

Learning from the Past to Predict the Future: Responses of European Diadromous Fish to Climate Change

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Abstract.—Climate change can have an effect on species distributions. The 1900 distribution and potential future distribution of diadromous fish in Europe, North Africa, and the Middle East were explored using generalized additive models (GAMs) and selected habitat characteristics of 196 basins. Robust presence–absence models were built for 20 of the 28 diadromous species in the study area using longitude, annual temperature, drainage surface area, annual precipitation, and source elevation as explanatory variables. Inspection of the relationship between each variable and species presence–absence revealed that the GAMs were generally interpretable and plausible. Given the predicted rise in annual temperature in climate models ranging between 1°C and 7°C by 2100, the fish species were classified according to those losing suitable basins, those gaining suitable basins, and those showing little or no change. It was found that the climate envelopes based on temperature and precipitation for diadromous species would, in general, be shifted farther northeastwards by 2100, and these shifting ranges were comparable with those assessed in other studies. The uncertain future of some species was highlighted, and it was concluded that conservation policy and management plans will need to be revised in the face of climate change.

Introduction

The past decade was the warmest of the last millennium, and temperatures will probably continue to rise in the future (IPCC 2007). The different scenarios outlined by the Intergovernmental Panel on Climate Change project an increase in global mean surface air temperature, relative to 1980–1999, of 1.1–6.4°C by 2100. Many studies covering a wide range of ecosystems have already attempted to understand and estimate the ecological consequences of climate change in various organisms. These studies have typically highlighted a change

in distribution and community structure (Thomas and Lennon 1999; Walther et al. 2002; MacKenzie et al. 2007).

Anadromous and catadromous fish rely on freshwater, estuarine, and marine ecosystems to complete their life cycles (McDowall 2009; Quinn et al. 2009). This unique life history characteristic has enabled them to adjust their distribution to cope with environmental changes and could allow them to do the same in a dynamic changing environment. Moreover, diadromous species are economically important in many parts of the world. The native range of the European eel *Anguilla anguilla* covers all of Europe and North Africa, and this species is exploited in all the countries

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in this area (Dekker 2003). Allis shad *Alosa alosa* are harvested by commercial fisheries throughout their range, extending historically from Morocco to Norway, in estuaries, in the middle sections of rivers, or in their resident form in lakes (Baglinière et al. 2003). Lampreys have long been considered a gastronomic delicacy in Europe, encouraging the development of commercial fisheries for these species (Kelly and King 2001). The river lamprey *Lampetra fluviatilis* is an important source of income for many fishermen in Sweden and Finland (Sjöberg 1980; Tuunainen et al. 1980), and the sea lamprey *Petromyzon marinus* is also a commercially important species in Spain and Portugal (Almeida et al. 2002).

Static modeling techniques can be used to assess the impact of global change on biodiversity distribution by predicting current species distributions and applying statistical models from current distribution to project future distributions under global change scenarios (i.e., Bakkenes et al. [2002] for plants, Hilbert et al. [2004] for birds, Chu et al. [2005] for fish, and Thuiller et al. [2006] for mammals). The model relates the current observed species distribution to a set of available environmental variables. Several modeling methods are available such as generalized linear models (GLMs), generalized additive models (GAMs), classification tree analysis, artificial neural network, or multiple adaptive regression splines. Some authors have compared the performance of these techniques in predicting species distribution (Olden and Jackson 2002; Thuiller 2003; Leathwick et al. 2006; Heikkinen et al. 2007). In most cases, GAMs provided a good stability and performance because of their flexible nonparametric or semiparametric framework to model the relationship between a response and one or more predictor variables (Hastie and Tibshirani 1990) and were easily interpretable.

The objectives of the work reported here were to develop a model that would relate the 1900 diadromous fish distribution to major climatic and physical factors using GAMs and then to project the distribution at the end of the 21st century under climate change. Our work focused on suitable climatic conditions without taking into account regional anthropic pressures such as the erection of dams in main stems (Gowans et al. 1999; Larinier 2001; Hill 2009), the deterioration in water quality in industrialized areas (Breine et al. 2007; Maes et

al. 2007; Woodland et al. 2009), or unsustainable fisheries (Masters et al. 2006). We chose to consider the distribution of diadromous fish species at the beginning of the 20th century before the main biodiversity erosion. The first warming period occurred worldwide between 1910 and 1945, with a temperature increase of 0.15°C per decade (IPCC 2007). Moreover, in Europe, the large dams policy (above 15 m) was started in the 1950s (CIGB/ICOLD 2003). Nevertheless, Hoffmann (1996, 2005) demonstrated that during the Middle Ages, increasing human populations and demand had already produced great change in many European fisheries and altered the freshwater biodiversity.

Methods

Study Area

We selected 196 river basins in Europe, North Africa, and the Middle East in a two-steps process: (1) we selected all the large rivers in the area according to the list of "major European river catchments" (31 basins exceeding 50,000 km² and draining two-thirds of the continent) provided by the European Environment Agency (www.eea.europa.eu), and (2) we selected medium-sized rivers to obtain a balanced geographical coverage (Figure 1). Basins ranged from Greenland in the west (Kapisillit River: 51.76°W) to Iran in the east (Gorgan Rud River: 54.04°E). Basins from Morocco, Algeria, Tunisia, and Egypt, as well as Greenland and Iceland, were added to our study to fully cover the distribution area of the diadromous species considered in this work. No other diadromous species were encountered in these regions. In North Africa, the river network is very scattered, especially in the desert country, Libya. We selected all the major basins (seven in all) in this region.

