FISH AND DIADROMY IN EUROPE

Poor water quality constrains the distribution and movements of twaite shad *Alosa fallax fallax* (Lacépède, 1803) in the watershed of river Scheldt

Joachim Maes · Maarten Stevens · Jan Breine

Abstract Worldwide, river fragmentation is primarily responsible for the decline of populations of migrating fish. In particular, anadromous fish species, which necessarily migrate to fresh water to reproduce, are endangered since many are no longer able to reach their natural spawning sites. In addition, pollution of rivers effectively prevents upstream or downstream movements and blocks access to spawning grounds. This article investigates how poor water quality interferes with the life history cycle of twaite shad *Alosa fallax fallax* (Lacépède, 1803), an anadromous clupeid fish, in the watershed of River Scheldt, a heavily impacted environment in West Europe. We used two models based on known ecological and environmental information to explain past and present twaite shad distribution within the watershed and to make inferences about a future population recovery and juvenile habitat value. We demonstrated that historical spawning areas satisfy water quality conditions necessary to support spawning and successful development of early life history stages of the twaite shad. However, poor water quality conditions just upstream the freshwater–saltwater boundary still act as an effective migration barrier for upstream movement. As a consequence, spawning grounds are inaccessible and the population is dominated by seasonal adults occurring in the lower estuarine part of the watershed. This article provides testable and diagnostic information to the watershed management in that it identifies habitat and water quality requirements needed to support the expected recovery of an endangered anadromous fish population.

Keywords Fish migration · Twaite shad · Logistic model · Bioenergetics model · Water pollution · Freshwater tidal reach · Anadromy · River Scheldt

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Introduction

Predicting changes in individual traits, population sizes, community interactions or ecosystem functioning is a challenging scientific task. Too often,

ecological theory fails at application (Hansson, 2003). Large simulation models with many variables and parameters may come closer but are hard to develop, hard to communicate and hard to understand (Grimm, 1999; Hansson, 2003). In a local context, biological inference from simple observations may still offer superior advice (Hansson, 2003). Empirical models may be more robust in predicting possible changes, especially when they describe changes along ecological gradients.

In this article, we used the latter strategy to make predictions about the future recovery of a migrating fish population in a heavily impacted and modified watershed. We summarized the known ecological and environmental information into simple models in order to predict migration opportunities and juvenile habitat quality. In particular, we focussed on the distribution of the twaite shad *Alosa fallax fallax* (Lacépède, 1803) in the basin of River Scheldt, a medium-sized West European lowland river with origin in France, main drainage area in Belgium and river delta in the Netherlands. The recent history of River Scheldt is characterized by a century of serious pollution and habitat deterioration. The major cause of environmental degradation of River Scheldt and its major tributaries can be linked to the high population density within the watershed combined with a historical lack of proper land use planning, especially in Flanders, the northern part of Belgium. Fragmentation of the landscape by roads and infrastructure constrains river channel dynamics. Scattered housing and the large amount of impervious cover limit the efficiency of wastewater treatment facilities. Livestock wastes accumulate in soils or run off into surface waters. As a result, exceptionally high nutrient loads reach the main river, especially in periods with increased rainfall (Struyf et al., 2004). The direct consequence is a hypoxic zone in the freshwater tidal area of the Scheldt. Dissolved oxygen levels reached an absolute minimum in the mid-1970s when the freshwater area of the river was virtually anoxic. Since then, and due to efforts to better treat wastewaters, average dissolved oxygen in the river increased by about 1 mg l^{-1} per decade (Van Damme et al., 1995).

Although seriously impacted, the river ecosystem still has important nature values. The estuary has a complete salinity gradient and includes extensive freshwater, brackish and salt marshes to its ecosystem. Tides penetrate as far as 160 km land inward and influence some of the major contributories of river Scheldt. It follows that, due to the absence of flow-regulating constructions, there are unique opportunities for migratory fish populations in the basin, all of which are now under threat or locally extinct. Sturgeon (*Acipenser sturio* L.), Atlantic salmon (*Salmo salar* L.) and allis shad (*Alosa alosa* L.) all disappeared by the end of the 1930s, while populations of twaite shad, flounder (*Platichthys flesus* L.) and smelt (*Osmerus eperlanus* L.) are confined to the brackish and marine parts of the estuary. Only the river lamprey (*Lampetra fluviatilis* L.) seemed to have persisted, as well as populations of more tolerant species such as eel (*Anguilla anguilla* L.) and three-spined stickleback (*Gasterosteus aculeatus* L.) (Van Damme et al., 1994).

Here, we focused on the ecological status of the twaite shad in the tidal part of the watershed of River Scheldt. Twaite shad is an iteroparous, anadromous fish species (Aprahamian, 1988). At maturity, adult shad gather in estuaries in April and May and move upstream to the head of estuaries or above to spawn from May to July (Aprahamian & Aprahamian, 2001; Oesmann & Thiel, 2001; Maitland & Hatton-Ellis, 2003). Once the eggs hatch nearby the spawning sites, the young fish quickly move downstream in the current to the quieter waters of the upper estuary, where they start to feed and grow (Aprahamian & Aprahamian, 2001; Gerkens & Thiel, 2001; Maitland & Hatton-Ellis, 2003). The juveniles are present in the estuary from July until they migrate seaward in the autumn (Aprahamian & Aprahamian, 2001). In the Elbe estuary, adult shad spawn in the tidal freshwater region, so that the spawning area and nursery for the juveniles spatially overlap. Historical evidence (Vrielynck et al., 2003) suggests that this was also the case for the shad population of the Scheldt basin.

In this article, we addressed the question as to why the life cycle of twaite shad in the watershed of the Scheldt is interrupted. In particular, we statistically investigated how poor water quality in the middle part of the River Scheldt between the lower estuary and the historical spawning grounds hinders the spawning run of mature shad. In addition, we modelled the future opportunities for growth of early juveniles in the estuary provided that migration

would end in successful spawning above historical spawning grounds in the freshwater tidal reaches of the watershed. We used field data of water quality and fish catches to construct an empirical model that described the presence or absence of adult fish as a function of environmental variation. Additionally, we modelled habitat quality for young-of-the-year fish using a spatially explicit model of growth rate potential. Using the models and assuming a further rise of, particularly, dissolved oxygen concentrations in the watershed, we illustrate how the models can be applied to provide future spatio-temporal distribution patterns. With this information, local watershed managers can anticipate to expected changes by identifying, delineating and protecting essential fish habitats.

