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Statistical modeling of seasonal and environmental influences on the population dynamics of an estuarine fish community

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Abstract A statistical modeling study was performed on the population fluctuations of the 15 commonest fish species frequenting the tidal Scheldt estuary in Belgium. These included marine juvenile and seasonal visitors, estuarine residents and diadromous fish species that were recorded on the filter screens of a power plant cooling-water intake between September 1991 and April 2001. The species population abundance was regressed against a candidate set of 6 environmental variables and 13 instrumental variables, accounting for seasonality and long-term trends present in the data. Population abundances of the different species were, in general, best described by seasonal variables. Seasonal components contributed, on average, up to 63.8% of the variance explained by the models. Ten species were found to show a slightly negative, though significant, trend over the period of the survey. Most models also included at least one environmental variable, and 25.4% of the explained variance could be attributed to environmental fluctuations. Of all physico-chemical variables, dissolved oxygen was the most important predictor of fish abundance, suggesting that the estuary suffered from poor water quality during the survey. Temperature, salinity, freshwater flow, suspended solids and chlorophyll *a* concentrations were minor determinants of fish abundance.

Introduction

Coastal and estuarine ecosystems are exposed to great environmental variability. As a result, the life cycles of marine organisms show clear seasonal patterns in growth, reproduction and abundance (Coma et al. 2000). This is especially evident in the fish faunas of temperate, macrotidal estuaries along the continental shelves of western Europe (Elliott and Hemingway 2002). These shallow transition zones between freshwater and marine environments provide nursery areas for juveniles and wintering or spawning grounds to which mature individuals return on an annual basis. Migrant species pass estuaries on their spawning migration to either fresh or saline waters.

The different use of North Sea estuaries by various fish species as well as the sequential immigrations of very large numbers of marine juveniles produce predictable seasonal patterns of population densities (Potter et al. 2001; Thiel and Potter 2001). Due to the limited number of truly estuarine fishes, it is thought that annual variability in the abundance of the different species that remain within estuaries is determined by recruitment processes at the sea or in rivers (Potter et al. 1997). The factors controlling the typical seasonal alteration in species composition in estuaries and, hence, the relative abundance of species with respect to each other, are still subject of debate. The consistency of the seasonal occurrence of different fish species in Holarctic estuaries has prompted researchers to explore direct relationships between species abundance and environmental variables such as temperature, flow regime, oxygen and nutrient concentrations, turbidity and salinity. Thiel et al. (1995) found temperature to be the best predictor of temporal changes in fish abundance and species composition in the Elbe estuary (Germany), while salinity correlated with the spatial distribution of estuarine fish communities. Also, in the Humber (UK), temperature appeared to be the best predictor of total fish abundance, while salinity influenced species richness and total biomass

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(Marshall and Elliott 1998). In a series of papers, Power et al. (2000a, 2000b, 2002) and Power and Attrill (2002, 2003) used multiple regression models to predict fish abundance in the tidal Thames (UK) based on a set of independent physico-chemical and seasonal variables. From their models, it became clear that the abundance of fish could not be predicted using physico-chemical variables alone. They recognized that estuarine species abundance is affected by a complex set of events within the estuary. Other researchers have even rejected the hypothesis that seasonal changes in estuarine fish assemblages are directly driven by variations in abiotic conditions (Potter et al. 1986), or at least recommend that such correlations should be interpreted with great care (Potter et al. 2001). They attribute seasonality in estuarine fish assemblages to the phasing of events that regulate spawning times and larval dispersal. The objective of this study was to analyze the long-term patterns of temporal use of the Scheldt estuary (Belgium, The Netherlands) by fish over the period 1991–2001. Since the beginning of the 1990s, the Scheldt estuary has benefited from enhanced water quality due to the deployment of a substantial wastewater treatment program by the Belgian authorities to meet the standard water quality imposed by European directives. At this time, regular sampling of fish commenced in the cooling water of the Doel power plant, Belgium. Cooling-water samples can be taken irrespective of weather conditions and are regarded as a valid alternative to more traditionally obtained beam trawl samples, certainly in areas where silty or muddy bottoms prevent adequate sampling (Henderson 1989). As a result, a dataset has become available consisting of monthly densities (numbers of individuals per volume of cooling water sampled) recorded between September 1991 and April 2001. By using multiple regression models, the relative impor-

tance of both seasonal and environmental variation in explaining the observed changes in fish density was evaluated. We restricted this analysis to the 15 most important fish species. These species represent different life-history categories and accounted for over 99% of the numbers caught. We particularly investigated the following hypotheses relating to the temporal distribution of fish species in the Scheldt estuary:

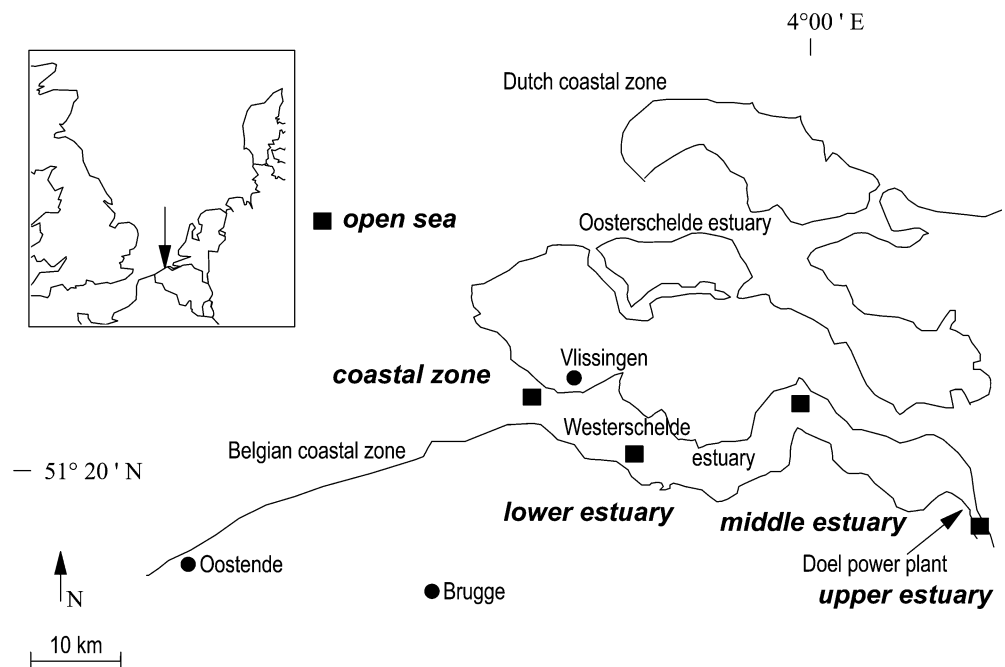
1. Seasonal patterns in the abundance of fish species using the estuary during a particular period of their life history are caused by sequential, obligate migrations that occur independently of estuarine environmental conditions (Potter et al. 1997).
2. Temperature is the most important environmental variable influencing the abundance of fish in the estuary (Attrill and Power 2002).
3. With regard to improvement in the water quality of the estuary, we expected that periods with low oxygen concentration would be characterized by low species densities (Möller and Scholz 1991).

Materials and methods

Study area

This study was undertaken in the brackish water part of the Scheldt estuary from 1991 to 2001. The Scheldt estuary (Fig. 1) is a macrotidal, coastal plain estuary with an average water depth of 11 m and a tidal range of 4–5 m. This results in strong currents that keep considerable quantities of silt in suspension. Salt water intrudes for about 100 km inland (Soetaert and Herman 1995). The lowest oxygen levels are measured in the upper estuary, where the heavy load of organic matter cataly-

Fig. 1 Map of the Scheldt estuary and indication of the sampling site. The lower estuary is delimited by the Belgian–Dutch border and the estuary mouth at Vlissingen. The upper estuary is situated upstream of the borderline. Samples were taken at the cooling-water intake of the nuclear power plant at Doel, Belgium



ses intense heterotrophic bacterial activity (Heip 1988). The lower estuary has a much better oxygenated water column, with oxygen saturation increasing from 50% at the Belgian–Dutch border to >90% at the mouth of the estuary.

Data collection

Fish were collected from the intake screens of the nuclear power station at Doel, situated on the west bank of the Scheldt estuary between Antwerp (Belgium) and the Belgian–Dutch border (Fig. 1). Cooling water is withdrawn through five intake apertures ($25 \text{ m}^3 \text{ s}^{-1}$) and filtered by two vertical traveling-screens, with a mesh size of 4 mm, to prevent larger organisms and debris from obstructing the condensers. Sampling was carried out monthly between September 1991 and April 2001. One day a month, an average of $500,000 \text{ m}^3$ of cooling water was screened over different samples to take into account tidal variation in intake numbers. Fish were separated from crustaceans and debris, identified to species level and enumerated. Sub-samples were necessary for counting fish in large catches. Total numbers of *Pomatoschistus minutus* and *P. lozanoi* were obtained by extrapolating the relative species composition of at least 50 randomly selected individuals that were identified to species level by using specific patterns of the papillae on the opercular bones (Hamerlynck 1990). Numbers of fish per sample were standardized to densities (i.e. numbers per 10^3 m^3 of cooling water). The effectiveness of the power station cooling-water intake for obtaining representative samples is demonstrated in Maes et al. (2001).

Environmental data that were included in the regression models were obtained from different sources. Water temperature ($^{\circ}\text{C}$) was measured coincident with the fish sampling. Monthly data for freshwater flow ($\text{m}^3 \text{ s}^{-1}$) were provided by the Flemish Administration for Waterways and Sea Affairs (AWZ). Salinity, suspended matter (mg l^{-1}), chlorophyll *a* ($\mu\text{g l}^{-1}$) and dissolved oxygen (mg l^{-1}) data were derived from the OMES database for the period 1994–2000 (S. Van Damme, personal communication) and from the Flemish Environmental Agency database for other months of the study period (<http://www.vmm.be>). Following Attrill et al. (1999), we also included 13 instrumental variables in the regression models. Twelve instrumental variables accounted for seasonality in the occurrence of fish. These variables assume a value of 1 for samples taken in the designated month and 0 otherwise. A trend variable was included measuring the number of months since September 1991.

Statistical analysis

We adopted the same statistical methodology as outlined in Attrill et al. (1999), since it facilitates compari-

sons between the Scheldt and Thames estuaries. Data on 6 environmental variables and 13 instrumental variables were used to build 15 multiple linear regression models of the form:

$$Y = b_0 + b_i + X_i + e_i \quad (1)$$

where Y represents the dependent variable (species density); b_0 stands for the model intercept; b_i are the regression coefficients associated with the independent, explanatory variables X_i ; and e_i is an error term, which is normally distributed around zero. Prior to statistical analysis, logarithmic [$\log_{10}(X+1)$] transformations were completed on the set of environmental and density data to approximate normal distributions.