Species Data

All over Europe, a pool of 28 diadromous fish species was encountered in the basins (Table 1; i.e., 25 anadromous species and 3 catadromous species). This list was based on the heuristic checklist of the freshwater fish of Europe (Kottelat 1997; Kottelat and Freyhof 2007) and the list of diadromous fish species established by McDowall (1988). Because of taxonomical uncertainties, all Baltic *Coregonus* species were pooled under the appellation *Corego-*

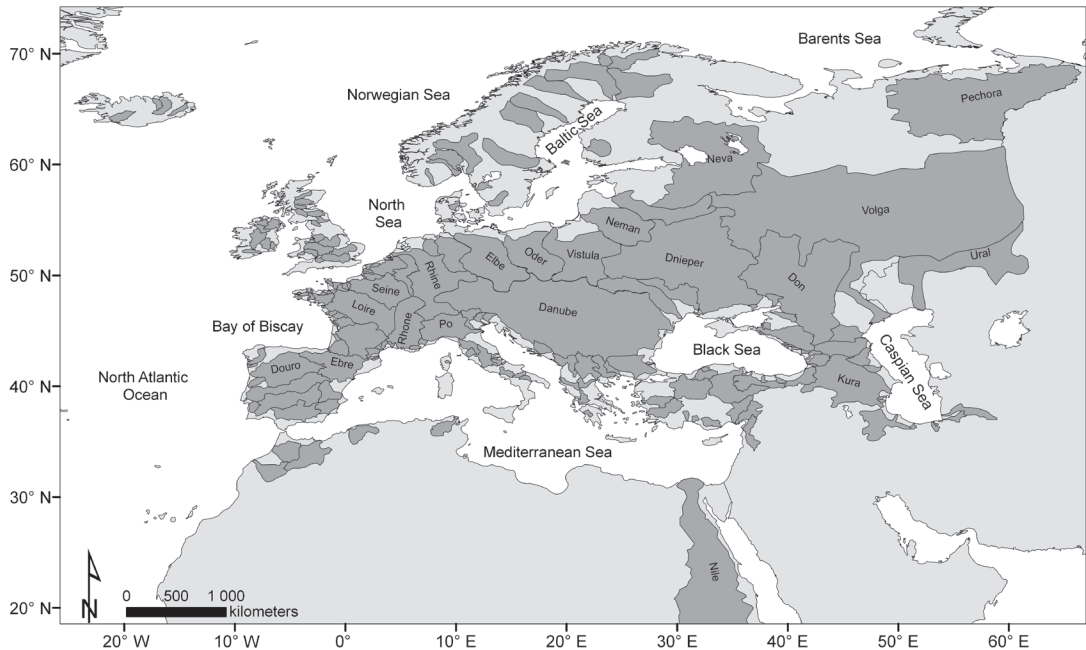


Figure 1.—The study area covering the whole of Europe, North Africa, and the Middle East. The names of the largest basins were provided. Nile (Egypt) and Kapisillit (Greenland) basins were truncated to offer a better visualization of the whole study area.

nus spp. Many species present high morphological variations. Thus, some taxonomists grouped similar species in groups or complexes while others recognized different species or subspecies for some local or regional variants. All the selected species demonstrated physiological and ecological capabilities to express diadromous tactics (McDowall 1988). In some cases, these tactics are not currently expressed (i.e., resident forms exist for some species).

A presence-absence database for these species at the beginning of the 20th century in the selected basins (EuroDiad 2.0 database) was produced from a literature review and was checked by national experts from the Diadfish network (www.diadfish.org). Béguer et al. (2007) used the first version of EuroDiad centered on Western Europe and provided the related reference list in their paper. This list constitutes a major overview of the literature types (thesis, scientific papers or officials reports about diadromous species distribution) that we used in our study. Brotons et al. (2004) demonstrated that models based on presence-absence

information were more relevant than presence-only modeling methods for mapping current species distributions under different conditions.

Explanatory Variables

Five types of variables (temperature, precipitation, longitude, basin surface area, and source elevation) were selected according to the amount of data available on a large scale and in accordance with theories regarding species response to environmental gradients and resources (Austin 2007). The description of the model variables and the references for where these data were located were provided in Table 2. Because of the amount of data, only the major references were cited. If data originated from Web sites, we searched for confirmation in peer review articles.

We selected three variables providing a physical description of the basins. Longitude at the mouth (Long) can be related to biogeographical history with two major events that profoundly affected fish extinction, dispersal, and speciation

Table 1.—Diadromous fish species studied. The list is taxonomically ordered according to Kottelat (1997) and Kottelat and Freyhof (2007). * represents the catadromous species compared to the anadromous species.

Family	Scientific name and authority	Common name
Petromyzontidae	<i>Caspiomyzon wagneri</i> (Kessler, 1870)	Caspian lamprey
Petromyzontidae	<i>Lampetra fluviatilis</i> (L., 1758)	River lamprey
Petromyzontidae	<i>Petromyzon marinus</i> L., 1758	Sea lamprey
Anguillidae*	<i>Anguilla anguilla</i> (L., 1758)	European eel
Acipenseridae	<i>Acipenser gueldenstaedtii</i> Brandt and Ratzeburg, 1833	Russian sturgeon
Acipenseridae	<i>A. naccarii</i> Bonaparte, 1836	Adriatic sturgeon
Acipenseridae	<i>A. stellatus</i> Pallas, 1871	Stellate sturgeon
Acipenseridae	<i>A. sturio</i> L., 1758	European sturgeon
Acipenseridae	<i>Huso huso</i> (L., 1758)	Beluga
Clupeidae	<i>Alosa algeriensis</i> Regan, 1916	
Clupeidae	<i>A. alosa</i> (L., 1758)	Allis shad
Clupeidae	<i>A. caspia</i> (Eichwald, 1838)	Caspian shad
Clupeidae	<i>A. fallax</i> (Lacépède, 1803)	Twaite shad
Clupeidae	<i>A. immaculata</i> Bennett, 1835	Pontic shad
Clupeidae	<i>A. kessleri</i> (Grimm, 1837)	Blackspined herring
Clupeidae	<i>A. tanaica</i> (Grimm, 1901)	
Clupeidae	<i>A. volgensis</i> (Berg, 1913)	Azon shad
Cyprinidae	<i>Vimba vimba</i> (L., 1758)	Vimba
Osmeridae	<i>Osmerus eperlanus</i> (L., 1758)	European smelt
Coregonidae	<i>Coregonus oxyrinchus</i> (L., 1758)	Houting
Coregonidae	<i>Coregonus</i> spp.	
Salmonidae	<i>Salmo caspius</i> Kessler, 1877	Caspian trout
Salmonidae	<i>S. labrax</i> Pallas, 1814	Black Sea salmon
Salmonidae	<i>S. salar</i> L., 1758	Atlantic salmon
Salmonidae	<i>S. trutta</i> L., 1758	Brown trout
Salmonidae	<i>Salvelinus alpinus</i> (L., 1758)	Arctic char
Mugilidae*	<i>Liza ramada</i> (Risso, 1826)	Thin-lipped mullet
Pleuronectidae*	<i>Platichthys flesus</i> (L., 1758)	European flounder

after the end of the Miocene: the Messinian salinity crisis (5 million years ago [Ma]) of the Mediterranean and the last glacial maximum (18,000 years ago) (Keith 1998; Reyjol et al. 2007). To test longitude as a predictor variable in our models, coordinates of the western basins were converted to negative values.