Materials and methods

Study area

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, which is presented in Fig. 1. The lower estuary (Westerschelde) is characterized by flood and ebb channels, separated by sandy or muddy intertidals. 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 does 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). The historical spawning sites, where twaite shad used to spawn until the 1930s above sandbanks (Vrielynck et al., 2003) are situated within the freshwater tidal reach of the watershed (Fig. 1).

Sampling

Between 1995 and 2004, we collected fish samples along the River Scheldt using pairs of fyke nets. Fish sampling sites are presented on a map in Fig. 1. 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. At each sampling site a pair of two fyke nets was deployed on the low water mark and emptied after 24 h. The fishing gear consisted of two 7.7 m fykes between which an 11-m lead net was suspended. The first hoop of each fyke is horseshoe 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 rising or falling tides, fish that encounter the leader net are guided into the fykes. Hence, both fish movements as well as mesh size influence the selectivity of fyke nets.

All fieldwork was done by trained fish biologists using a standardized protocol. Between 1995 and 2004 fishing occurred for 48 h at each site between March and October, yielding a total of 114 samples. Fish captured were identified on site using a single field guide (Nijssen & 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).

Environmental data that was included in the different models was obtained from different sources. Water temperature (°C) was measured coincident with the fish sampling. Dissolved oxygen (mg l^{-1}) data was provided by Van Damme et al. (2005) for the period 1995–2000 and downloaded from the Flemish Environmental Agency internet database for other months of the study period (www.vmm.be). Freshwater flow rate data (m^3 s^{-1}) was obtained from the Dutch Rijkswaterstaat database (www.waterbase.nl).

Models

We used two models to predict the basin wide distribution patterns of twaite shad and juvenile habitat value, respectively. Presence or absence of adult shad was modelled using logistic regression
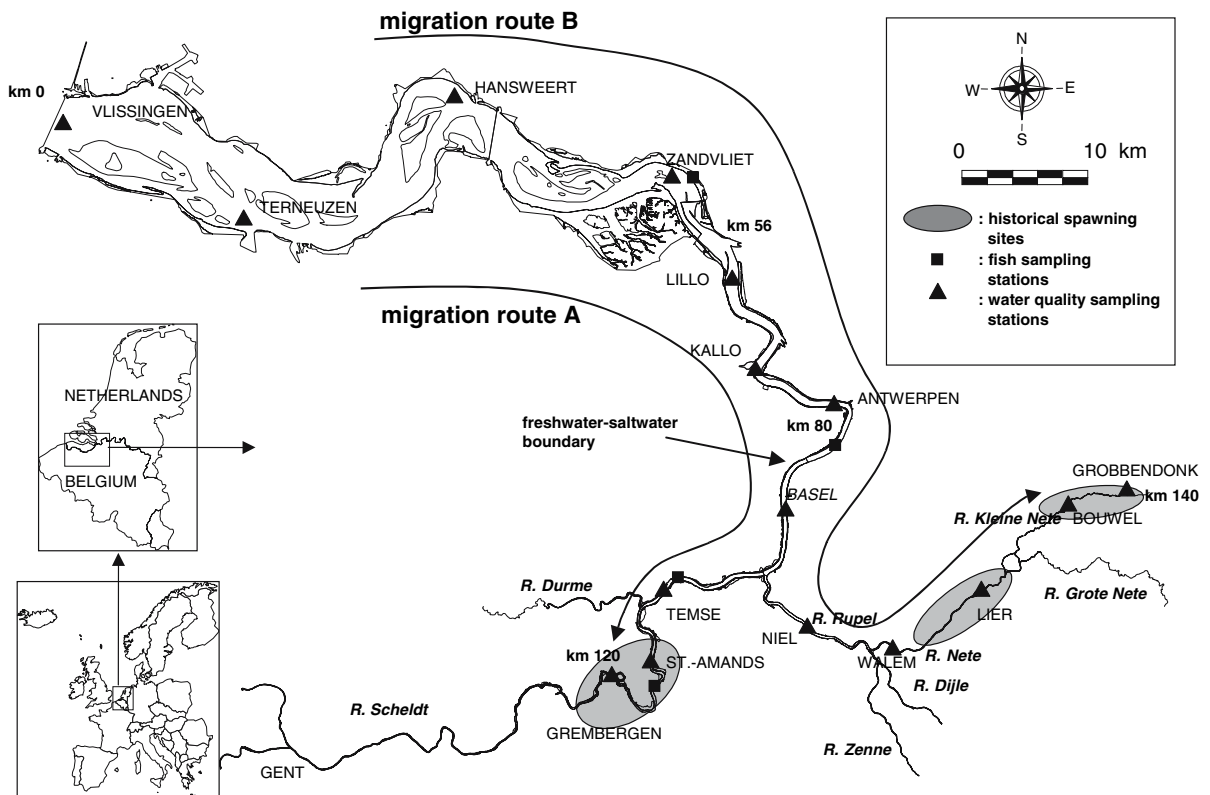
Fig. 1 Map of the tidal part of the Scheldt basin indicating the River Scheldt and tributary rivers. End point of the rivers represent the tidal limit. The map shows the fish sampling stations (squares) and the water quality sampling stations (triangles). Historical spawning sites of twaite shad are indicated as well based on a review of Vrielynck et al. (2003). Km indications measure the distance to the river mouth

based on field samples. In the model, a binary response variable (presence/absence) was expressed as a linear combination of freshwater flow, temperature and dissolved oxygen concentration through a logit link function. A priori, we expected that the response of twaite shad to oxygen concentration was increasing, following a logistic S-shaped function. In estuarine fish species, the avoidance of low oxygen concentration differs, as some species exhibit an avoidance threshold, while others exhibit a graded response (Wannamaker & Rice, 2000). A graded response is best modelled using linear regression, but this technique is less appropriate to model binary data such as the presence or absence of species. Stier & Crance (1985) constructed habitat suitability models for *Alosa sapidissima* (Wilson, 1811) and assumed a threshold response for dissolved oxygen following a study by Chittenden (1973). We expected an opposite relationship with freshwater

flow, following observations that the upstream movement behaviour of American shad decreases at stream velocities above 1 m s^{-1} (Stier & Crance, 1985). Similarly, Acolas et al. (2006) observed that migration activity in allis shad increased while temperature increased and water flow decreased, and slowed when temperature decreased. The response to temperature was assumed to follow a bell shaped curve which can be approximated by a second order polynomial, which results in a temperature optimum. The model design is:

$$\text{logit } p = \log_e [p/(1-p)] = b_0 + b_1 \times [O_2]$$
$$+ b_2 \times Q + b_3 \times T + b_4 \times T^2 + \varepsilon \qquad (1)$$

where p is the probability to capture adult twaite shad in a fish fyke over a 24 h period; $[O_2]$ represents the dissolved oxygen concentration (mg l^{-1}), Q represents the average monthly freshwater flow or debit

(m^3 s^{-1}) and T is the ambient temperature (°C). ε is the error term. The regression parameters b_i were estimated using the maximum likelihood procedure. Model goodness of fit was evaluated using the model deviance. It is defined as $-2 \times (L_M - L_S)$ 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. Under the null hypothesis that the logistic model is true, the deviance is χ^2-distributed. The null hypothesis of $b_i = 0$ was tested using the Wald statistic. The fishing gear that was used captures pelagic species at low efficiency, hence we consider the predictions as lower limits.