We used a forward stepwise regression procedure to select explanatory variables for inclusion in the models (Sokal and Rohlf 2001). The forward stepwise selection method begins with one predictor and adds new ones, one at a time, until no significant improvement occurs in the model's predictive ability. The addition of variables to the model is based on an F -statistic. Variables exceeding a pre-specified F -to-enter value are added to the model. At each time step, variables, previously entered in the model, are removed again if they exceed a pre-specified F -to-remove. We used default values suggested in the statistical software Statistica 6.0 for F -to-enter and F -to-remove. The procedure stops when F -to-enter values become non-significant at the probability level of 0.05. Note that in stepwise regression models redundant variables—variables that are highly interrelated to other variables—will be down-weighted. Relative partial sums of squares (RPPS) indicated the relative amount of variance explained by individual explanatory variables, with the effect of other variables statistically removed (Sokal and Rohlf 2001). Accordingly, RPPS values can be used to assess the independent contribution of each explanatory variable to the total explained model variance as indicated by R^2 . All the linear models were tested for statistical significance at the $\alpha=0.05$ level using an F -test (Sokal and Rohlf 2001). The residuals were visually inspected for normality.

Incident correlations among physico-chemical variables and between physico-chemical variables and the trend variable were made using Spearman rank correlation tests.

Results

Water quality

Between September 1991 and April 2001, salinity varied between 0.5 in January 1995 and 15 in August 1996 (Fig. 2C), and water temperature from 1°C to 24.7°C (Fig. 2A). Freshwater flow rates into the estuary ranged between 35 and $403 \text{ m}^3 \text{ s}^{-1}$ (Fig. 2B) and increased significantly over time (Spearman rank correlation test; $N=116$; $r=0.21$; $P=0.02$). Turbidity levels were mod-

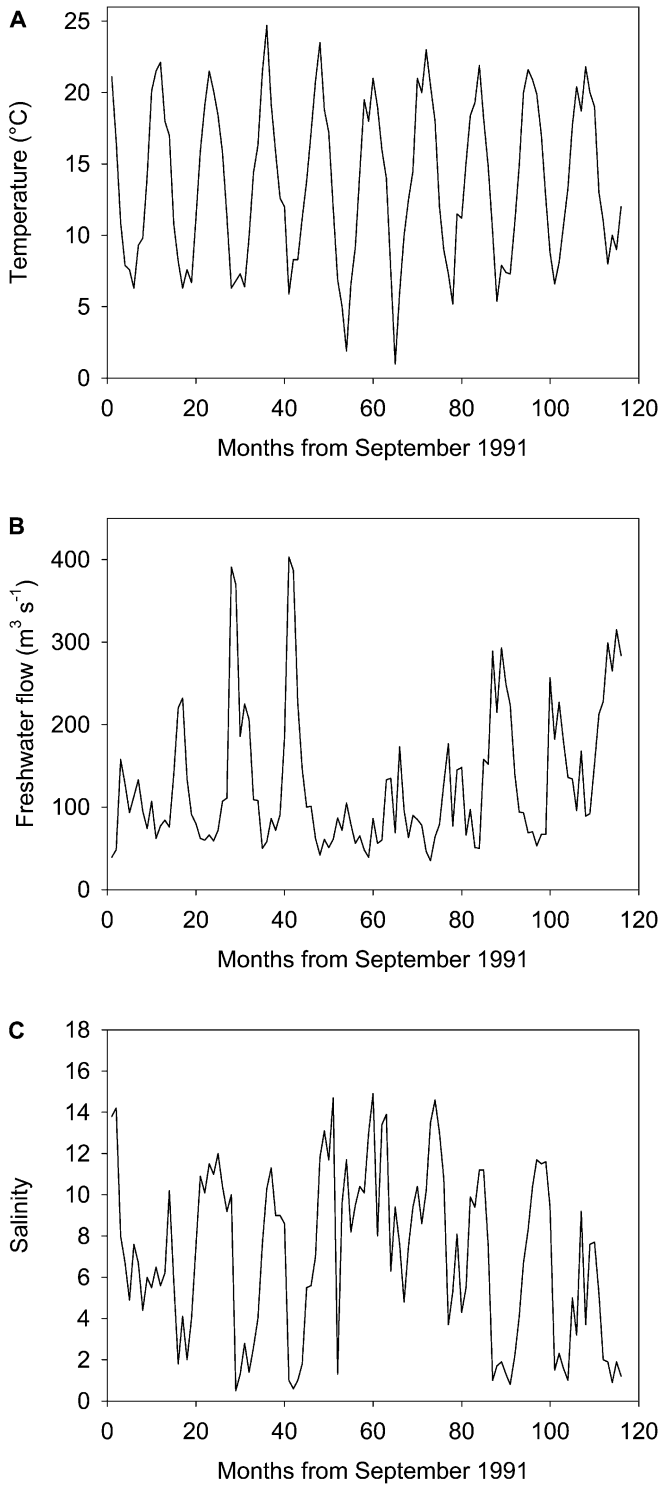


Fig. 2 **A** Water temperature, **B** freshwater flow and **C** salinity near the sampling site, recorded over the period between September 1991 and April 2001

erate throughout the study period, ranging between 18 and 230 mg suspended matter l^{-1} (Fig. 3B). Chlorophyll *a* concentrations peaked in spring and summer months and were lowest during the winter (Fig. 3A). Dissolved oxygen fluctuated around 5 mg l^{-1} (Fig. 3C)