According to the species–area theory (MacArthur 1984; Angermeier and Schlosser 1989), the surface area of the drainage basin (Surf) should influence the number of species present in a basin. Increasing the sample area includes additional habitat types with groups of different species.

The source elevation of a basin (Elv) is an element of topography informing about the altitude range encountered in a basin (Leopold et al. 1995). Combined with precipitation, it represents the hydraulic potential of the river. This has consequences

for habitat characteristics and how demanding are the swimming skills required.

We selected two factors to define the climate experienced in the basins: air temperature at the mouth and precipitation across the whole basin. Air temperature in a certain range is a good proxy for water temperature. A linear relationship was found to exist between air temperature above 0°C and corresponding water temperature (Preud'homme and Stefan 1993; Pilgrim et al. 1998; Erickson and Stefan 2000). However, at low air temperature, stream temperatures often reach 0°C as an asymptote, and at high air temperature, strong evaporative cooling causes a flatter stream temperature–air temperature relationship (Mohseni and Stefan 1999). Precipitation informs about the amount of water a basin receives (Leopold et al. 1995). Discharge data are

Table 2.—Predictor variables, unit, range, and source data used in generalized additive model training.

Variable name and description	Unit	Mean	Minimum	Maximum	References
Climatic variables averaged over 1901–1910					Mitchell and Jones 2005 (CRU TS 2.1 database)
<i>At the outlet</i>					
TempAnn—annual air temperature	°C	11	4.8	20.2	
TempSum—summer air temperature	°C	18.9	6.2	30.1	
TempWin—winter air temperature	°C	3.5	–18	14	
<i>On the whole basin</i>					
PrecAnn—annual precipitation	mm/month	63.3	8.2	156.1	
PrecSum—summer precipitation	mm/month	55.9	0	172.1	
PrecWin—winter precipitation	mm/month	65.9	19.2	148.4	
Physical variables					
Long—longitude at the outlet	° (decimals)	14.1	–51.8	54.0	http://earth.google.com
Surf—surface drainage area	km ²	57,600	52	3,350,000	www.rivernet.org
Elv—elevation at the source	m	1,181	3	4,014	The Time atlas of the world, comprehensive edition 1975

difficult to obtain on so large a scale and models enabling precipitation to be converted into discharge are finalized at the local scale only and cannot currently be applied to regions.

We compiled historic data from the CRU TS 2.1 (Mitchell and Jones 2005) database, which consists of 1,200 monthly grids of observed climate for the period 1901–2002, covering the global land surface at 0.5-degree resolution. Temperature and precipitation data used in our models were averaged over 10 years between 1901 and 1910 to smooth interannual variability. As stated in the introduction, this decade was before the first warming period registered during the 20th century (IPCC 2007). Climate data were not available on a European scale before 1900. Precipitation across the whole basin corresponded to the average for all the grids contained in the basin. This calculation was performed with ArcGIS 9.0 and the Zonal Statistics tool (ESRI 2004).

Annual air temperature/precipitation (TempAnn/PrecAnn) at the river mouth and across the whole basin, respectively; the mean over the three summer months (June, July, and August—TempSum/PrecSum) and the mean over the three winter months (December, January, and February—TempWin/PrecWin) were tested separately.

Distribution Models of Diadromous Fish

Model building.—From among the various methods for predicting and explaining the presence–absence of species in relation to environmental variables (Guisan and Zimmermann 2000), we used GAMs (Hastie and Tibshirani 1990), which are semiparametric extensions of GLMs. Generalized additive models are more flexible; they permit both linear and complex additive response shapes, as well as combinations of the two within the same model (Wood and Augustin 2002).

In order to evaluate the quality of predictions for each species, we divided the original database into two subsets: calibration and validation. The first, a random sample from 75% of the total database, was used to calibrate (train) the models, whereas the second, constituted with the remaining data (25%), was used to evaluate (test) model predictions.

We used R software (R foundation core team 2005), the gam package (Hastie 2005), and some custom functions to implement the GAMs.

For each species, we examined all possible combinations of the five environmental variables, without posing and testing only plausible approaches, and selected the best models using the Akaike information criterion (Burnham and Anderson 2002). Interactions between variables were not relevant and were therefore not included in the analysis. To circumvent predictor colinearity, we added the three temperature/precipitation expressions (annual, summer, and winter) to the model separately.

We applied a binomial distribution of error via a logistic link function. A cubic smoothing spline method was chosen to smooth the studied variables, using a maximum of two degrees of freedom to avoid overfitting.

To obtain the relative importance of the predictors (their rank) in our models, we assessed the residual deviance change after excluding each variable in turn from the final model (Virkkala et al. 2005).

Model evaluation.—To assess the overall classification success of the model, we first derived a confusion matrix to tabulate the observed and predicted presence-absence patterns in order to provide a summary of the number of correct and incorrect classifications from the model (Fielding and Bell 1997). Using this matrix, five prediction success metrics were produced: (1) the percentage of sites where the model correctly predicted the presence-absence of each species was assessed (% well classified), (2) the percentage of sites where presences were correctly predicted was defined as model sensibility, (3) the percentage of sites where absences were correctly predicted was defined as model specificity; (4) the kappa coefficient measures the correct classification rate (proportion of correctly classified presences and absences) after the probability of chance agreement has been removed (Cohen 1960). Landis et al. (1977) proposed a scale to describe degree of concordance: 0.81–1.00, almost perfect; 0.61–0.80, substantial; 0.41–0.60, moder-

ate; 0.21–0.40, fair, and <0.20, fail; (5) area under the curve (AUC) relates true positive proportion (sensibility) and false positive proportion (1-specificity) over a wide and continuous range of threshold levels, which make it a threshold-independent measure (Fielding and Bell 1997). The AUC ranges from 0.5 for models with no discrimination ability to 1 for models with perfect discrimination. An appropriate guide for classifying the accuracy of AUC is Swets (1988): 0.90–1.00, excellent; 0.80–0.90, good; 0.70–0.80, fair; 0.60–0.70, poor; 0.50–0.60, fail. Last, we used the percentage of deviance, explained (DevExp) by our final models (Virkkala et al. 2005),

$$\text{DevExp} = \frac{\text{Null model deviance} - \text{final model residual deviance}}{\text{Null model deviance}} \times 100$$

as the sixth evaluation method.