Since adult shad is, at present, not able to spawn, we assessed the possible habitat value of the estuary for juveniles using a bioenergetic growth model. The assumption is that growth rate potential can be used as a criterion to evaluate habitat suitability (Brandt et al., 1992). In spatially explicit habitat models, the growth rate potential describes the amount of growth achievable by a size and species-specific predator when placed in a predetermined habitat characterised by a particular suite of environmental conditions (Roy et al., 2004). Several authors have used growth rates potential of habitats to describe the relative quality of habitats and environments for fish populations in lakes, rivers and estuaries (Brandt et al., 1992; Luo et al., 2001; Höök et al., 2003). We used the basic Wisconsin bioenergetics-modelling framework (described by Kitchell et al., 1977) to develop a model of juvenile twaite shad. Bioenergetics models balance the flow of energy through an individual fish over consumption, growth, and energy loss (respiration, specific dynamic action, egestion and excretion). We refer to Hanson et al. (1997) for a complete description of bioenergetic models for fish. We used parameters of the congeneric *Alosa pseudoharengus* (Wilson, 1811) (Stewart & Binkowski, 1986) and of herring *Clupea harengus* L. (Rudstam, 1988) to model the bioenergetics of twaite shad (Table 1). Following Luo et al. (2001), oxygen dependence of maximum consumption was modelled as a hypothetical function based on the general concept of fish physiological processes in response to stress (Bartell, 1990):

$$f(\mathrm{DO}) = \left[1 + \exp \left(4.77 - 1.59 \times [\mathrm{O_2}] \right)^{-1} \right] \qquad (2)$$

This function limits consumption by 50% at a DO of 3 mg l^{-1} (Stier & Crance, 1985).

Environmental scenarios

Models were used to predict spatially explicit probabilities of past and present distributions and to assess juvenile habitat value. Past conditions referred to the year 1990. Present conditions refer to the situation as observed in 2003. We also made predictions based for 2010 assuming that observed historical trends in dissolved oxygen concentration between 1989 and the present will continue into the future. In each case, we focussed on two possible migration routes, which adult shad should follow in order to reach historical spawning sites (Fig. 1). The first route (route A) leads shad to spawning grounds situated in the tidal, freshwater part of river Scheldt at 120 km of the river mouth. The second route (route B) leads shad to an historical spawning area in a smaller tributary river (Kleine Nete), situated 140 km upstream. We estimated future environmental conditions using a statistical model, assuming that temperature and river flow in 2010 can be approximated using monthly averages for the period 1993–2004 and that DO in 2010 can be approximated using monthly averages for the period 1989–2004 superimposed on a long-term linear trend. Predicted oxygen concentrations in 2010 satisfied the following equation:

$$[\mathrm{O_2}] = \alpha \times \mathrm{Trend} + \beta_j \times \mathrm{Month}_j + \varepsilon \qquad (3)$$

Equation 3 is a general linear model with the oxygen concentration $[\mathrm{O_2}]$ as dependent variable, with slope α and intercept $\beta_j \times \mathrm{Month}_j$. Trend as continuous predictor variable, which measures the number of days that passed since 1 January 1989 divided by 30. The categorical variable Month_j takes 12 different codes (January, …, December) and was encoded into 12 binary variables. These variables assume a value of one for samples taken in the designated month, zero otherwise. As a result, categorical predictors either increase or decrease the model intercept but the slope α remains unaffected. It follows that, under the null hypothesis of a non-significant slope α, oxygen concentrations are estimated as monthly averages. ε is the error term, which is normally distributed around zero. Models were constructed for 16 fixed-sampling stations situated in the watershed (Fig. 1).

Table 1 Parameters used in the twaite shad bioenergetics model

Symbol	Description	Value	Unit
P-value	Proportion of maximum consumption	0.27	Dimensionless
Ca	Intercept for maximum consumption	0.8464	$g\ g^{-1}\ d^{-1}$
Cb	Exponent for maximum consumption	−0.3	Dimensionless
f(T)	Temperature dependence of maximum consumption		Dimensionless
	$f(T) = f(K1,\ K2,\ K3,\ K4,\ T1,\ T2,\ T3,\ T4)$		
f(O$_2$)	Oxygen dependence of maximum consumption		Dimensionless
	see text for description		
K1	Proportion of maximum consumption at T1	0.17	Dimensionless
K2	Proportion of maximum consumption at T2	0.98	Dimensionless
K3	Proportion of maximum consumption at T3	0.98	Dimensionless
K4	Proportion of maximum consumption at T4	0.01	Dimensionless
T1	Temperature for K1 in f(T)	3	°C
T2	Temperature for K2 in f(T)	27	°C
T3	Temperature for K3 in f(T)	27	°C
T4	Temperature for K4 in f(T)	32	°C
Ra	Intercept for maximum standard respiration	0.00367	$g\ g^{-1}\ d^{-1}$
Rb	Exponent for maximum standard respiration	−0.2152	Dimensionless
RQ	Slope for temperature dependence	0.0548	Dimensionless
	of standard respiration		
RTO	Coefficient for swimming speed dependence	0.03	$s\ cm^{-1}$
	on metabolism		
RTL	Cut-off temperature at which the activity relationship changes	9	°C
RK1	Intercept for swimming speed above the cut-off temperature	15	$cm\ s^{-1}$
RK4	Mass dependence coefficient for swimming speed	0.13	Dimensionless
	at all water temperatures		
ACT	Intercept for a 1 g fish at 0°C of the relationship for swimming	3.9	$cm\ s^{-1}$
	speed versus mass at water temperatures less than RTL		
BACT	Temperature dependence coefficient of swimming speed	0.149	$°C^{-1}$
	at temperatures below RTL		
SDA	Specific dynamic action coefficient	0.175	Dimensionless
Fa	Proportion of consumed food egested	0.16	Dimensionless
Ua	Proportion of assimilated food excreted	0.1	Dimensionless