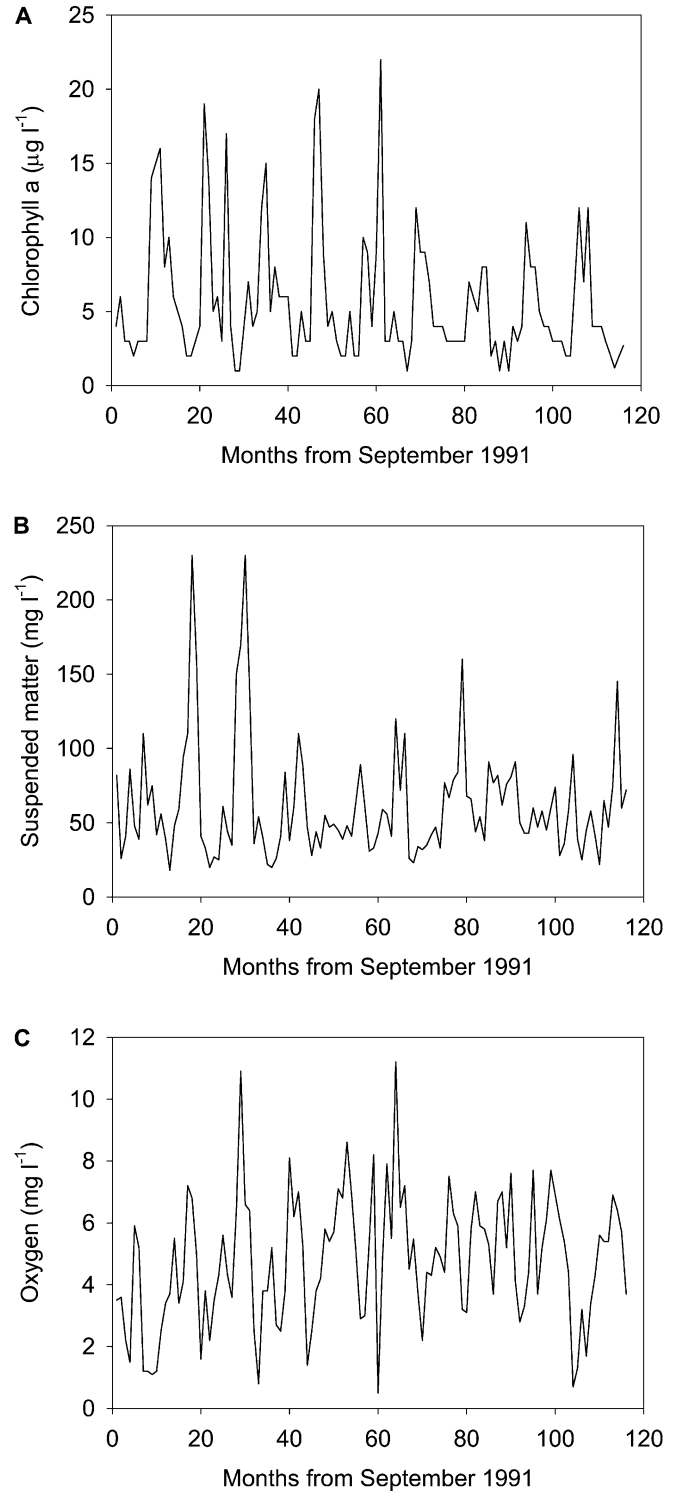


Fig. 3 **A** Chlorophyll *a*, **B** suspended matter and **C** dissolved oxygen near the sampling site, recorded over the period between September 1991 and April 2001

and showed a significant increasing trend over time (Spearman rank correlation test; $N=116$; $r=0.23$; $P=0.01$). Almost all environmental variables were significantly interrelated to each other, with the highest correlation occurring between freshwater flow and

salinity (Spearman rank correlation test; $N=116$; $r=-0.73$; $P<0.001$).

General catch statistics and model results

The abundance of the entire fish community fluctuated between 0.07 and 528 individuals per 1,000 m³ cooling water surveyed. Species characteristics for the 15 species included in this study are given in Table 1. Six species were categorized as marine juveniles, which use the estuary primarily as a nursery. Four species were estuarine residents while another four were either anadromous or catadromous. *Sprattus sprattus* was the only marine seasonal visitor. The most common species were the demersal gobies *Pomatoschistus minutus* and *P. microps* and the pelagic clupeids *Clupea harengus* and *S. sprattus*.

Regressing the population abundance against a candidate set of 6 environmental variables and 13 instrumental variables produced significant models ($P<0.01$) explaining between 9% and 64% of the variance as indicated by R^2 . Variables contributing significantly at the $\alpha=0.05$ level to the prediction of species abundance, regression model coefficients, relative partial sums of squares and model diagnostics are given in Table 2. Except for *P. microps*, models always included at least one environmental variable (Table 2). Temperature, salinity and flow rate were selected for six species. Suspended matter was selected for three; chlorophyll *a* for four; and dissolved oxygen for eight species. Dissolved oxygen was the most important explanatory predictor variable, relating positively to six fish species and negatively to *Anguilla anguilla* and *Gasterosteus aculeatus*. Inspection of the relative partial sums of squares showed that environmental variables had moderate to weak explanatory power. On average, 25.4% of the explained variance could be attributed to environmental fluctuations. All models had strong seasonal components, and seasonal instrumental variables contributed, on average, to 63.8% of the variance explained by the models (Table 2). Months between September and December were each selected for eight species, mostly with positive

regression coefficients, indicating that the study area is a preferred fish habitat during the fall. Ten species were found to show a slightly negative, though significant, trend over the period of the survey (Table 2). The abundance of *Liza ramada* increased significantly over time. On average, the trend variable accounted for 10.8% of the explained variance of the models.

Species-specific model results

As an example, model predictions were plotted against field observations for four fish species (Fig. 4). In general, predicted abundance fluctuations matched the field abundance, but observed peak abundances often fell outside the model confidence limits.