Model Predictions under Climate Change Scenario

To examine future species distributions, we used the TYN SC 2.03 data set (Mitchell et al. 2004), which comprises monthly grids of modeled climate for the period 2001–2100 and covers the global land surface at 0.5-degree resolution. The control scenario represented the evolution of surface climate over the 21st century under the assumption that the mean climate remained fixed at 1961–1990 levels. The 20 climate change scenarios were made up of all permutations of five global climate models (GCMs) with four emission scenarios (IPCC 2000) (A1FI, A2, B2, B1).

Potential future distributions were projected by changing climate as predicted by the HadCM3 GCM under one of the most pessimistic and frequently used scenarios (A2). Temperatures and precipitation were averaged over 30 years from 2070 to 2099 in order to smooth interannual variability. The climate model resulted in a rise in annual temperature in our study area of between 1°C and 7°C and a reduction in annual precipitation for the southern basins in particular of up to 1% and 47%. Annual precipitation, on the contrary, increased in the same range for the northern basins of our set.

To transform probability values for each model into presence-absence, we used the threshold T , maximizing kappa statistics (Fielding and Bell 1997).

Results

Successful Model Building and Evaluation

For 20 species, we built robust models, including climatic variables and allowing predictions into the future. During calibration, all the models presented high AUC values (0.86–1), indicating their good accuracy. In the same way, kappa values (0.62–1) indicated substantial to almost perfect model discrimination ability. On average, final models explained 72% of deviance (Table 3).

The validation of single species models received high AUC values (0.70–1). The AUC values did not differ greatly between the calibration and the evaluation data set in the different species. However, kappa values were always weaker during the validation phase. Models were almost perfect for three species (sea lamprey, Adriatic sturgeon, and Atlantic salmon), substantial for eight species, moderate for seven species, and fair for two species (Table 3). All the selected variables were highly significant ($P < 0.001$). Longitude was included in all the GAMs models built for the 20 species. However, other variables also emerged as important predictors of species distribution. Temperature was retained in 15 models and was in fact the most explanatory variable for six species (rank 1). Surface drainage area was selected in 12 models mainly in rank 2 (eight species); precipitation was included in seven models and source elevation in one model. Relationships between species presence–absence and each predictor variable varied from simple increasing or decreasing trends to more complex unimodal trends. Unimodal characterizes a symmetrical or nonsymmetrical distribution that has only one mode (Table 4).

Successful Model Predictions under Climate Change Scenario

Predictions for the 20 modeled species revealed responses that were species-dependent. Nevertheless, these species could be placed into three categories: those gaining suitable basins with an expansion of the 1900 presence area of between 10% to 30%, those losing suitable basins with a contraction of between 16% and 92%, and those showing little or no change (Figure 2).

The expected trend of northward expansion was apparent for twaite shad and thin-lipped mullet, with no decreasing trend in the southern part of

their distribution area and a gain of suitable basins in the southern Baltic as well as in Ireland, Scotland, and Iceland (Figure 3a).

Caspian lamprey distribution decreased with the disappearance of this lamprey in the southern Caspian Sea (in Iran and Turkmenistan). Changes in the distribution of Russian sturgeon and stellate sturgeon tended to show the eradication of these species from small basins in the Black Sea and Caspian Sea. Potential suitable basins for Acipenseridae were recorded in Scandinavia, such as the Neva River near the Gulf of Finland or the Vistula River in Poland. However, these basins were a long way from the present distribution of these sturgeons. *Coregonus* spp. remained in the extreme northern part of its distribution area (Gulf of Bothnia and northern Norway). Future potential distribution for vimba *Vimba vimba* indicated a regression in small basins of the Black Sea and Caspian Sea and a northward movement in the Baltic. Arctic char *Salvelinus alpinus* remained present only in the four basins studied in Iceland and in the Altä River in northern Norway (Figure 3b). In the same way, the European smelt *Osmerus eperlanus* model tended towards a high rate of disappearance of this species across its entire distribution area with a potential new refuge in Iceland. The model for Allis shad indicated a major decrease in suitable conditions in Morocco, Portugal, and Spain but a northward expansion into Scotland and Iceland. For the European river lamprey distribution area, a decrease mainly in southern France around the Bay of Biscay was predicted. Next, the model projected a stable presence area, particularly in the British Isles. Model predictions for Atlantic salmon highlighted a disappearance from the Iberian Peninsula, the basins around the Bay of Biscay, and the small basins bordering the English Channel. In the same way, future predictions for sea lamprey highlighted a decrease in presence of this lamprey in Italian basins and in the Iberian Peninsula (Figure 3c). For brown trout *Salmo trutta*, the resident populations were predicted to disappear for the most part in all the countries bordering the Mediterranean up to the Charente River. The European flounder *Platichthys flesus* model tended towards a disappearance of this species in all the countries bordering the Black Sea and the Mediterranean (Figure 3d).

Adriatic sturgeon, Azov shad *Alosa tanaica*, Black Sea salmon *S. labrax*, Caspian trout *S. caspius*,

Table 3.—Summary of the final generalized additive models selected to explain the distribution of the diadromous fish. Calibration: training set (147 basins) considered to compute the model; validation: testing set (49 basins) considered to validate the model. *T* is threshold. Kappa values were calculated using the optimal threshold (*T*) that yielded maximum values for each of the models based on the model calibration data. The list is ordered taxonomically according to Kottelat (1997) and Kottelat and Freyhof (2007). AUC = area under the curve; DevExp = percent of deviance, explained.

