencies of diadromous fish species at the different sampling stations, according to Fig. 1. Species were subdivided into two groups: common species for which regression models were produced and rare species, which sporadically returned in the fishing gear. A total of 112 samples, collected between 1995 and 2004 was broken down over 4 sampling sites. In 2005, seven samples were collected and used as validation of the regression models. These frequencies are presented in parentheses

Species	No. of fish samples							
	Zandvliet $n = 51$		Antwerp $n = 26$		Temse $n = 25$		Hamme $n = 10$	
	Present	Absent	Present	Absent	Present	Absent	Present	Absent
Species with regression models								
European eel	42 (0)	9 (1)	17 (2)	9 (0)	4 (2)	21 (0)	1 (2)	9 (0)
European smelt	36 (1)	15 (0)	0 (0)	26 (2)	0 (0)	25 (2)	0 (0)	10 (2)
Flounder	51 (1)	0 (0)	8 (2)	18 (0)	2 (0)	23 (2)	0 (0)	10 (0)
Thinlip mullet	25 (0)	26 (1)	1 (0)	25 (2)	0 (0)	25 (2)	0 (0)	10 (2)
Three-spined stickleback	13 (0)	38 (1)	9 (1)	17 (1)	2 (1)	23 (1)	3 (1)	7 (1)
Twaite shad	22 (0)	29 (1)	1 (0)	25 (2)	0 (0)	25 (2)	0 (0)	10 (2)
Species without regression models								
Atlantic salmon	1	50	0	26	0	25	0	10
Brown trout	6	45	0	26	0	25	0	10
River lamprey	2	49	2	24	0	25	0	10
Sea lamprey	1	50	0	26	0	25	0	10

Possible interactions between DO and temperature were accounted for by considering the product between these two variables. Further, one categorical predictor variable was entered in the model accounting for seasonal effects. Statistically, this variable was encoded in three binary variables assuming a value of 1 for samples taken in the designated season and zero otherwise. The complete model design is:

$$\begin{aligned}\text{logit } P &= \log_e[P/(1-P)] \\ &= [\beta_0 + \beta_{1J}(\text{season})] + \beta_2 \times \text{DO} + \beta_3 \times T + \beta_4 \times F \\ &\quad + \beta_5 \times T^2 + \beta_6 \times T \times \text{DO} + \varepsilon \end{aligned} \tag{1}$$

where P is the probability to capture a species in a fish trap over a 24 h period; DO represents the dissolved oxygen concentration (mg L^{-1}), F is the monthly averaged river flow ($m^3\ s^{-1}$) and T is the ambient surface water temperature (°C). ε is the error term of the model. The model's intercept is given by the term $\beta_0 + \beta_{1J}$(season), where season represents the three binary variables spring, summer and fall each with slope β_{1J}. As a result, the categorical predictors either increase or decrease the model intercept with β_{1J} but the different slopes $\beta_{2,\ldots,6}$ of the continuous predictor variables remain unaffected. The intercept β_0 represents the model for winter samples, for which the three binary variables are zero.

Initially, full models for each species were fitted using the maximum likelihood statistic that is available in STATISTICA 7 (Statsoft). Next, we used the procedure of best subsets in order to fit all possible models ($N = 63$). From this list, we selected the model with the lowest Akaike's information criterion (AIC) (Johnson and Omland, 2004). This minimal adequate model was used in further model applications.

Model goodness-of-fit was evaluated using the model deviance. The deviance is defined as $-2(L_M - L_S)$ where L_M denotes the maximized log-likelihood value for the model of interest, and L_S is the log-likelihood for the saturated model (a saturated model has n parameters and fits n observations perfectly). Under the null hypothesis that the logistic model is true, the deviance is χ^2-distributed. Inference for single parameters is based on the Wald statistic. The null hypothesis is that a single parameter β_i equals 0.

Contrary to the ordinary least squares statistic, the maximum likelihood statistic does not result in a typical R^2 value. Alternatively, the model performance was evaluated by assessing the percentage of correctly classified occurrences and non-occurrences. Hereto, we used $P = 0.5$ as cut-off value. The final models were additionally evaluated by comparing the model predictions with the presence and absence data of the considered fish species during the field campaign of 2005. Again, we used $P = 0.5$ as cut-off value, i.e. predicted probabilities >0.5 were considered as present.