Model symbols and conventions correspond with the Wisconsin Bioenergetics Model (Hanson et al., 1997). The model describes growth during the first year for all weights of twaite shad between 0.25 g and 5 g. Prey (zooplankton) and predator energy density were set at 2,580 J g^{-1} (Hanson et al., 1997) and 5,233 J g^{-1} (Stewart and Binkowski, 1986), respectively

Results

Distribution of twaite shad in the Scheldt basin

Regular sampling of fish populations in the estuary of River Scheldt using fyke nets started in 1995. Adult twaite shad first appeared in samples in 1996. Since then, annual landings, initially rose until 1999 but fluctuated strongly during the remainder of the study period (Fig. 2A). Pooling monthly data shows that

shad abundance generally peaked in June and August. Twaite shad left the estuary before November to winter in the North Sea (Fig. 2B). Total shad body length averaged 38 cm (Fig. 2C). The 0-group shad (<10 cm) were never caught. The spatial distribution of twaite shad appeared to be limited to the saline and brackish parts of the estuary. So far, no shad have been captured in the part of the Scheldt basin upstream the city of Antwerp. Apparently, adult shad were unable to reach upstream historical spawning
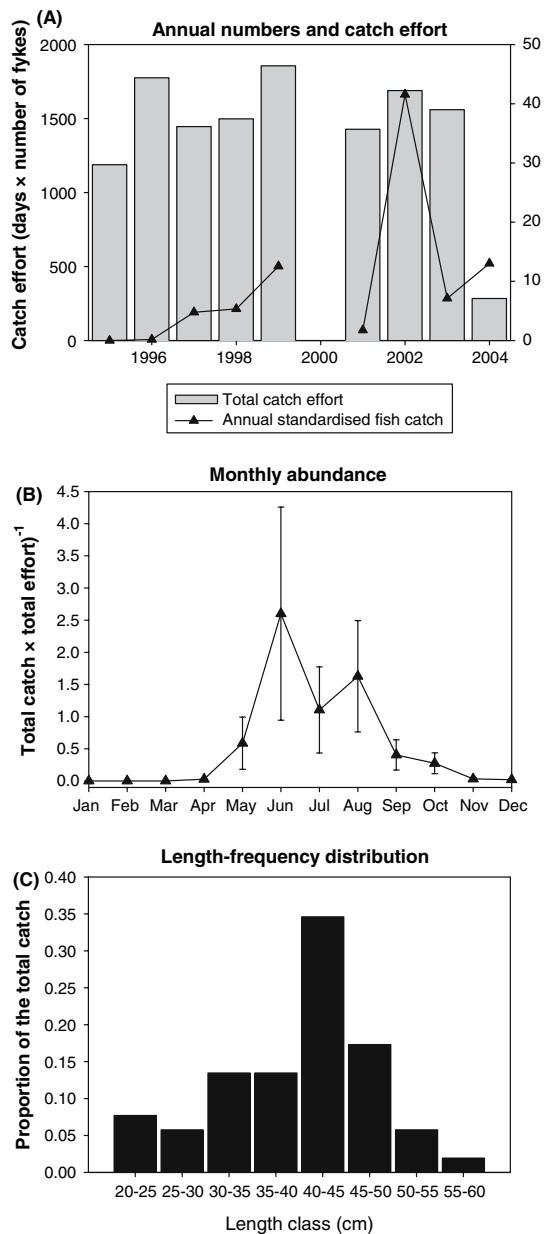
Fig. 2 Abundance patterns and population structure of twaite shad in the Scheldt estuary based on fyke net data taken between 1995 and 2004 at a permanent fish monitoring station in the Scheldt estuary (km 58, Fig. 1). (**A**) Total annual catch effort (number of fishing days × number of fyke nets) and standardised annual catch (numbers of shad per 100 fishing days using 1 fyke net). (**B**) Average monthly distribution of adult shad (error bars are standard deviations). (**C**) Length frequency distribution of shad over 5 cm length classes ($N = 1260$)

sites which are situated in the tidal freshwater part of the River Scheldt and in the tributaries of the Scheldt (River Nete and River Kleine Nete, Fig. 1).

Logistic model

Logistic regression with the presence of twaite shad in fyke nets as dependent variable and ambient oxygen concentration, freshwater flow and temperature as independent predictor variables yielded a statistically significant model. The model deviance was 68.7, with 108 degrees of freedom. Since $\chi^2_{p = 0.05}$ is 85.7, we accept the logistic regression with equation logit $(p) = -10.85 + 0.77 \times [O_2] - 0.014 \times Q + 0.67 \times T - 0.014 \times T^2 + \varepsilon$. Increasing dissolved oxygen significantly affected the probability to capture adult shad in fyke nets, given temperature and flow (Wald test: $df = 108$; $W = 16.5$; $P < 0.001$, Fig. 3). Shad were negatively affected by high river flow rates, given temperature and DO (Wald test: $df = 108$; $W = 4.01$; $P < 0.05$, Fig. 3). Essentially, this variable does not affect the probability of capturing shad in fyke nets since freshwater flow rates rarely exceed 400 m³ s⁻¹. The likelihood for shad to occur in fyke nets increased with temperature, reflecting their seasonal occurrence between April and October (Fig. 3).
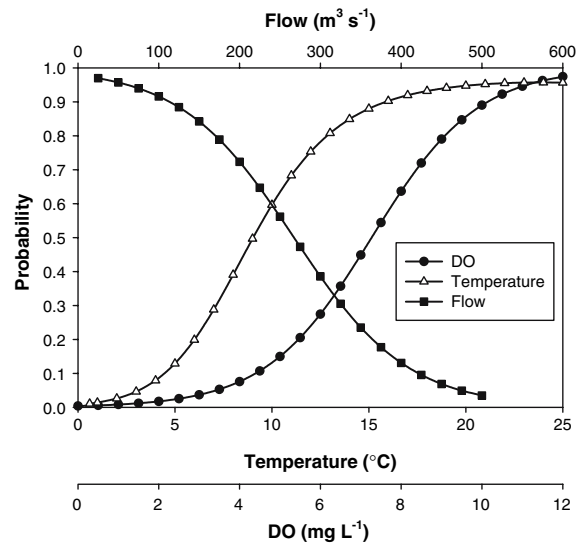

Fig. 3 Logistic response of twaite shad occurrence as a function of temperature, dissolved oxygen (DO) and monthly river flow. Probabilities represent the statistical likelihood to capture twaite shad in 24 h fyke net samples. Probabilities are calculated using Eq. 1 and are presented along three univariate axes, given constant values for the two other environmental variables (DO = 10 mg l⁻¹; temperature = 15.4°C, river flow 121 m³ s⁻¹)