Species	T	Calibration					Validation					
		% well classified	Sensitivity	Specificity	Kappa index	DevExp (%)	% well classified	Sensitivity	Specificity	Kappa index	AUC	
Caspian lamprey	0.50	99	100	99	0.92	0.99	85	94	50	98	0.54	0.74
River lamprey	0.41	92	96	88	0.83	0.96	66	80	78	81	0.59	0.91
Sea lamprey	0.50	97	100	94	0.94	0.99	75	94	90	100	0.87	0.95
European eel	0.72	99	100	93	0.96	0.99	80	94	95	83	0.73	0.90
Russian sturgeon	0.40	98	90	100	0.94	0.99	82	90	50	93	0.39	0.72
Adriatic sturgeon	0.32	99	83	99	0.83	0.99	83	100	100	100	1	1
Stellate sturgeon	0.37	94	87	96	0.81	0.97	65	94	50	100	0.64	0.74
European sturgeon	0.37	77	80	77	0.54	0.82	25	77	53	91	0.47	0.72
Beluga	0.51	98	96	98	0.92	0.98	78	94	67	96	0.54	0.80
Allis shad	0.59	90	85	92	0.78	0.94	51	82	71	88	0.59	0.94
Twaite shad	0.40	81	99	62	0.62	0.86	37	75	78	72	0.50	0.81
Azov shad	0.16	95	100	95	0.67	0.98	64	90	33	98	0.40	0.73
Vimba	0.36	93	85	95	0.80	0.97	65	87	40	100	0.51	0.70
European smelt	0.61	96	97	99	0.90	0.99	77	86	67	93	0.63	0.90
Coregonus spp.	0.13	100	100	100	1	1	96	96	75	98	0.73	0.86
Caspian trout	0.10	100	100	100	1	1	99	96	100	96	0.73	0.98
Black Sea salmon	0.46	97	87	98	0.86	0.99	71	98	100	98	0.66	0.98
Atlantic salmon	0.20	99	99	96	0.94	0.99	88	94	100	87	0.88	0.98
Brown trout	0.69	86	83	93	0.69	0.92	43	79	83	67	0.48	0.86
Arctic char	0.25	99	100	99	0.97	0.99	91	94	100	93	0.79	0.96
Thin-lipped mullet	0.59	91	93	87	0.80	0.95	49	83	79	92	0.61	0.91
European founder	0.48	95	99	82	0.85	0.97	66	86	93	67	0.63	0.88

Table 4.—Variables selected in final models showing nature of the relationship between each continuous variable and diadromous fish presence-absence. For each variable, numbers indicate its relative contribution (Rank) to the model. (s) represents smooth term of generalized additive models. Effect represents with a letter (P, positive; N, negative; U, unimodal with an intermediate optimum) the direction of the effect. For climatic variables, Type informs on the expression (Annual, Summer, or Winter) retained in the final model. The list is taxonomically ordered according to Kottelat (1997) and Kottelat and Freyhof (2007).

Species	Long			TempAnn TempSum TempWin			Surf			PrecAnn PrecSum PrecWin			Elv	
	Rank	Effect		Rank	Type	Effect	Rank	Effect		Rank	Type	Effect	Rank	Effect
Caspian lamprey	1	P												
European river lamprey	1(s)	U		2(s)	Annual	U				2(s)	Annual	U	3	N
Sea lamprey	1(s)	U		3(s)	Summer	U				2(s)	Annual	U		
European eel	1(s)	U												
Russian sturgeon	1(s)	P		3(s)	Annual	U	2	P						
Adriatic sturgeon	1(s)	U								2(s)	Annual	P		
Stellate sturgeon	1	P		3(s)	Annual	U	2	P						
European sturgeon	2(s)	U					1(s)	U		3	Annual	P		
Beluga	1	P					2(s)	P		3	Annual	P		
Allis shad	1(s)	N		2(s)	Summer	U	3(s)	U						
Twaite shad	1(s)	N		3(s)	Annual	P	2(s)	U						
Azov shad	1(s)	P		3(s)	Annual	U	2(s)	P						
Vimba	1(s)	P		3(s)	Winter	U	2(s)	P						
European smelt	3(s)	U		1(s)	Summer	U	2(s)	U						
Coregonus spp.	2(s)	U		1(s)	Annual	N	3(s)	U						
Caspian trout	1(s)	P												
Black Sea salmon	1(s)	P					2(s)	P		2(s)	Annual	U		
Atlantic salmon	2(s)	U		1	Annual	N	3(s)	U		3(s)	Annual	U		
Brown trout	1(s)	U					2(s)	P						
Arctic char	2	N		2(s)	Winter	N	3	P						
Thin-lipped mullet	2(s)	U		1(s)	Annual	P								
European flounder	2(s)	U		1(s)	Summer		U			3(s)	Annual	U		

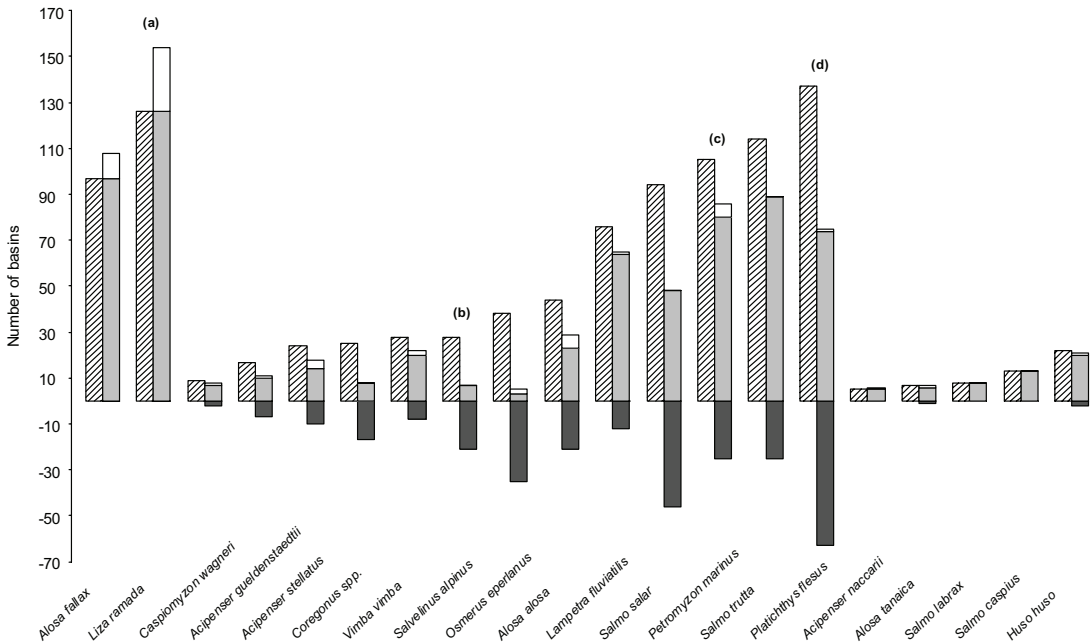


Figure 2.—Changes in distribution predicted for each species by generalized additive models. Hatched bars represent the number of basins where the species occurred in 1900. Light gray bars represent basins where the species remained in 2100 under climate change. White and dark gray bars represent respectively the number of basins gained and lost by a species in 2100 under climate change. Letters indicate the species for which a map was produced in Figure 3. The species were sorted to highlight groups according to response to climate change. Within a group, the species were sorted by increasing frequency of occurrence in the study area.

and beluga remained stable without clear expansion or contraction of their distribution area under global change.