2.5. Model applications

We used the minimum adequate logistic regression models in three different applications. Firstly, we used the regressions in order to predict the occurrence of anadromous and catadromous species along the entire river gradient. Probability values P can be calculated based on eq. (2), where e is the natural exponent:

$$P = e^{\text{logit}(P)} / \left[1 + e^{\text{logit}(P)}\right] \tag{2}$$

Monthly water quality data of 22 stations (Fig. 1) were entered in eq. (2) in order to produce species specific spatially and temporally explicit probability plots. For simplicity, we used only environmental data for the year 2003 to demonstrate the applicability of the model. The contour plots were used to better visualize the migration opportunities of diadromous fish in River Scheldt.

In a second application, we tested the effect of several environmental scenarios with respect to increased oxygen

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concentration in the middle section of the estuary (between km 80 and km 100, Fig. 1). For this river section, we modified the DO input data series of 2003 by assuming either an increase in DO by 10% or by assuming minimum dissolved oxygen concentrations ($5\ \mathrm{mg\ L^{-1}}$ and $6\ \mathrm{mg\ L^{-1}}$). A threshold of $5\ \mathrm{mg\ L^{-1}}$ corresponds to a legally established DO minimum for surface waters in Flanders (Belgium) (VLAREM II, 1995).

In a recent report, the European Commission concludes that the establishment of DO criteria for fish, amongst others, is a prior research theme in order to fully implement the European water framework directive (Heiskanen and Solimini, 2005). Therefore the final application of the statistical model is an attempt to infer preliminary DO criteria for migrating fish. Such minimum requirements with respect to dissolved oxygen for fish have yet to be established in Flanders, an autonomous region of Belgium competent for environmental policies (VLAREM II, 1995). In this paper we applied the models in order to calculate the minimum required concentration of dissolved oxygen to yield a capture probability of at least 50%. This calculation was performed for each species separately assuming temperature and freshwater flow conditions averaged over the season of maximum occurrence in the samples for the period 1994–2005.

3. Results

3.1. General fish catch statistics

A total of 112 fish samples was taken between 1995 and 2004 at four different sampling stations in the tidal Scheldt capturing 10 diadromous fish species (Table 1). Four anadromous species occurred irregularly in the fyke nets: two lamprey species (river lamprey *Lampetra fluviatilis* and sea lamprey *Petromyzon marinus*) and two salmonids (Atlantic salmon *Salmo salar* and sea-run brown trout *Salmo trutta*). These species were not further considered in the statistical models and applications. Thinlip mullet, European smelt (*Osmerus eperlanus*) and twaite shad returned more frequently in the samples but their distribution was limited to the brackish reaches of the estuary downstream the freshwater saltwater front situated near Antwerp (Fig. 1, Table 1). Flounder, eel and stickleback (*Gasterosteus aculeatus*) moved further upstream and the latter two species occurred throughout the study area (Table 1).

3.2. Logistic regression models

Logistic regression with the presence or absence of species in fyke nets as dependent variable and ambient oxygen concentration, temperature, river flow and season as independent predictor variables yielded statistically significant models (Table 2). Summary statistics for the environmental variables that were used as predictors in the regression models are given in Table 3. In all cases, the minimal adequate models had a lower AIC than the full models (Table 2). Full models had a higher percentage of correct classifications when field data was compared with model predictions, but in general the

Table 2
Logistic regression models. For each species, we present the model diagnostics, the explicit description of the minimal adequate model and the final regression parameters of the minimal adequate model. Model diagnostics are Akaike's information criterion for the full model with all predictor variables (AIC_{FM}) and for the minimal adequate model (AIC_{MM}). For the minimal models, we present the model deviance (Dev_{MM}) together with the Chi-squared statistic ($\chi^2_{P=0.05}$) for the appropriate degrees of freedom (df). The full model has 103 degrees of freedom. Recall that significant models have a Deviance < χ^2. A second set of diagnostics are the percentage of correct classifications of presence and absence and the percentage of correctly predicted occurrences of the validation data set. Final model parameters (with standard error) are presented at the bottom of the table

Species	AIC_{FM}	AIC_{MM}	Dev_{MM} ($\chi^2_{P=0.05}$, df)	Correct absent	Correct present	% Correct validation	Minimal model
Flounder	114.4	106.4	102.4 (135.4, 110)	80.4%	82.0%	71.5%	logit $P = \beta_0 + \beta_6 \times T \times \mathrm{DO}$
Stickleback	112.5	106.7	96.7 (132.1, 107)	87.1%	48.1%	85.7%	logit $P = [\beta_0 + \beta_{1,f}(\mathrm{season})] + \beta_5 \times T^2$
Thinlip mullet	117.2	112.1	108.1 (135.4, 110)	91.9%	3.8%	100.0%	logit $P = \beta_0 + \beta_6 \times T \times \mathrm{DO}$
Twaite shad	80.8	77.3	71.3 (134.4, 109)	95.5%	52.2%	100.0%	logit $P = \beta_0 + \beta_4 \times F + \beta_6 \times T \times \mathrm{DO}$
Eel	150.0	142.6	132.6 (134.4, 109)	60.4%	70.3%	57.1%	logit $P = \beta_0 + \beta_2 \times \mathrm{DO} + \beta_6 \times T \times \mathrm{DO}$
Smelt	118.3	109.7	103.7 (134.4, 109)	86.8%	58.3%	100.0%	logit $P = \beta_0 + \beta_5 \times T^2 + \beta_6 \times T \times \mathrm{DO}$