The abundance of *Dicentrarchus labrax* was strongly seasonal (82% of the explained variance) and related positively to freshwater flow (Table 2). *Pomatoschistus* sp. abundance displayed a pronounced seasonal trend, while environmental variables were unimportant in the models. *P. lozanoi* responded positively to dissolved oxygen. The *P. minutus* model had positive slopes for temperature and salinity and negative slopes for freshwater flow and suspended matter. Models for clupeids also had important seasonal elements. Seasonal instrumental variables constituted 78.4% and 82.6% of the explained variance by *C. harengus* and *S. sprattus* models, respectively. Seasonality was further evident in *Syngnathus rostellatus* (67% of the explained variance) and *L. ramada* (63% of the explained variance). The model of *S. rostellatus* included temperature (positive coefficient) and suspended solids (negative coefficient). *L. ramada* abundance was significantly influenced by freshwater flow and dissolved oxygen. Flatfish abundance was more affected by environmental variables, although the seasonal component explained most of the variance in *Limanda limanda* and *Solea solea* models. *L. limanda* abundance increased with increasing oxygen concentration and decreased with increasing freshwater flow. Dissolved oxygen, suspended matter and salinity positively affected *S. solea* abundance. Environmental

Table 1 Species characteristics for the 15 fish species included in this study. Life-cycle categories were assigned following Elliott and Dewailly (1995) (*MJ* marine juvenile; *MS* marine seasonal; *CA* catadromous/anadromous; *ER* estuarine resident). The total catch column provides the total number of fish caught over the entire survey period (September 1991–April 2001)

Species	Common name	Life-cycle category	Total catch
<i>Anguilla anguilla</i>	Eel	CA	3,264
<i>Clupea harengus</i>	Herring	MJ	351,889
<i>Dicentrarchus labrax</i>	Sea bass	MJ	21,824
<i>Gasterosteus aculeatus</i>	Three-spined stickleback	CA	6,054
<i>Lampetra fluviatilis</i>	River lamprey	CA	769
<i>Limanda limanda</i>	Dab	MJ	1,411
<i>Liza ramada</i>	Thin-lipped grey mullet	MJ	1,060
<i>Osmerus eperlanus</i>	Smelt	CA	13,269
<i>Platichthys flesus</i>	Flounder	ER	4,318
<i>Pomatoschistus lozanoi</i>	Lozano's goby	MJ	109,169
<i>Pomatoschistus microps</i>	Common goby	ER	651,638
<i>Pomatoschistus minutus</i>	Sand goby	ER	713,032
<i>Solea solea</i>	Sole	MJ	1,117
<i>Sprattus sprattus</i>	Sprat	MS	175,959
<i>Syngnathus rostellatus</i>	Nilsson's pipefish	ER	141,362

Table 2 Regression model coefficients (*b*) and relative partial sum of squares (*RPSS*) for independent variables selected by a forward stepwise regression. *RPSS* were used to partition the variance over instrumental and environmental variables. Model diagnostics include explained variance (*R*²) and *F*-statistics. All models were significant at *P* < 0.01 (for full taxonomic names, see Table 1)