Species Failing during the Modeling Process

First, no models were established for *Alosa algeriensis*, Caspian shad, blackspined shad, Volga herring, and houting because of their too narrow distribution range (presence in only two to four basins over the 196 investigated). The Pontic shad model was not mentioned because of poor results during the validation phase. The kappa value inferior to 0.20 indicated that the model failed especially in the prediction of presences.

Second, the model for European sturgeon *Acipenser sturio* was not sufficiently relevant to perform an accurate prediction, with only 25% of deviance explained by this model and the weakest kappa and AUC values during the calibration

phase (Table 3). Finally, climatic variables were not significant in the European eel model; thus prediction under climate change scenario could not be performed (Table 4).

Discussion

The Model Approaches and the Use of GAMs

Presence-absence models performed well (i.e., discriminated successfully between presences and absences for 20 species out of 28). The level of discrimination in these models was good to excellent (AUC values 0.86–1) during the calibration phase. The high calibration kappa values confirmed the good discrimination ability of the models. Furthermore, predictions made for the independent validation data set successfully predicted occurrence for these species. Both validation AUC values and validation kappa values ranged from fair to excellent. Our overall con-

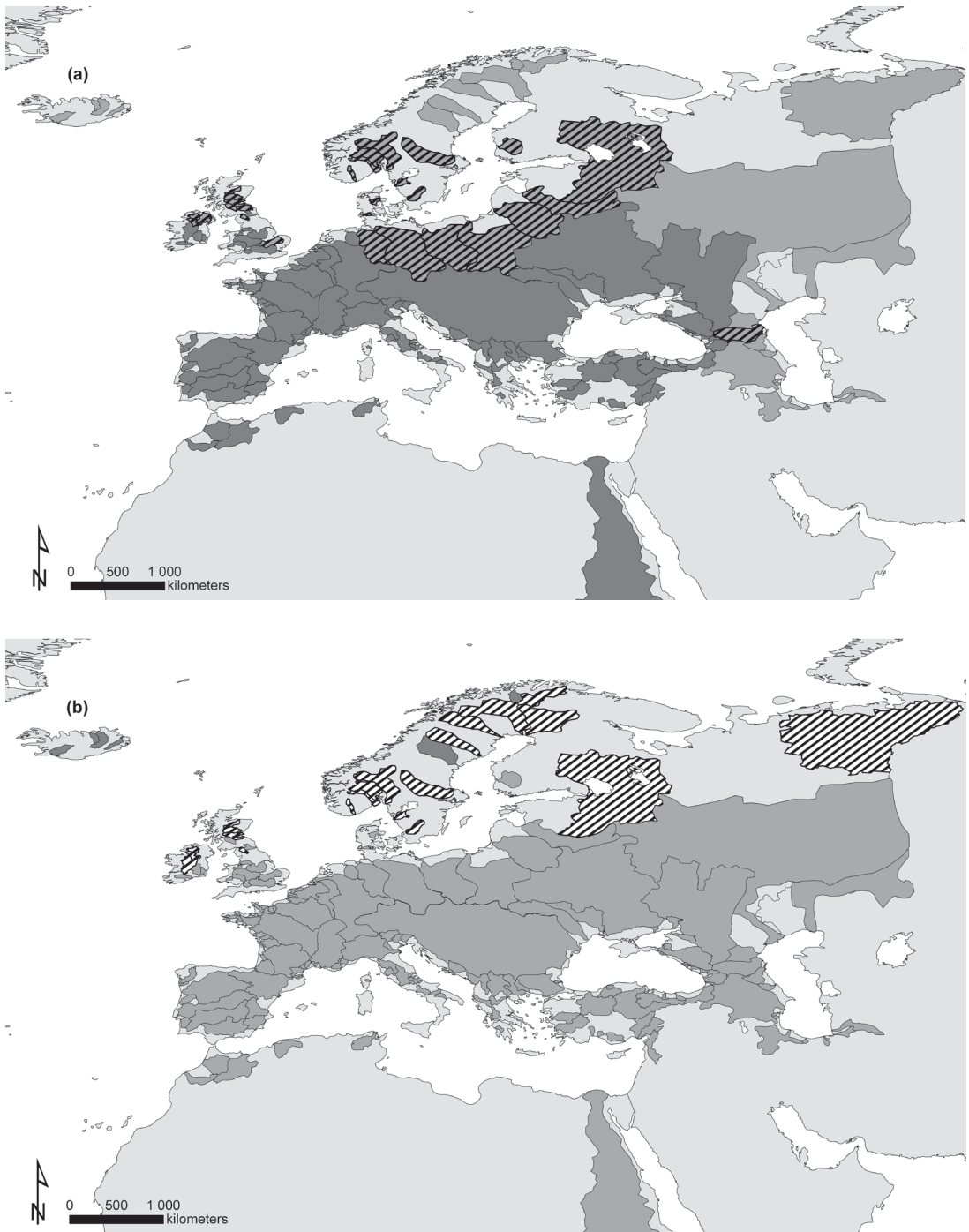


Figure 3.—Projected future potential distribution for (a) thin-lipped mullet, (b) Arctic char, (c) sea lamprey, and (d) European flounder. Dark gray color corresponds to stable suitable basins, clear gray to stable unsuitable basins, hatched with a white background to loss of suitable basins, and hatched with a gray background to gain of suitable basins. Nile (Egypt) and Kapisillit (Greenland) basins were truncated to offer a better visualization of the whole study area.