Model parameters

	β_0	β_1 Spring	β_1 Summer	β_1 Fall	β_2	β_3	β_4	β_5	β_6
Flounder	−2.688 (0.556)								0.049 (0.009)
Stickleback	0.339 (0.693)	0.803 (0.441)	0.609 (0.755)	−0.243 (0.511)				−0.008 (0.003)	
Thinlip mullet	−2.749 (0.554)								0.022 (0.006)
Twaite shad	−3.178 (1.195)						−0.013 (0.007)		0.040 (0.010)
Eel	−0.541 (0.461)				−0.269 (0.132)				0.032 (0.009)
Smelt	−2.517 (0.614)							−0.006 (0.002)	0.045 (0.010)

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Table 3
Summary statistics. Average (standard deviation) of the continuous predictor variables used in the logistic regression analysis. Sampling stations are presented in Fig. 1

	Sampling station			
	Zandvliet	Antwerp	Temse	Hamme
No. of samples	51	26	25	10
Temperature (°C)	16.1 (4.6)	15.2 (5.9)	14.8 (5.9)	14.0 (5.6)
Dissolved oxygen (mg L^{-1})	5.8 (1.7)	2.7 (1.9)	2.8 (2.0)	5.4 (2.9)
River flow ($m^3 s^{-1}$)	110.5 (60.0)	132.3 (70.4)	134.8 (71.0)	108.8 (55.8)

Wald statistics for individual parameters estimated when fitting a full model through the data were not significant. In contrast, minimal adequate models were statistically significant (deviance < Chi-squared for a given degrees of freedom at a significance level of $P = 0.05$) and yielded significant regression coefficients as well.

All species but three-spined stickleback showed a significantly increasing response to the interaction of DO and temperature (Table 2). It follows that the capture probability in the fyke nets increased when the product of DO and temperature increased. For European eel this interaction was negatively corrected for increasing DO concentrations (Table 2). For smelt, the square of temperature negatively influenced the interaction effect (Table 2). The probability to capture twaite shad decreased significantly when freshwater flow increased (Table 2). The model for stickleback was different from the other models in that it was the only for which the categorical predictor (season) remained in the model as explaining variable (Table 2). This fixed seasonal pattern was negatively influenced by the square of temperature, suggesting that stickleback avoided the summer warm waters of the estuary.

In general, the reduced models performed well in that the percentage of correctly classified occurrences and non-occurrences was relatively high (Table 2). This is illustrated in Fig. 2 which plots the field observations against modelled probabilities along a temperature and DO gradient. The model for thinlip mullet is the only exception with 3.8% of the presence correctly classified (Table 2). We used the models to predict the presence or absence of the considered species in fyke net observations made in the year 2005, outside the modelled period. Again, models correctly classified between 57% and 100% of the cases (Table 2).

3.3. Model applications

3.3.1. Spatio temporal probability plots

The minimum adequate logistic regression models were used in three different applications. Firstly, we plotted capture probability distributions of the different species for the tidal part of River Scheldt adopting environmental conditions for the year 2003 (Fig. 3). Probabilities to capture fish in 24 h samples based on fyke nets are presented in a two-dimensional plane where distance to sea represents a spatial axis, and time in months a temporal axis. In agreement with the results of the model fitting procedure, spatial patterns dominate above seasonal effects due to the presence of spatial gradients of temperature and, particularly, of dissolved oxygen concentration in the estuary. The probability plots for almost all species suggest that capture probabilities are predicted to reach a minimum in the oxygen poor zone in the middle estuary while modelled probabilities are higher in the lower and upper parts of the estuary. For stickleback, a seasonal pattern emerged with maximum predicted probabilities throughout the estuary during winter. The predicted distribution patterns based on logistic regressions with environmental variables as predictors clearly show how the low DO zone in the middle part of the tidal Scheldt may interfere with the migration opportunities for fish that necessarily move between the ocean and freshwater habitats in order to successfully complete their life history.