Model variables	<i>D.labrax</i>		<i>P.microps</i>		<i>L.limanda</i>		<i>A.anguilla</i>		<i>P.flesus</i>		<i>C.harengus</i>		<i>L.fluviatilis</i>		<i>P.lozanoi</i>	
	RPSS	<i>b</i>	RPSS	<i>b</i>	RPSS	<i>b</i>	RPSS	<i>b</i>	RPSS	<i>b</i>	RPSS	<i>b</i>	RPSS	<i>b</i>	RPSS	<i>b</i>
Intercept		-0.111	1.066		0.089		-0.008	0.212		-0.084		0.044		-0.477		
Temperature						10.9	0.030	11.9	-0.039				12.7	-0.010	13.0	0.229
Salinity								22.6	-0.040							
Oxygen					11.2	0.048	8.4	-0.025	11.5	0.041	5.7	0.480				
Flow	7.4	0.113			19.5	-0.060										
Chlorophyll <i>a</i>							12.1	0.026			4.1	0.255				
Suspended matter																
Jan	4.7	0.064									13.5	0.729				
Feb											9.6	0.516	22.8	0.023		
Mar									7.7	0.018	5.1	0.275	42.0	0.043		
Apr	4.5	0.061	7.5	-0.294			36.3	0.069					9.2	0.009		
May			10.7	-0.442			15.3	0.031							9.0	-0.217
Jun			8.0	-0.333												
Jul			10.2	-0.421												
Aug	15.2	0.218					16.9	0.034							9.8	0.236
Sep	18.7	0.255	8.8	0.347							6.3	0.338			18.1	0.417
Oct	14.3	0.194	13.8	0.545	13.3	0.037					11.4	0.613			21.0	0.484
Nov	15.0	0.204	11.7	0.463	33.5	0.092			11.4	-0.026	19.2	1.035			12.4	0.286
Dec	9.6	0.131	7.7	0.303	22.5	0.062			15.6	-0.036	17.6	0.951			8.9	0.204
Trend	10.6	-0.001	21.6	-0.007					19.3	-3×10 ⁻⁴	7.5	-0.003	13.2	-1×10 ⁻⁴	8.0	-0.002
Model diagnostics																
Adjusted <i>R</i> ²	0.341		0.426		0.146		0.286		0.089		0.538		0.565		0.275	
<i>F</i>	7.624		10.377		4.918		8.681		6.241		14.440		30.942		6.473	
Variance partitioning																
Environmental variables	7.4%		0%		30.7%		31.4%		46.0%		9.9%		12.7%		13.0%	
Seasonal variables	82.0%		78.4%		69.3%		68.6%		34.7%		82.6%		74.1%		79.0%	
Trend variable	10.6%		21.6%		0%		0%		19.3%		7.5%		13.2%		8.0%	
Model variables																
	<i>S.rostellatus</i>		<i>P.minutus</i>		<i>O.eperlanus</i>		<i>S.solea</i>		<i>S.sprattus</i>		<i>L.ramada</i>		<i>G.aculeatus</i>			
	RPSS	<i>b</i>	RPSS	<i>b</i>	RPSS	<i>b</i>	RPSS	<i>b</i>	RPSS	<i>b</i>	RPSS	<i>b</i>	RPSS	<i>b</i>	RPSS	<i>b</i>
Intercept		0.712		0.994		0.587		-0.078		1.485		-0.053		0.689		
Temperature	5.7	0.206	5.5	0.565					7.5	0.459			19.4	-0.251		
Salinity			6.5	0.359			18.4	0.022								
Oxygen					24.0	0.201	16.1	0.039			8.1	0.014	8.7	-0.123		
Flow			6.4	-0.515	13.2	-0.080			5.6	-0.413	16.9	0.021				
Chlorophyll <i>a</i>					13.0	-0.080							12.9	-0.133		
Suspended matter	10.5	-0.333	3.6	-0.327			11.5	0.023								
Jan			3.5	-0.254					11.6	0.765						
Feb			5.1	-0.366					7.2	0.476			8.4	0.076		
Mar			9.1	-0.656	11.5	0.062	11.3	0.018	4.5	0.296						
Apr			14.3	-1.036									13.6	-0.123		
May			18.3	-1.390									8.5	-0.081		
Jun			17.0	-1.287												
Jul			7.2	-0.546			33.6	0.055	2.9	0.198						
Aug	22.8	0.603	3.6	-0.270					3.5	0.243						
Sep	27.9	0.702					9.1	0.014	6.2	0.407	7.7	0.009				
Oct	16.2	0.409							9.5	0.625	31.9	0.036				
Nov									17.5	1.153	23.3	0.026				
Dec									15.5	1.024			6.2	-0.057		
Trend	16.9	-0.004			21.4	0.001			8.5	-0.005	12.0	1×10 ⁻⁴	22.3	-0.002		
Model diagnostics																
Adjusted <i>R</i> ²	0.538		0.639		0.152		0.192		0.556		0.149		0.397			
<i>F</i>	23.331		18.008		4.429		5.528		12.085		7.350		10.491			
Variance partitioning																
Environmental variables	16.2%		21.9%		67.0%		46.0%		13.1%		25.0%		41.0%			
Seasonal variables	66.9%		78.1%		11.5%		54.0%		78.4%		62.9%		36.7%			
Trend variable	16.9%		0%		21.4%		0%		8.5%		12.0%		22.3%			

variables contributed to 46% of the explained variance of modeled *Platichthys flesus* abundance, with significantly negative regression slopes for temperature and salinity, while a positive correlation was found for dis-

solved oxygen. Models for *Osmerus eperlanus* and *Gasterosteus aculeatus* also had significant environmental influences. Significant negative correlations were apparent between *G. aculeatus* abundance and temper-