Spatio-temporal distribution patterns of twaite shad in the Scheldt basin

The logistic model was used to plot basin-wide probability distributions of adult twaite shad occurrence under past, present and future environmental conditions. DO concentrations for 2010 were predicted using linear regression models for 16 stations situated in the tidal watershed of the Scheldt (Fig. 1). Model parameters and diagnostics of the regression models are presented in Table 2. All models were significant at $P < 0.001$ and the explained variance varied between 36% for station Lier to 75% for station Terneuzen. Five stations in the watershed, of which three in River Scheldt and two in River Kleine Nete, displayed a slope that was not significantly different from zero (Table 2). DO predictions for these stations calculated for the year 2010 are therefore approximated as monthly averages. The regression slopes for other stations were significantly positive (Table 2), evidencing an increasing DO trend in the watershed. As an example, we presented the historical and predicted time series of DO for two water quality stations. In Fig. 4, we regressed the DO time series against the number of days since 1 January 1989 using Eq. 3. At Basel, a station in the River Scheldt nearby the freshwater–saltwater boundary (Fig. 1), DO displays a significantly positive trend (see slope α, Table 2). Hence DO predictions for 2010 are based on historical monthly averages superimposed on an increasing long-term trend. At station Grobbendonk, situated in River Kleine Nete (Fig. 1) at the limit of the tidal range in the Scheldt basin, the trend in DO has a non-significant slope (slope α, Table 2), so predictions for 2010 are estimated using monthly means for the period 1989–2005. Figure 5 summarizes the spatial trends in DO by presenting the annually averaged DO concentrations as a function of distance to the river mouth for the two possible migration routes. Data for 1990 and 2003 is based on field measurements, while DO predictions for 2010 are based on the general linear model. Between 1990 and 2003, the annual average DO concentration clearly increased in the river part upstream km 40 and DO conditions are expected to improve by 2010.

Environmental variables (temperature, DO and river flow) were used as input to make inferences about the spatial and temporal distribution of shad in the basin. Probabilities to capture shad 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 (Fig. 6). Superimposed on these contour plots, we indicated the spatio-temporal spawning window, which corresponds to the presumed geographical position of the spawning areas along the spatial axis and the possible spawning period along the temporal axis. In general, habitat suitability of adult twaite shad in the basin was predicted to increase with time. In 1990, poor DO conditions, especially in the middle part of the river, confined the distribution of twaite shad to the lower estuary (km 0–60). Capture probabilities in more upstream areas along migration route A, were zero (Fig. 6). The spawning areas situated in River Kleine Nete (migration route B) already satisfied water quality requirements but again, a zone of hypoxia between km 60 and km 100 was unsuitable for twaite shad and possibly prevented movements between the upstream river parts upstream km 100 and the lower estuary downstream of km 60.

In 2003, the situation improved relative to 1990 and model results suggest that the spatio-temporal distribution of available twaite shad habitat in the basin expanded, particularly along migration route A (Fig. 6). Conditions at historical spawning grounds probably allowed spawning but poor water quality in the middle estuary (km 80–km 100) was predicted to block upstream movements. Again, twaite shad were unable to reach historical spawning sites, although these sites satisfy to boundary conditions for shad presence.

The entire river gradient between the ocean and freshwater spawning sites is predicted to become a suitable habitat for twaite shad by the year 2010 (Fig. 6). DO in the middle estuary (at about km 100) is expected to increase (Fig. 5), creating a time window during which the probability to pass this part of the river increases.

Juvenile habitat value

We used the observed and predicted environmental data for the three years considered in order to assess growth rate potential for young-of-the-year twaite shad. These simulations are based on a bioenergetic model that was parameterized for juvenile shad. We

Table 2 Regression model coefficients and diagnostics of a general linear regression model which predicts the concentration of dissolved oxygen for 16 water quality sampling stations in the Scheldt basin according to Eq. 3

Sampling station	Distance to the river mouth (km)	F	DF	R^2	α	β_1 Jan	β_2 Feb	β_3 Mar	β_4 Apr	β_5 May	β_6 Jun	β_7 Jul	β_8 Aug	β_9 Sep	β_{10} Oct	β_{11} Nov	β_{12} Dec
Vlissingen	0	30.2	186	0.64	0	10.37	10.24	10.17	10.39	9.95	8.39	7.71	7.48	7.14	7.78	8.80	9.03
Terneuzen	21.5	36.8	129	0.75	0	10.52	10.22	10.03	9.85	9.41	7.99	7.20	7.08	7.04	7.75	8.76	8.78
Hansweert	37.3	37.0	180	0.69	0	10.89	10.43	9.96	9.88	9.49	8.45	7.67	7.42	7.37	8.05	9.02	9.07
Zandvliet	57.5	7.4	100	0.41	0.010	7.10	6.49	5.63	4.32	3.52	3.30	4.03	3.38	4.33	4.64	4.61	4.70
Lillo	64.8	10.0	104	0.48	0.014	5.76	6.12	4.39	3.00	1.92	2.32	2.80	2.88	3.37	3.12	3.14	3.57
Kallo	70.3	10.9	103	0.51	0.015	5.21	4.55	3.61	2.12	1.17	1.41	1.69	1.88	1.77	2.06	2.20	2.53
Antwerpen	76.1	17.0	152	0.54	0.018	3.30	3.12	2.39	0.99	0.28	0.68	0.54	0.51	0.62	0.68	0.68	1.27
Basel	90.5	22.6	177	0.58	0.019	3.56	3.20	2.35	0.65	0.37	-0.16	0.32	-0.51	-0.46	-0.34	0.56	0.91
Temse	99.8	10.4	89	0.53	0.008	6.32	6.47	5.06	3.06	1.78	1.36	1.69	1.94	1.91	1.77	1.83	3.05
St.-Amands	110.7	11.5	133	0.46	0.016	4.19	4.82	4.43	1.87	0.97	0.51	0.68	0.71	0.56	0.41	1.03	1.86
Grembergen	121.6	26.3	154	0.65	0.026	3.93	3.67	3.34	2.76	0.75	0.50	0.96	1.00	0.88	0.86	1.30	1.89
Niel	96.0	17.0	148	0.55	0.017	2.68	3.80	2.39	0.71	-0.02	-0.17	-0.53	0.29	-0.22	-0.39	0.70	0.91
Walem	106.9	10.9	170	0.39	0.008	7.54	6.39	5.87	5.23	3.62	2.59	2.46	2.76	2.61	2.62	4.83	4.30
Lier	115.6	5.0	73	0.36	0.001	8.82	7.33	8.57	6.83	6.70	6.43	5.69	5.29	5.09	6.31	7.83	6.94
Bouwel	129.7	5.9	91	0.37	0	12.27	10.73	11.10	8.70	8.37	7.80	7.84	7.88	8.19	9.44	10.19	9.37
Grobbendonk	140.0	13.3	226	0.38	0	10.16	9.44	9.35	8.77	7.87	7.31	6.75	7.01	7.01	8.16	8.94	8.37