3.3.2. Environmental scenarios

In a second application, we focused on an area with poor water quality between km 80 and km 100 where untreated waste water of the Brussels capital region reaches the Scheldt. We assumed three different scenarios in terms of DO relative to the 2003 situation: a 10% increase and an increase to at least 5 mg L^{-1} and 6 mg L^{-1}, respectively (Fig. 4). Since DO as predictor variable was retained in the all models but one, mostly in the interaction term with temperature, it follows that the probability to capture fish in nets was predicted to increase if the concentration of DO increased (Fig. 4). This was especially evident for twaite shad and smelt. The model suggests that if water quality meets the baseline requirements, which are legally adopted by the Flemish Region, fish captures of all species are expected to increase substantially. Only for stickleback, we were unable to relate an increment in DO to increased probability of occurrence.

3.3.3. DO criteria

The logistic models were finally applied to infer minimum river DO concentrations at which the probability to capture a species was at least 50% during the season of peak migration (Table 4). Under these assumptions, thinlip mullet seemed to be the most sensitive species with a 50% probability of occurrence in the nets when DO reaches 6.2 mg L^{-1} given a temperature of 20.5 °C. Smelt and twaite shad needed DO concentrations of at least >5 mg L^{-1} while there is a 50% probability to catch flounder if DO was at least 2.7 mg L^{-1}. Eel was the most tolerant species. DO was absent as variable in the stickleback regression model, so no value was derived for this species.

4. Discussion

Historical research by Van Damme et al. (1994) and by Vrielynck et al. (2003) suggests that at the beginning of the 20th century, ten anadromous and three catadromous species frequented the Scheldt basin, albeit with different population sizes (De Selys-Longchamps, 1842, 1867; Bottemanne, 1884; Poll, 1945). Sturgeon *Acipenser sturio* and allis shad

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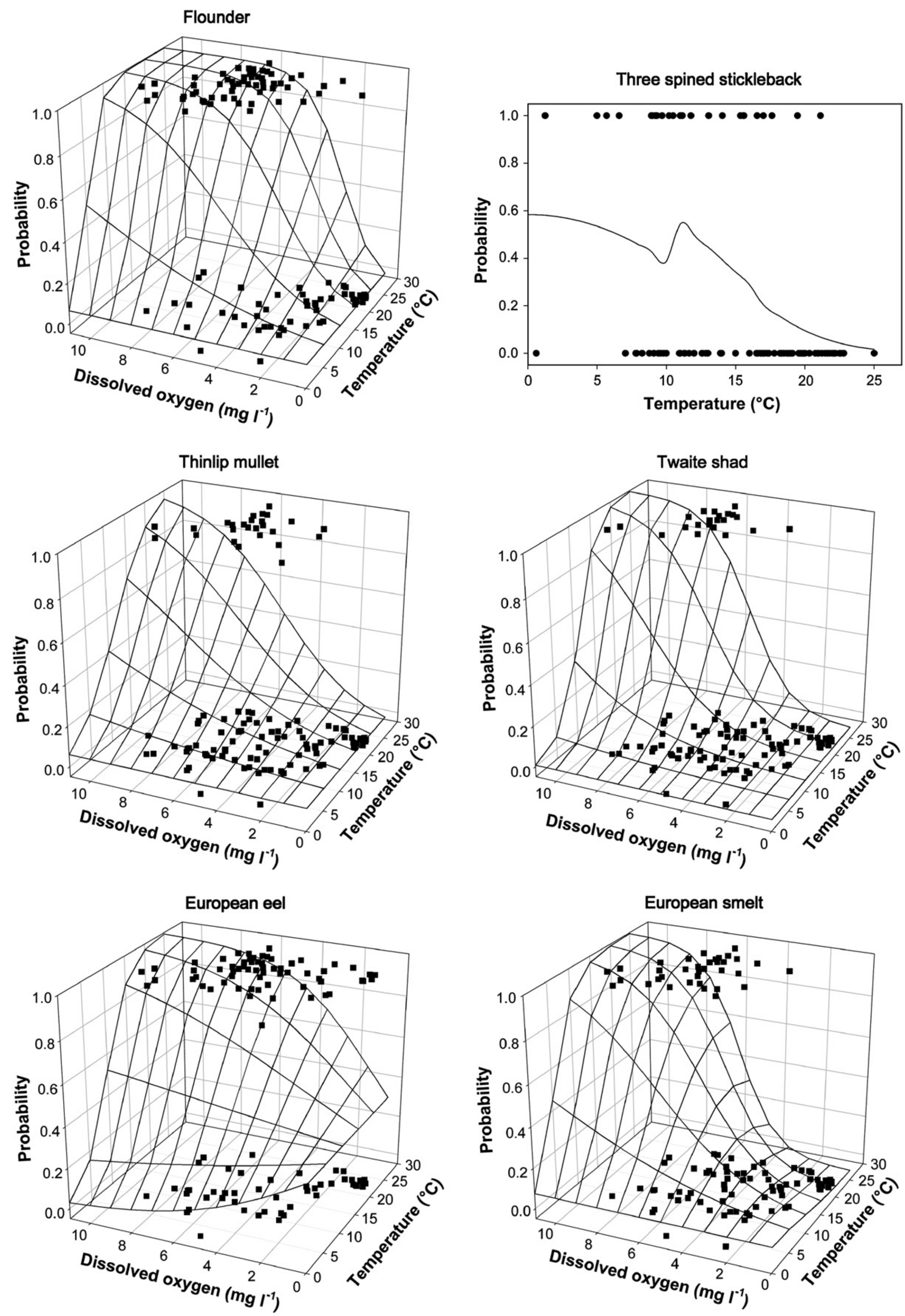