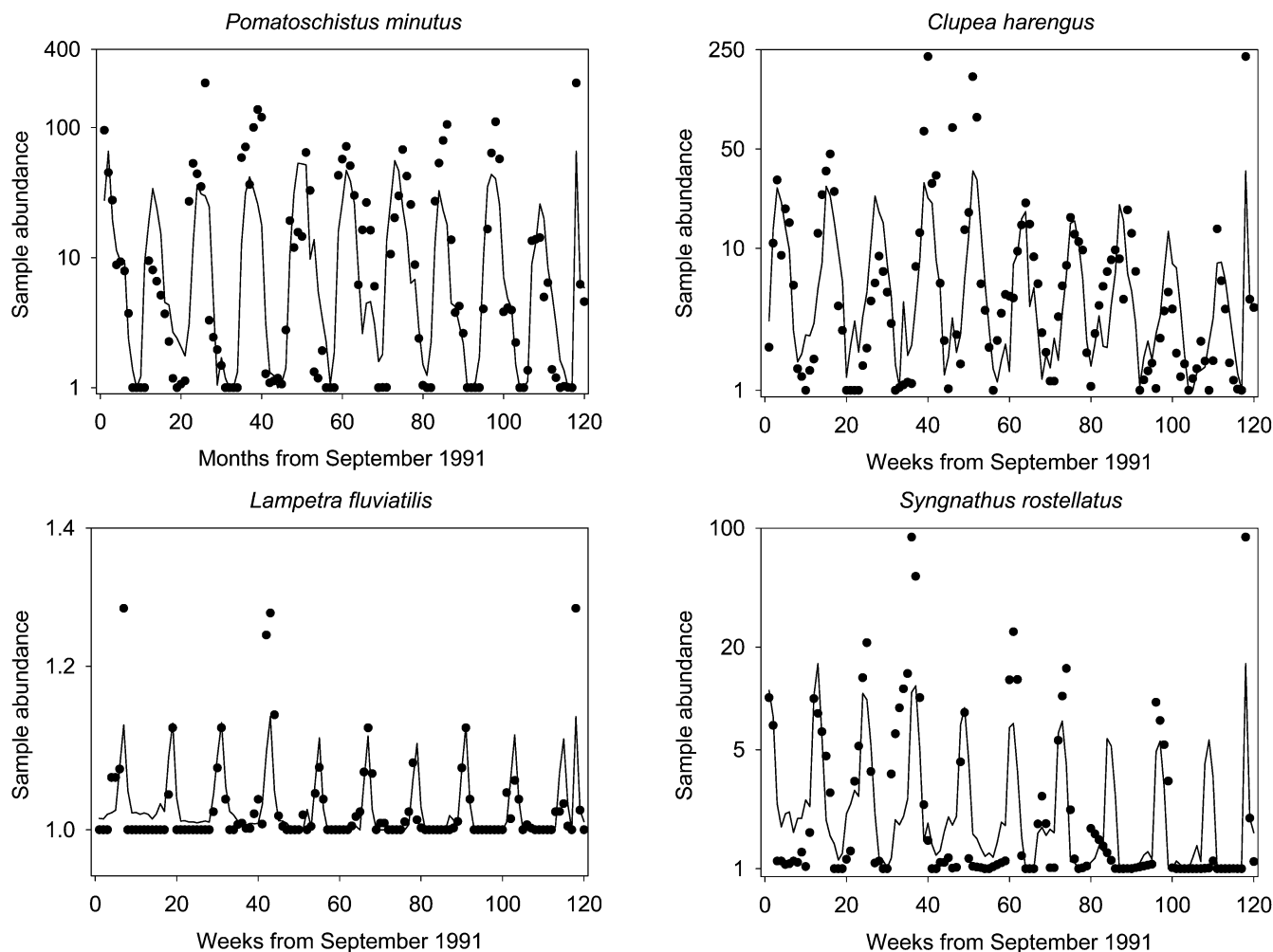


Fig. 4 Model predictions (*lines*) against field observations (*dots*) of the sample abundance (numbers per 1,000 m³ of cooling water sampled + 1) for four fish species

ature, dissolved oxygen and chlorophyll *a* levels. Four environmental variables were included in the *O. eperlanus* model, with negative model slopes for salinity, freshwater flow and chlorophyll *a* and a positive model slope for dissolved oxygen. Finally, models of the catadromous *Anguilla anguilla* and the anadromous *Lampetra fluviatilis* showed clear seasonal components, but some influence of physico-chemical parameters was also apparent.

Discussion

The study of factors that cause temporal fluctuations in the population density of organisms is a primary goal of ecology. Such fluctuations may be explained by density-dependent mechanisms or density-independent factors, mostly climatic forcing. In estuarine ecology, most effort has been directed towards the explanation of spatial and temporal distribution patterns as a function of density-independent factors. This is due to the very nature of

estuarine ecosystems, since they are strongly believed to represent an extreme environment to the organisms that they harbor (Day et al. 1989). The two most important abiotic variables in an estuary are the tides and salinity. Tidal forcing produces a spatial gradient from the sub-tidal channel to the highest parts of salt marshes, whereas the diffusion of salt into the river mouth results in a salinity gradient from the freshwater zone to the marine parts of estuaries, where the salinity is close to full-strength seawater. The spatial and temporal distribution of planktonic and benthic communities largely responds to these two gradients. Marine, estuarine and freshwater plankton are swept up and downstream by the tides, but may eventually end up in zones where they suffer salinity stress and die (Soetaert and Herman 1994; Muylaert and Raine 1999). Temporal changes in salinity caused by stochastically pulsed events, mainly increased rainfall, control the populations of estuarine benthic organisms (Ysebaert et al. 2002). As a result, the occurrence of most estuarine organisms and, hence, also estuarine biodiversity relate well to spatial and seasonal changes in salinity (Attrill 2002), and salinity may thus represent an unambiguously density-independent factor to explain part of the abundance of plankton and benthos in a certain zone of the estuary.

Partitioning the explained variance over the set of independent variables indicated that physico-chemical parameters and, in particular, salinity were not the major determinants of fish abundance in the Scheldt estuary. Still, a substantial literature reports on significant relationships between environmental data and the abundance of fish populations in estuaries (Blaber and Blaber 1980; Henderson 1989; Cyrus and Blaber 1992; Hamerlynck et al. 1993; Marshall and Elliott 1998; Thiel et al. 1995; Maes et al. 1998; Cabral et al. 2001). It appears, however, that short-term studies ignore seasonal patterns in the data, but focus instead on a coupling between environmental variation and fish abundance. An analysis of the present data for the period 1994–1995 (Maes et al. 1998) identified temperature, salinity and dissolved oxygen as forces structuring the fish community of the Scheldt estuary. Other studies dealing with short-term datasets confirm the importance of physico-chemical factors as explanatory variables. A statistical examination of environmental influences on the fish community of the Humber estuary between April 1992 and November 1994 indicated that salinity was the dominant factor influencing the distribution of fish, with temperature also having a major influence (Marshall and Elliott 1998). Similar results were obtained for the Elbe based on samples taken between 1989 and 1992 (Thiel et al. 1995). The present assessment of long-term data of the fish fauna of the Scheldt estuary, however, resulted in models with strong and predictable seasonal components and parallels findings reported for the Thames. In a series of papers, Power et al. demonstrated that seasonal instrumental variables significantly influenced the abundance of flatfish (Power et al. 2000a), clupeids (Power et al. 2000b), *Agonus cataphractus* (Power et al. 2002), gadids (Power and Attrill 2002) and *S. rostellatus* (Power and Attrill 2003). Seasonality was also evident in statistical models of Crustacea populations frequenting the Thames estuary (Attrill et al. 1999), but, in their models, environmental variables, in particular temperature, had a more pronounced influence on species abundance than in our models. The importance of temperature as a critical resource has led to the assumption that estuaries serve as thermal refuges for juvenile fishes (Attrill and Power 2002). Faster spring warming and autumnal cooling of the estuarine water body relative to the water of the North Sea create temperature differentials that can be exploited by mobile organisms such as fish and crustaceans to enhance growth (Attrill and Power 2002).