Sampling stations refer to the nearest city and are situated at different distances (km) to the mouth of the river (Fig. 1). All models were significant ($P < 0.001$) as evaluated using an F test. DF refers to the degrees of freedom; R^2 presents the explained variance by each model. Regression slopes (α) different from zero were significant ($P < 0.05$), slopes equal to zero were not significant. Model intercepts (β_j) differ for each month and can be interpreted as the concentration of dissolved oxygen if the variable 'trend' in Eq. 3 is equal to zero
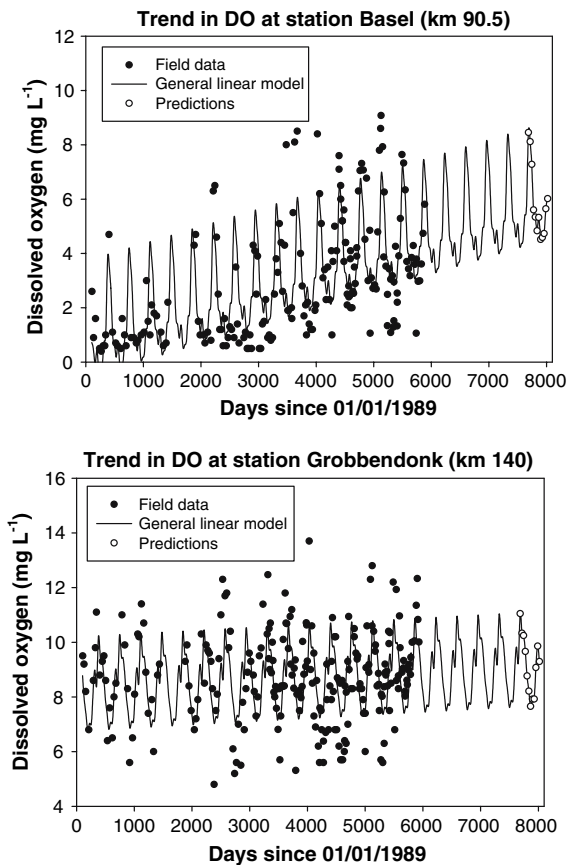
Fig. 4 Observed field data (black dots) and modelled trend of dissolved oxygen (DO) at two water quality stations in the Scheldt watershed (Basel and Grobbendonk) since 01/01/1989. The trendline is based on a general linear regression model according to Eq. 3. At station Basel, DO increased significantly with time (see α, Table 2) while at station Grobbendonk, the trend in DO has a non-significant slope (α, Table 2). The model was used to project DO concentrations for the year 2010 (white dots)

Fig. 5 Past (1990), present (2003) and predicted (2010) annual mean concentration of dissolved oxygen (DO) along two possible migration routes (route A, route B, see Fig. 1) as a function of distance to the sea. The data for 1990 and 2003 is based on DO water samples at 16 stations in the Scheldt basin (Fig. 1). Predicted values for the year 2010 were calculated using a general linear model (GLM) given in Eq. 3

assumed young shad with total body weights of 0.5 and 1.5 g, respectively. Spatial changes of juvenile growth rates are illustrated in Fig. 7. The calculations were made for the entire estuary including the tidal freshwater part which extents to Gent along route A and to Grobbendonk along route B (Fig. 1).

Similar spatial patterns for the two considered body weights emerged but the scales differed since both consumption and resting metabolic rate scale with body weight. The spatial distribution of habitat offering optimal growth rates was predicted to increase over the years. In the lower estuary (<40 km) where water is fully saturated with oxygen, differences in mean growth rates reflected differences

in mean annual temperatures. Slower growth rates in 2003 predicted for this part of the estuary were produced by above-average summer temperatures following the heat wave in Europe.

The opportunity for growth of young shad gradually decreased in upstream direction as a result of deteriorated DO conditions relative to the downstream part of the watershed. Nearby the historical spawning sites in the upstream parts in the upstream tributary Kleine Nete along migration route B, environmental conditions permitted positive growth rates for the three years that were included in the simulation. Habitat quality nearby spawning sites in the tidal freshwater reach of river Scheldt (Fig. 7, route A) was low in 1990 but is expected to increase

by 2010 as a result of the expected increase in DO concentration.

Discussion

Two important conclusions derived from this study. First, historical spawning sites in the Scheldt basin already satisfy water quality conditions necessary for spawning and successful development of early life history stages of twaite shad. However, available habitat still showed a bimodal distribution along the river gradient. Poor water quality conditions just upstream the freshwater–saltwater boundary still acted as an effective migration barrier for both upstream and downstream movements. A second conclusion is that there is a reasonable possibility that the twaite shad population recovers by the end of this decade. These conclusions are based on a number of assumptions with respect to twaite shad life history, habitat utilization and expected environmental recovery. We consider these assumptions before discussing model applications.

Model assumptions

In this article, we used water temperature, river flow and DO as spatio-temporal input in order to make predictions of juvenile and adult-habitat distribution within the watershed. These variables represent key ecological resources for the twaite shad population. Temperature directly or indirectly controls physiological rates, hatching success (Maitland & Hatton-Ellis, 2003), juvenile growth rate (Aprahamian, 1988), year class strength (Aprahamian & Aprahamian, 2001), juvenile seaward migration (Limburg, 1996), adult upstream movements (Aprahamian, 1988). More generally, temperature also relates to natural mortality of teleost fishes (Pauly, 1982) as well as to prey abundance. DO influences the behaviour of twaite shad through physiological tolerances. Twaite shad is reported as sensitive to pollution, but few data appear to be available (Maitland & Hatton-Ellis, 2003). The modelled logistic response to dissolved oxygen reported in this article suggests that adult shad become seriously stressed at DO less than 3 mg l^{-1}, a concentration at which the capture probability is less than 10%. This parallels the situation in the Elbe

estuary (Germany) where twaite shad were absent in fish samples taken at sites where DO felt below 3 mg l^{-1} (Möller & Scholz, 1991). Stier & Crance (1985) used 5 mg l^{-1} DO as threshold level for adult American shad *Alosa sapidissima*. It is unclear whether the relationship between low DO and twaite shad occurrence is causal. Eggs and larvae do not tolerate poor oxygen conditions, so there is a clear fitness consequence when adults take the risk to continue upstream migration and face low DO concentrations. A similar conclusion may be drawn to explain the negative relationship between increasing river flow and shad presence. As appears to be the case with other migratory species (Maitland, 2003), high flows are likely to be detrimental to populations of twaite shad by limiting the access spawning grounds and by lowering recruitment after spawning, probably due to downstream advection of eggs and larvae.