Fig. 2. Modelled (gridded surface) versus observed (dots) fish occurrence of six species as a function of temperature and dissolved oxygen. Fish occurrence is the presence or absence of fish captured in fyke nets at four sampling sites in River Scheldt between 1995 and 2004 ($N = 112$). The modelled surface is based on the minimal adequate models based on equation 1 using the fitted parameters as in Table 2. We assumed average river flow conditions (Table 3). DO was not retained as explaining predictor variable in the stickleback model so only the binary response to temperature was given.

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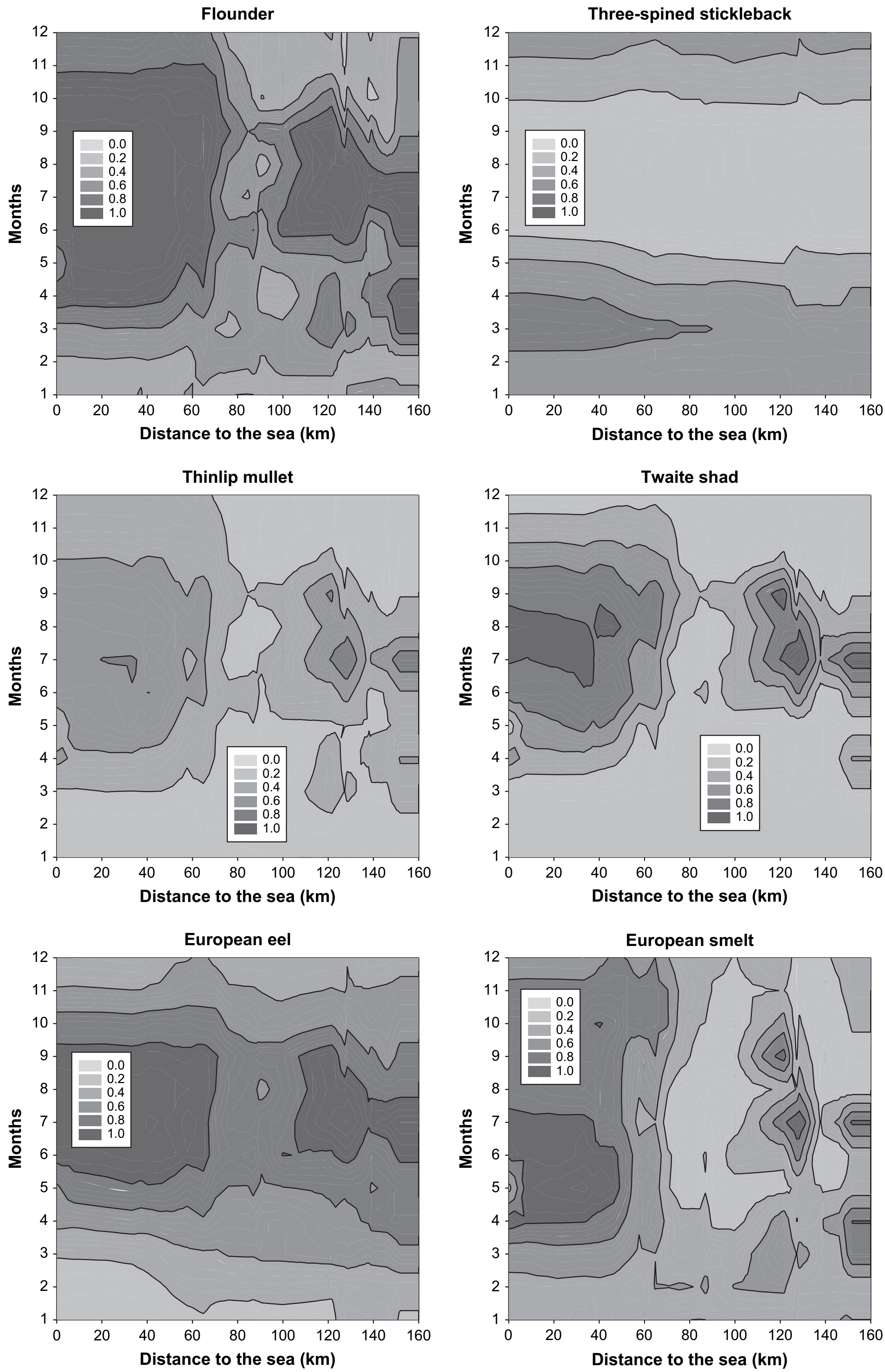