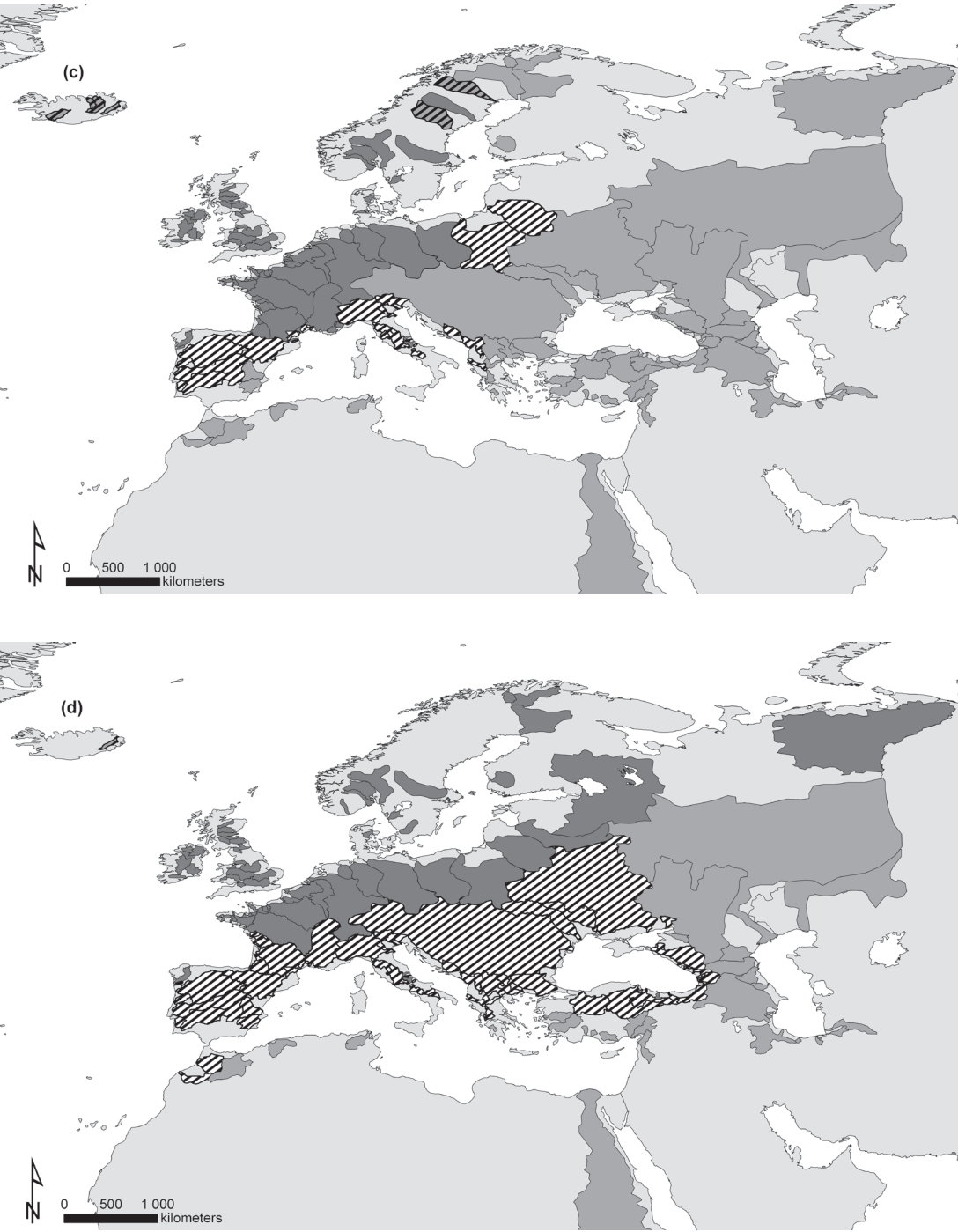


Figure 3.—Continued.

clusion is that GAMs were successful in describing and predicting the occurrence of most species.

No models could be established for *Alosa algeriensis*, Caspian shad, blackspined shad, Volga herring, and houting because of the rarity of these species in the study area (i.e., only one to four basins with these species in the study area). Indeed, in our database EuroDiad 2.0, *A. algeriensis* is only recorded in North Africa, Caspian shad is endemic to the southern Caspian Sea, blackspined shad and Volga herring spawn in the Caspian Sea, mainly in two northern rivers, and houting is recorded in a few basins in Germany and the Netherlands. To establish models with high discrimination abilities for these species, we would have to enlarge and detail our database in these specific regions.

The Pontic shad model failed during the validation phase with a null kappa value. Source elevation was retained as a predictor with a bimodal response curve (low and high optima) indicating a variable that was too distal with no direct physiological effect. A more ecologically relevant variable related to source elevation has to be found to build a distribution model for pontic shad. The European eel model included only longitude as an explanatory variable, mainly because the species was recorded as present in most of the basins. In further study, an abundance index should be used.

Environmental Variables and Their Relevance in the Modeling Process

The individual response functions for the continuous variables presented in Table 4 are u-shaped (bimodal) as well as bell-shaped (unimodal) and truncated versions of these functions. These results are in agreement with Austin's (2007) conclusions. Inspection of the relationship between each variable and species presence-absence revealed that the GAMs were generally interpretable and plausible.

Longitude was retained in each model, mainly in first rank. The eight species endemic to the Caspian Sea had a positive correlation between their probability of presence and longitude. This is in accordance with the biogeographical history and particularly with the formation of the present Ponto-Caspian region 5 Ma. It is now widely accepted that during the Messinian (7.1–5.3 Ma; Berggren et al. 1995), the Mediterranean (Tethys) was at least partially dried up (Hsü et al. 1973, 1977). Hsü (1972)

has suggested that Paratethys, a northern arm of the Mediterranean extending from the Rhone basin to the Caucasus, dried up too. This phenomenon resulted during the Pliocene (5.3–1.8 Ma; Berggren et al. 1995) in the formation of the Black Sea and Azov Sea, the Balaton Lake in Hungary, the Caspian and the Aral seas, and the development of a highly endemic fauna in this area. However, under the climate change scenario used in our study, Baltic basins were predicted to become suitable for Beluga, Russian, and stellate sturgeons. These basins, which are in the same range of longitude as the Ponto-Caspian region, are not connected to this region. This result underlined the necessity to find a more relevant proxy for endemism and biogeographical history (Oberdorff et al. 1997, 1999).

Temperature was used in 15 models. For the species described as coldwater species in the literature, Atlantic salmon, brown trout, Arctic char (Klemetsen et al. 2003), and *Coregonus* spp. (Svärdson 1970), models were mainly established using the winter temperature as an explanatory variable with a decreasing trend for this variable. Two species retained the annual temperature with an increasing trend. Indeed, for twaite shad, temperature appears to play an important role in the onset of spawning, with a range of 18–22°C (Aprahamian et al. 2003). Thin-lipped mullet is recorded in all the temperate and tropical seas entering lagoons and estuaries and rivers between temperatures of 8–24°C (Keith and Allardi 2001). Temperature appeared to have an influence for nine other species with bell-shaped response curves. Both annual and summer temperatures were retained equally in these models. Optimal temperatures registered for each species were in accordance with ecological observations (European river lamprey and sea lamprey [Maitland 1980], Russian sturgeon and stellate sturgeon [Holcik 1989], Allis shad and Azov shad [Hoestlandt 1991], vimba [Zayanchkauskas 1970], European smelt [Nellbring 1989], and European flounder [Fonds et al. 1992]).