To model estuarine habitat suitability of young-of-the-year twaite shad using a fresh body weight of either 0.5 g or 1.5 g, we assumed that the consumption rate was constrained by DO. Although we did not know the exact nature of this relationship, there is evidence low DO directly restricts consumption in fish (Secor & Niklitschek, 2001; Poon et al., 2001). Under hypoxia, fish have difficulties in supporting any activity that requires aerobic respiration and they shift to anaerobic pathways for energy expenditure (Poon et al., 2001). Feeding and, in particular, digestion of food are energetically demanding processes which need to be stopped during periods of hypoxia. Hence, it seemed appropriate to include a sigmoid function in the bioenergetic model to restrict food consumption.

In order to translate model results into predictions for a nearby future, we accepted that a linear path in the concentration of dissolved oxygen is a realistic environmental scenario to approximate future DO conditions. An analysis of monthly DO measurements taken between 1989 and 2005 at 16 sampling stations in the watershed corroborates the hypothesis of linearly increasing oxygen. The increasing trend is the result of increased efforts to clean wastewaters. Although global warming may affect DO in rivers on the long term, we do not expect sudden near-future declines in DO. At present, DO simulation models are under construction for the estuary of River Scheldt but so far, they are unavailable for predictions. Until then, a statistical model may be the only effective alternative to produce extrapolations.
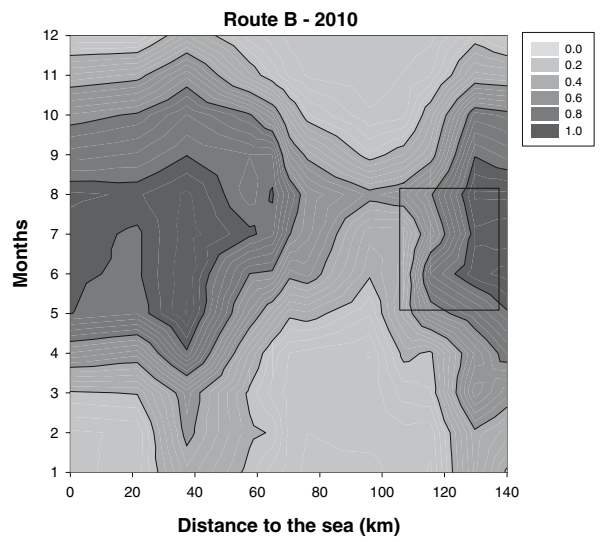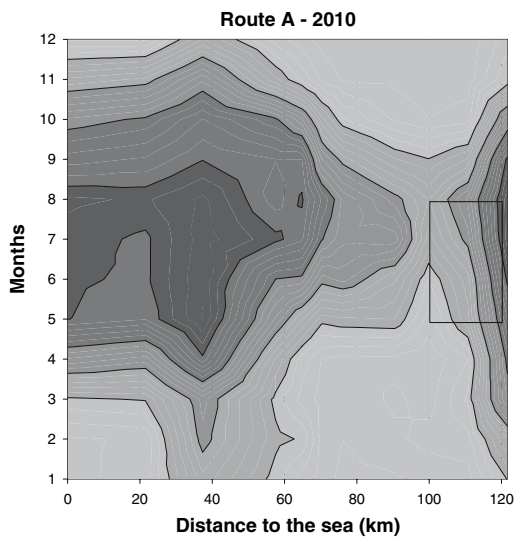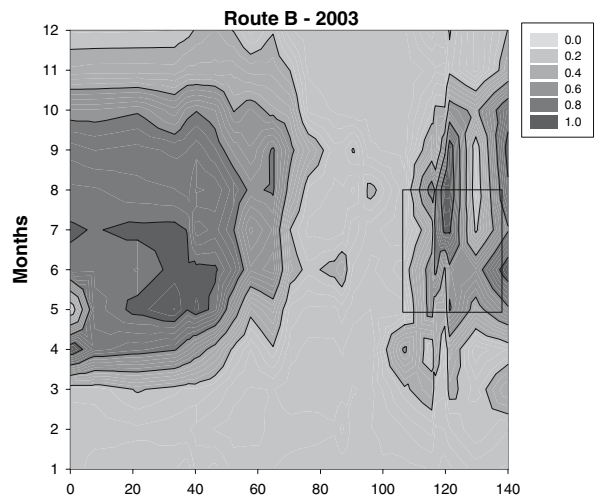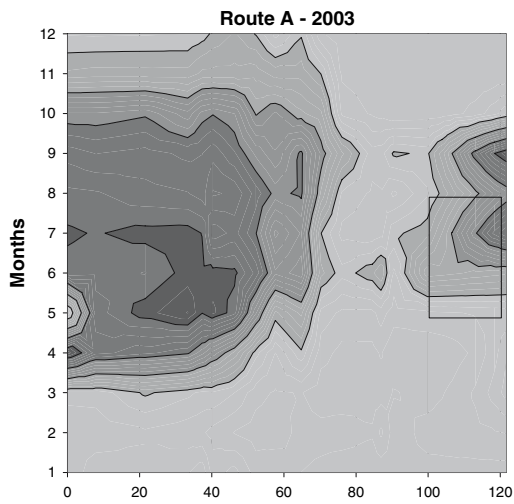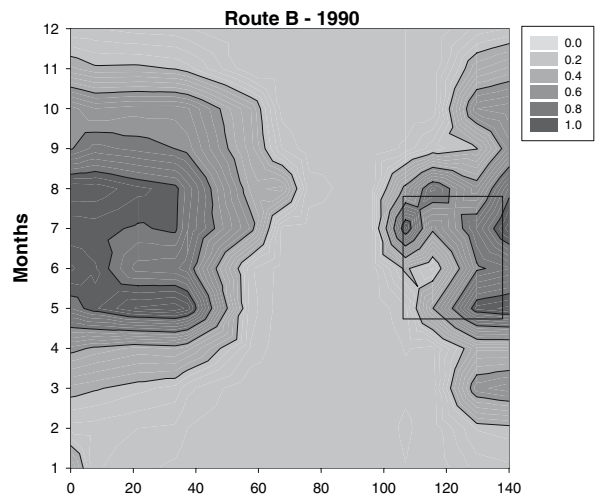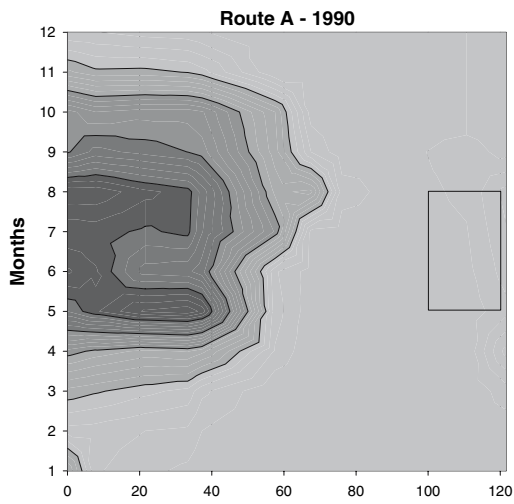
◀ **Fig. 6** Spatio-temporal capture probabilities of adult twaite shad along two river gradients (migration route A and B). Contours define space-time areas with similar catch probability. The spatial axis represents the distance to the sea (river mouth at 0 km and most upstream area at 140 km). The temporal axis represents the months of the year (Jan = 1, …, Dec = 12). Probabilities vary between 0 and 1. Three environmental scenarios simulate conditions for 1990, 2003 and 2010. Rectangles delineate historical spawning areas along the spatial axis and time available for reproduction along the time axis