In this study, temperature was not the dominant factor influencing fish abundance, as the series of studies for the Thames estuary suggested. This is possibly due to two notable differences between this study and the one on the Thames estuary: a different climatic regime during the respective survey periods and local differences in water quality. Inspection of annual patterns of the North Atlantic Oscillation Index (NAOI) showed, in general, high index values between 1991 and 2001 (Hurrell et al. 2003), corresponding to wet and relatively

warm winters in the Northeast Atlantic. This contrasts with the more variable pattern of the NAOI for the period during which the fish fauna of the Thames was monitored (1977–1992), with a series of colder winters in the middle part of the study period. Accordingly, the limited variability in annual climatic winter conditions probably restricted the temperature range included in this study. Hence, the influence of temperature on the population abundances may be underestimated in this study. A second, important difference is that studies of the Thames estuary report on the post-recovery period, while the Scheldt estuary is still in recovery. Our results showed indeed that, of all environmental variables included in the models, dissolved oxygen (DO) was a primary determinant of fish abundance. As the levels of DO in the estuary increased, the abundance of six fish species increased, confirming our a priori hypothesis. The concentration of DO near the study site increased from an annual average of 3.2 mg l^{-1} in 1992 to 5.4 mg l^{-1} in 1999, followed by another decline in 2000. Marine fish become stressed at DO levels $< 4.5 \text{ mg l}^{-1}$ (Poxton and Allouse 1982), values occurring in 47% of the records. Our results suggest that particularly flatfish as well as *Osmerus eperlanus*, a species related to salmonids, suffered from hypoxic events in the estuary as the population abundance of these species related positively to DO. It shows that the estuary still suffered from hypoxia during the survey period, in spite of efforts to treat household and industrial wastewaters. The importance of DO as a factor explaining fish abundance in the estuary also gives support to ongoing research efforts to use fish communities as indicators for estuarine water quality. Two species, *Anguilla anguilla* and *Gasterosteus aculeatus*, responded negatively to increased DO. They both are tolerant to low levels of DO (Möller and Scholz 1991) and possibly shifted to more-upstream but less-oxygenated habitats during the study period.

Other environmental variables were only minor determinants of fish abundance. Neither salinity nor any other environmental resource contributed much to the variance explained by the models. One can argue that the response of fish to changes of these variables is not linear, as assumed in multiple linear regression models, but approaches an optimum. It follows that non-linear quadratic models would be more appropriate to describe the relation between environmental variables and species density, but using polynomial models did not improve the explained variance as indicated by R^2 .

Platichthys flesus, *Osmerus eperlanus* and *Gasterosteus aculeatus* were the only species for which an important link existed between the physico-chemical environment and fluctuations in population abundance. Two of these species, *O. eperlanus* and *G. aculeatus*, are categorized as diadromous fish (Elliott and Dewailly 1995). However, similar to *P. flesus*, they appear to spend a considerable period of their life history in the brackish water part of the Scheldt estuary. Consequently, the population dynamics of these species are likely to be limited by estuarine environmental conditions.

The strong seasonal components in most models suggest that annual recruitment patterns of marine and estuarine resident fish species into the study area and the passage of diadromous fish species through the area occur independently from environmental conditions within the estuary. These migration patterns result in seasonally consistent changes in species composition, which are typically found in all Holarctic, macrotidal, estuarine fish faunas (Thiel and Potter 2001). Ordination of fish data for the Elbe and Severn estuaries (Potter et al. 1997; Thiel and Potter 2001) suggested that the main factors controlling seasonality in the marine component of the estuarine fish community are the spawning times of the respective species and the time their larval and juvenile stages need to recruit into the estuary. Analysis of the Thames data further revealed that the annual realized abundance of marine fishes in the estuary is regulated mainly by temperature (Attrill and Power 2002), while low levels of DO are of primary importance in cases of polluted river systems, as demonstrated by this study. The seasonality observed in the fluctuations of dominant estuarine resident fish species such as *Pomatoschistus* sp., *Syngnathus rostellatus* and *Platichthys flesus* parallels the patterns found for marine species, suggesting that these species spawn outside the study area, presumably near the mouth region or on coastal habitats. Consequently, it is concluded that the temporal distribution of fishes in estuaries is highly predictable and largely independent of estuarine environmental conditions, suggesting that factors outside estuaries regulate the fish community structure. Future studies of estuarine ichthyofaunas would therefore benefit from the inclusion of upstream or marine fluctuations in environmental variables and life-history strategies (Maes et al. 2004).

A final note relates to the observed negative trend in the abundance of ten species, which seems to contrast with gradual improvements in water quality. This negative trend possibly reflects a decreased supply of post-larval and juvenile stages to the estuary. However, no such trend was found in the abundance of seven of the most common species of the Forth estuary between 1982 and 2001 (Greenwood et al. 2002). The latter observation plus the fact that the negative trend was found to be significant for pelagic, demersal and benthic species, with either marine or estuarine life-history styles, suggests that changes in the estuary itself are likely responsible for the decline, rather than decreased recruitment. It seems that the overall improved water quality of the upper Scheldt estuary has led to increased availability of habitats situated upstream of our study site. Furthermore, Appeltans et al. (2003) showed that *Eurytemora affinis*, a dominant prey item in fish stomachs, recently shifted to areas with lower salinity, where it is also common in other, more oxygenated estuaries. The dispersal of fish over a larger area due to improved water quality and the redistribution of prey resources possibly resulted in a decrease of fish abundance at our sampling station.

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