Surface of the drainage basin appeared to have an influence on continental diadromous fish distribution. This variable was selected with an increasing trend in 12 models out of 20. This could be related to the species-area theory (MacArthur 1984; Angermeier and Schlosser 1989) and more precisely to environmental heterogeneity. Increasing the sample area includes additional available habitat types

(Williams 1964). Nevertheless, probability of presence decreased for five species for very large basins more than 200,000 km². There may be a trade-off between habitat availability and stream hydraulicity. Moreover, species presenting this decrease were among the smallest ones, such as Allis shad, twaite shad, European smelt, and *Coregonus* spp.. For example, Allis shad cannot swim upstream if the speed of the current exceeds 2 m/s, and they cannot jump (Cassou-Leins 1981). The spawning sites of twaite shad are homogeneous, sandy, and muddy, indicating a low stream velocity (Hoestlandt 1991).

Precipitation was included in 7 models out of 20, and annual precipitation was the only selected expression. This variable is easily available on a large temporal and spatial scale and acts as surrogate for a more proximal variable such as depth or a linked factor like current speed or associated granulometry. Indeed, the two species that presented an increasing trend with this variable are sensitive to stream depth during spawning periods. During both the seaward and the spawning migration, the beluga normally travels in the deepest parts of the riverbed (Holcik 1989; Vecsei et al. 2002). In rivers, Adriatic sturgeon seeks out deep pools with high flow rates (Bronzi et al. 2005).

Elevation acted only for European river lamprey, which exhibited a decreasing trend with this variable. *Ammocoetes* live in rivers where they burrow in the silt bottom either in the main channel or along the bank. Moreover, in Scandinavian rivers, average flow rates over the burrows of *Lampetra* sp. have been recorded at 0.08–0.1 m/s (Hardisty 1986). These elements of their ecology suggest a preference for rivers with a low hydraulic potential.

Limitations of the Approach

Accurate absence data in particular are often difficult to obtain (Hirzel et al. 2002). A species may be undetected even though it was present, especially for inconspicuous species. Nevertheless, most diadromous fish species are not very small in size and all of them can be caught by fishermen; therefore, the existence of cryptic populations is very unlikely. A mobile species could be absent from the site only temporarily. However, for each basin in our data set, we collected several references to its fish fauna from different dates. In some cases, authors neglect rare species or species whose distribution is

limited to the lower reaches of basins. Thus, in the case of contradictions between data sources of the same quality, data indicating presence were favored in our study. Furthermore, difficulties might arise when working with historical data. As historical records mostly originate from opportunistic sampling, they show sampling biases (e.g., certain localities have been investigated more frequently than others or no information is available on the exact locality of the survey) (Lütolf et al. 2006). Thus, we chose to investigate species presence–absence on a large scale (basin scale) to reduce the sources of error in our data. To go further in the predictions of diadromous fish distributions, an abundance index should be used to split the presences into several classes such as rare, moderate, or abundant levels. In this way, a population predicted to be still present but in strong decline could be detected, which was not possible with presence–absence data.

It is important to remember that the protocol developed in our study corresponds to projections of a pristine situation in a changing global environment, focusing on the climatic suitability of the habitat. Our models show habitat changes and infer changes in fish distributions. However, the potential success of these species depends on other crucial factors such as the distance to cover and their dispersion tactics (Solomon and Shugart 1993; Bakkenes et al. 2002). Further studies on variations in life history traits along a latitudinal gradient could address the issue more precisely and could provide information on the possibility of the predicted distribution being filled by the species according to the dynamic of its populations (Lassalle et al. 2008). Furthermore, this study does not include any estimates of the regional anthropic pressures that are placed on aquatic ecosystems, such as the erection of dams in main stems (Gowans et al. 1999; Larinier 2001; Hill 2009), the deterioration in water quality in industrialized areas (Breine et al. 2007; Maes et al. 2007; Woodland et al. 2009), or unsustainable fisheries (Masters et al. 2006). However, there are two main limitations to the inclusion of these variables into the modeling process: first, finding relevant proxies and then, developing evolution scenarios for these variables in the future.

There are at least three sources of uncertainty inherent in the modeling process presented in this paper and other published studies (Thuiller 2003): uncertainty based on climate change scenarios, un-

certainty based on the modeling techniques, and uncertainty based on the selection of the threshold to transform probability values into presence–absence form. We tried to minimize the two sources of error that we could control. First, the modeling technique used in this work (GAMs) allowed us to fit realistic descriptions of relationships between species and environmental predictors with complex and nonlinear response curves (Hastie and Tibshirani 1990; Austin 2007). Moreover, rather than simply following the conventional decision threshold of 0.5 (Oberdorff et al. 2001), we examined thresholds with 0.01 accuracy for each of our models and selected the probability level that gave the highest Cohen's kappa values (Fielding and Bell 1997). To show the range of possibilities, it would be necessary to test all the emission scenarios from the most optimistic to the most pessimistic.

Implications for Management

Our results showed that basins that were suitable in 1900 could become unsuitable under climate change. There are species for which the existence of suitable space is predicted to be sufficiently reduced to cause serious concern and thus further support their conservation. This category would include Nordic species such as Arctic char and European smelt, which are currently classified as LR (low risk) and DD (data deficient), respectively, in the International Union for the Conservation of Nature (IUCN) World Red Data Book (IUCN 2006). These Nordic species are at the border with the Arctic region and thus do not have new territories to colonize if they were to face global warming (Figure 3b). More generally, 20 European diadromous fish species are listed under the 2006 IUCN red list and the most threatened are also protected by European and national laws. Consequently, restoration and management plans have been set up to reduce harmful impacts on species, to sustain populations by stocking, or to reintroduce an extinct species into a basin (Lyle and Maitland 1997; Prignon et al. 1999; Kirschbaum and Gessner 2000). Action plans aim to reverse the trend for the remaining populations, but also to restore the species to their historical range (i.e., 1900). Therefore, in the light of the distribution changes predicted by our models, we argue that global warming issues should be included in diadromous fish conservation or restoration plans (Rochard et al. 2009).

In conclusion, models were established for almost all diadromous fish species recorded in Europe, North Africa, and the Middle East. In accordance with ecological theories, five variables related to physical habitat and climate were retained as explanatory variables in GAMs. Predictions at the end of this century under the global warming assumption revealed a shift in distribution for many diadromous species. The modeled species could be placed mainly into three categories: those losing suitable basins, those gaining suitable basins, and those showing little or no change. This first assessment of future diadromous fish distributions provides useful guidelines for their conservation and management.

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