Finally, we assumed that, once shad will reach historical spawning sites, they will successfully spawn. Hence, twaite shad were assumed to show sufficient plasticity in spawning behaviour and habitat requirements. Historical evidence shows that in the basin of River Scheldt twaite shad used to spawn in or just above the tidal reach (Vrielynck et al., 2003). Sand banks appeared to act as preferred spawning substrate, but probably any zone in the freshwater reach where egg retention is sufficiently

high may provide suitable spawning sites. Retention zones may comprise areas with slower flow in shallow fast flowing waters as well as deep areas in the tidal part of the river where net particle displacement is limited due to periodic upstream flood currents. This would explain the variety of spawning habitats and substrates that are reported for European estuaries and rivers (Caswell & Aprahamian, 2001; Gerkens & Thiel, 2001).

Applications for watershed management

Once conditions are restored and ecosystem stressors are removed, fish populations may recover and recolonise watersheds quickly (Eklöv et al., 1998). Here, we predicted that twaite shad, an endangered and protected fish species, will probably recover after an absence of nearly one century. We consider twaite shad as a indicator species showing the possibilities of ecosystem recovery to a society, which has no more collective memory of migrating fish species. The species was historically abundant, is sensitive to pollution and necessarily needs the whole river gradient for completion of the life history. Its predicted return to historical spawning sites would be an important milestone after decades of decline and an environmental success.

We demonstrated that it is possible to make acceptable predictions about a future population recovery with limited information. The models that were used yielded testable predictions and should convince river managers to take a number of necessary steps in order to support the expected recovery. First, it is clear that at present the mid part of the estuary is the most critical part in which hypoxia and high temperature conditions cause severe habitat fragmentation. Movements of adults are blocked and the total nursery area for young-of-the-year fish is reduced. This part of the river should receive prompt attention. Second, the bioenergetics model can be applied to identify and protect essential habitats as nursery areas for early life history stages. The approach to couple habitat quality to growth rate potential has proven its value in applied ecosystem management issues (Brandt et al., 1992; Luo et al., 2001; Höök et al., 2003; Niklitschek & Secor, 2005). Amongst other factors such as field measurements of fish density or an estimate of habitat related survival,
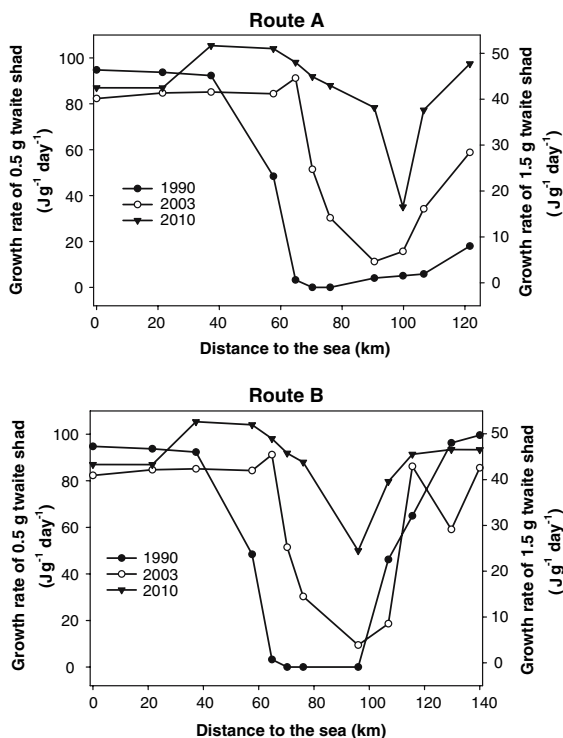

Fig. 7 Spatially explicit annually averaged growth rates (J g^{-1} day^{-1}) of juvenile twaite shad (0.5 and 1.5 g body weight) along two river gradients (migration route A and B, see Fig. 1). Three environmental scenarios simulate conditions for 1990, 2003 and 2010. The spatial axis represents the distance to the sea

the calculation of spatially explicit growth rates is a suitable proxy to identify nursery areas for young fish (Beck et al., 2001). Especially for habitats where juveniles are absent because of a lack in connectivity between adult habitats at sea and spawning and nursery sites in fresh water spatially explicit bioenergetic growth models may offer an valuable alternative to the more classic habitat quality estimates that are based on direct fish densities measured in the field. Finally, in anticipation of population recovery, a survey of suitable spawning habitats and substrate is clearly needed to support successful restoration of the twaite shad population in the Scheldt basin.

The predictor variables used in the models represent true ecological recourses and data of dissolved oxygen, temperature and river flow is commonly, and often freely, available in databanks. The empirical models are simple and straightforward and can be used directly by watershed managers. Clearly, species distributions are affected by biotic interactions, and in particular, by the distribution and abundance of their prey. This interaction was not included in this study since predator prey relations require considerable modelling and assumptions about the distribution and behaviour of prey and predators. Therefore, practical use of models that include biotic interaction may be limited.

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