Fig. 3. Modelled spatially and temporally explicit capture probabilities of six fish species occurring in the tidal Scheldt basin. Contours define space-time areas with similar catch probability. The spatial axis represents the distance to the sea (river mouth at 0 km and most upstream area at 160 km). The temporal axis represents the months of the year (Jan = 1, …, Dec = 12). Probabilities vary between 0 and 1. Probabilities were calculated using minimal adequate logistic regression models according to equation 1 using parameters as in Table 2.

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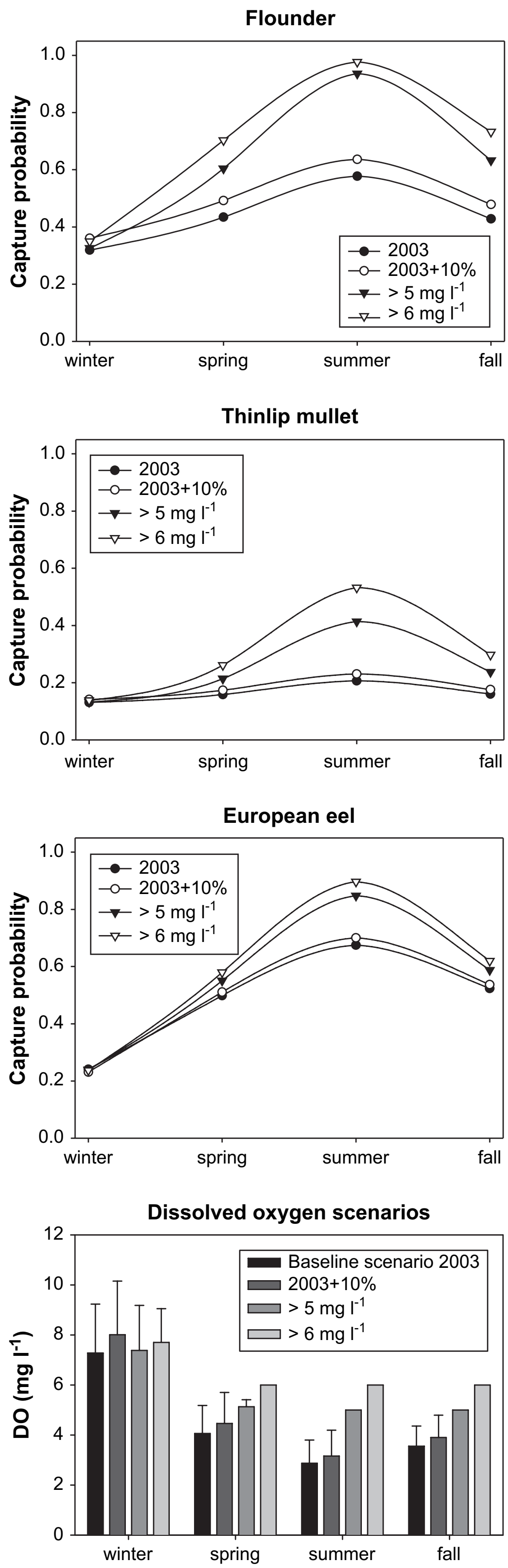

Fig. 4. Environmental scenarios. If oxygen concentration of the tidal River Scheldt between km 80 and km 100 is increased by 10% or if a minimum DO concentration of 5 or 6 mg L^{-1} is imposed, capture probabilities for most diadromous species increase. Probabilities are presented as seasonal averages based on monthly calculations. The barplot compares the average seasonal DO concentration for the baseline scenario based on values for 2003 with three other scenarios. The error bars are standard deviations.

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Table 4
Preliminary criteria of dissolved oxygen for migrating fish species. These criteria ($DO_{P=0.5}$) correspond with a capture probability of 50% assuming that the other environmental predictor variables (temperature and river flow) can be substituted by their average value during the season of maximum occurrence. DO was not retained in the model for three-spined stickleback, so no concentration was defined for this species

Species	Season of maximum occurrence	Seasonal temperature (°C)	Seasonal river flow ($m^3 s^{-1}$)	$DO_{P=0.5}$ ($mg L^{-1}$)
European eel	Summer	20.5		1.3
European smelt	Fall	17.0		5.5
Flounder	Summer	20.5		2.7
Thinlip mullet	Summer	20.5		6.2
Three-spined stickleback	Spring	11.6		
Twaite shad	Summer	20.5	77.6	5.1

Alosa alosa were once probably quite abundant, but extirpated during the first two decennia of the 1900s, mainly as a result of increased water pollution. Populations of sea lamprey, Atlantic salmon, sea trout and houting *Coregonus oxyrhynchus* were probably constrained by available spawning substrates in the river basin and hence, had relatively small population sizes compared to the neighbouring populations of the rivers Rhine and Meuse (De Groot, 2002). Individuals of these first three species sporadically returned in fyke net catches between 1995 and 2004. Other populations of diadromous species persisted, although some of them are now confined to the lower reaches of the estuary that are situated downstream of the freshwater saltwater front. This is the case for thinlip mullet, European smelt and twaite shad. Adults of the latter two species occur in the lower estuary but seem unable to reach upstream spawning sites. Thinlip mullet as well as flounder are catadromous but catadromy is in neither species obligate. They both spawn offshore and young of the year move upstream to estuaries and, if possible, above the tidal limit. River lamprey, European eel and three-spined stickleback were the only diadromous species with a confirmed closed life cycle in the basin (Van Damme et al., 1994; Maes et al., 1998, 2005). Sticklebacks probably form a metapopulation with migrating forms from the *trachurus* type and resident forms, but they were not separated in the field. Numbers of river lamprey were highly underestimated by the fishing method used in this study since there is evidence that migrating individuals moved through the subtidal navigation channel. Sampling at a power station cooling water inlet (Maes et al., 2005) confirmed the presence of upstream moving adult spawners and seaward moving juveniles.

The occurrence and spatiotemporal distribution of diadromous fish species in the Scheldt basin were explained in this paper as a function of three environmental variables. In particular, the interaction between dissolved oxygen and temperature proved to be a statistically significant predictor of fish capture probabilities. The interpretation is that under summer warm conditions in the watershed, dissolved oxygen is a limiting factor. In particular, hypoxic events in the tidal freshwater part of the estuary just above the freshwater saltwater boundary prevented upstream migration movements of both anadromous spawners and catadromous young of the year on their way to either spawning substrates or nursery areas. As shown by our assessment of DO criteria, tolerances were species specific. Eel, stickleback, and flounder were the most tolerant species and their distribution shows that they are able to move through the zone of low DO. Twaite shad, smelt and mullet were much more sensitive to low DO concentrations and did not penetrate as far upstream. Clearly, this conclusion should be interpreted within the context of the possible limitations of this study. Observational studies like this one do not prove causality. In this study, we essentially made a statistical correlation between two datasets that were spatially and temporally unmatched. This approach is, however, not necessarily flawed. The water quality measurements that were used in this study were derived from a consistent water quality monitoring network using standardized sampling and analysis protocols. The data cover sufficiently the study area in order to capture the prevailing spatial and seasonal trends. This would have been impossible by sampling and analysing water only during fishing occasions. Vice versa, it can be argued that the fish fauna of a sample is a reflection of the average water quality at one site, so that fish community data is summarized in biotic indices to evaluate water quality (Deegan et al., 1997; Hughes et al., 2002; Harrison and Whitfield, 2004; Breine et al., 2007). Therefore we claim that, by using environmental data from a database that is maintained by a governmental agency, the present statistical models can be applied to derive the spatially and temporally explicit probability plots as presented in this study, to validate the models against future water quality data or to make new predictions within the watershed.

In an application of the logistic regression models we inferred DO concentrations for which the probability of the presence of diadromous fish in diurnal fyke net samples is 50% and we proposed this data as preliminary DO criteria for fish in watershed. Clearly, this approach lacks an experimental basis. Under the assumption that DO criteria apply during periods of peak migration, minimum values vary between 1.3 and 6.2 $mg L^{-1}$ while the average was 4.2 $mg L^{-1}$. In Fig. 4, we showed that scenarios with a dissolved oxygen concentration of at least 5 and 6 $mg L^{-1}$, respectively, substantially increased the capture probability of fish occurrence relative to the situation as observed in 2003. Based on these results, we suggest a minimum dissolved oxygen concentration of 5 $mg L^{-1}$ throughout the tidal part of the river basin for migratory fish. This minimum corresponds to the regional (Flemish) baseline water quality requirement. More field evidence on DO tolerances in estuarine fishes is presented by Möller and Scholz (1991), who used stow nets to sample fish along a DO gradient during summer and fall in the Elbe estuary (Germany). Fish were found to concentrate downstream the area of hypoxia. Species specific DO preferences were between 1.2 and 3 $mg L^{-1}$ for eel, between 3 and 4 $mg L^{-1}$ for flounder, between 4 and 5 $mg L^{-1}$ for 0 group shad and >5 $mg L^{-1}$ for smelt. Turnpenny et al. (2004) estimated lethality and tolerances of estuarine fishes to low DO concentrations in the Thames estuary using an experimental set-up in the laboratory and in the field. So, other than in this study, avoidance of low DO by fish has been directly tested. Based on the overall test results, a minimum DO standard of 1.5 mg L^{-1} was suggested for the tidal Thames. A number of species among which the smelt seemed unexpectedly tolerant to low concentrations of DO. This value is clearly lower than the 5 mg L^{-1} suggested by this study based on empirical field data. Although experimental trials can be interpreted in a straightforward manner, empirical field data have the advantage that possible fitness consequences are included. Diadromous fish species possibly tolerate low DO concentrations but may skip spawning when environmental conditions nearby the reproductive habitats are unfavourable for eggs or early life history stages. Such behaviour is common in many fishes (Jørgensen et al., 2006).

4.1. Applications for watershed management

Ecological rehabilitation of the diadromous fish fauna requires applicable knowledge that can be used to identify limiting factors for population recovery. Here we demonstrated that it is possible to make acceptable predictions about the future spatiotemporal distribution of migrant fishes with relatively limited information. The models that were used yield testable predictions. Empirical models of the probability of presence or absence of species rather than of fish abundance warrant straightforward interpretation and avoid inclusion of density dependent effects or recruitment variability. Predictor variables used in the models represent true ecological recourses and data of dissolved oxygen and temperature is commonly, and often freely, available in databanks.

A first essential step for river management that derives from this study is to increase the concentrations of DO in the freshwater tidal estuary of the watershed. The model results suggested that an increment of DO to a baseline concentration of 5 mg L^{-1} considerably increases the opportunity for diadromous fish species to pass the middle part of the estuary. At present, this area still receives the untreated municipal waste water of the Brussels capital region through the contributories Zenne and Rupel (Van Damme et al., 2005). A 1.5 million inhabitant equivalent waste water treatment plant of Brussels is under construction. Therefore, it is believed that once the waste load of this major source of pollution is treated, the water quality of the tidal Scheldt where the river Rupel discharges into the Scheldt will improve consistently (Van Damme et al., 2005) and hence, the basin wide distribution of migratory fish.

Decreasing chemical and biological oxygen demand by the ongoing wastewater treatment programs seems evident but is not the only solution. Estuaries are natural collectors of organic waste and the transformation of ammonia and particulate and dissolved organic matter depletes the available DO. In estuaries, aeration of water is an important source of oxygen (Van Den Bergh et al., 2005). Aeration is more efficient in areas with a high surface to volume ratio such as marshes and flood control areas. Restoration of these habitats, although generally not essential in the life history of diadromous species, is likely a crucial measure to support fish migration. In anticipation of a population recovery, a survey of suitable spawning habitats and substrate is another requirement to support successful restoration.

Migrant fish are considered as important indicators of ecosystem recovery, especially in our society, which has hardly a collective memory of migrating fish species. The return of species that were once so abundant that they were used as fertilizer would be an important milestone after decades of decline and an environmental success.

Acknowledgements

This paper benefited from several fish monitoring projects funded by VIBNA (Association of Industrial Companies of North Antwerp), AMINAL Afdeling Bos en Groen (Flemish Environmental Administration), the Institute of Forestry and Game Management. This paper is a contribution to the European Interreg IIIb North Sea project Harbasins, aiming at harmonizing European river basin management.

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Please cite this article in press as: Maes, J. et al., Modelling the migration opportunities of diadromous fish species along a gradient of dissolved oxygen concentration in a European tidal watershed, Estuar. Coast. Shelf Sci. (2007), doi:10.1016/j.ecss.2007.03.036