

# Anticipating the impact of climate change on fish communities

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## Introduction

**A**s indicated in the previous chapters, recent climate trends (first chapter) have already progressed sufficiently to cause considerable effects on fish communities in the lakes and rivers of continental France, at multiple levels of scale from individuals to communities (second chapter). Given the major conservation and/or economic issues surrounding certain species and the role played by fish in aquatic ecosystems, the need to assess the future impact of the trends on fish populations has taken on crucial importance.

A number of models have been developed recently to assess the impact of climate change on species distribution and thus anticipate its effects. Most of these models are based on the notion of niche for each species. A niche may be defined as the multi-dimensional space representing both the position occupied by a species in a given environment and all the conditions required to sustain the species (Hutchinson, 1957). The geographic areas offering these conditions correspond to the potential range of the species (fundamental niche). However, within the fundamental niche, a number of factors limit the dispersal of the species (geographic barriers, etc.) and its survival (predation, pathogens, etc.) to a more limited, effective range, called the realised niche.

Among the existing models, species distribution models (SDM) input the data describing the effective range of species (realised niche) and add a number of measured environmental variables such as the climate, topography or soil type in order to statistically model the ecological envelopes in which the species can live (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). These envelopes then serve as filters in selecting areas that in the future will offer favourable conditions for various species (Pearson and Dawson, 2003; Jeschke and Strayer, 2008). A basic hypothesis underlying these models is that the species have achieved stability (equilibrium) within their environment (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). This is because the data used to build the models are generally collected over a relatively short period and a limited geographic zone. The data thus constitute a "snapshot" of the effective distribution of species and the models do not take into account colonisation dynamics and limiting factors such as environmental disturbances (e.g. pollution, land use, droughts) and past events (e.g. glacial periods), which can lead to situations where an equilibrium does not prevail. In addition, the future distribution does not take into account any new interactions between species (e.g. predation, competition) or their capabilities to disperse or to adapt to changes in the environment. When used in conjunction with environmental-change scenarios, these models produce projections for the zones where the combinations of variables are potentially favourable for a species. These zones must therefore not be interpreted as the future range of the species, but rather as potentially favourable habitats in the future (Guisan and Thuiller, 2005).

Contrary to statistical models, mechanistic (matrix or individual-based) or hybrid models attempt to reproduce a part of the processes by incorporating ecophysiological traits and/or demographic data specific to the species (Kearney and Porter, 2004; Buckley, 2008) (see Box 8). These approaches are based primarily on the physiological tolerance limits of species (Guisan and Thuiller, 2005; Kearney, 2006) and can be used to determine, for example, the climatic limits to the range of a species. The advantage of these types of model is that they do not depend on the observed distribution of a species and some explicitly take into account adaptive and evolutionary processes. In other words, they model the fundamental niche of the species. However, they require a great deal of knowledge and data on the ecology and physiology of the organisms, information that is not always available. For this reason, these models should, at this point, be seen as research topics rather than as management tools.

The purpose of this chapter is to present the approach adopted by statistical distribution models and the main results of these models, without neglecting the other modelling approaches. The results inform on the potential effects, over the coming century, of climate change on the distribution of the fish in France.



## Distribution models

### General structure

The basic ideas behind distribution models are fairly simple in that the models describe the link between:

- the environmental variables known to influence species distribution;
- the data on species distribution, drawn from atlases and inventories.

Statistical models produce a probability of occurrence for a species as a function of the environmental variables. They can subsequently be used to model the effective distribution of the species (realised niche), then to project the changes in favourable habitats (potential distribution) over space and time (see Figure 38).

Figure 38

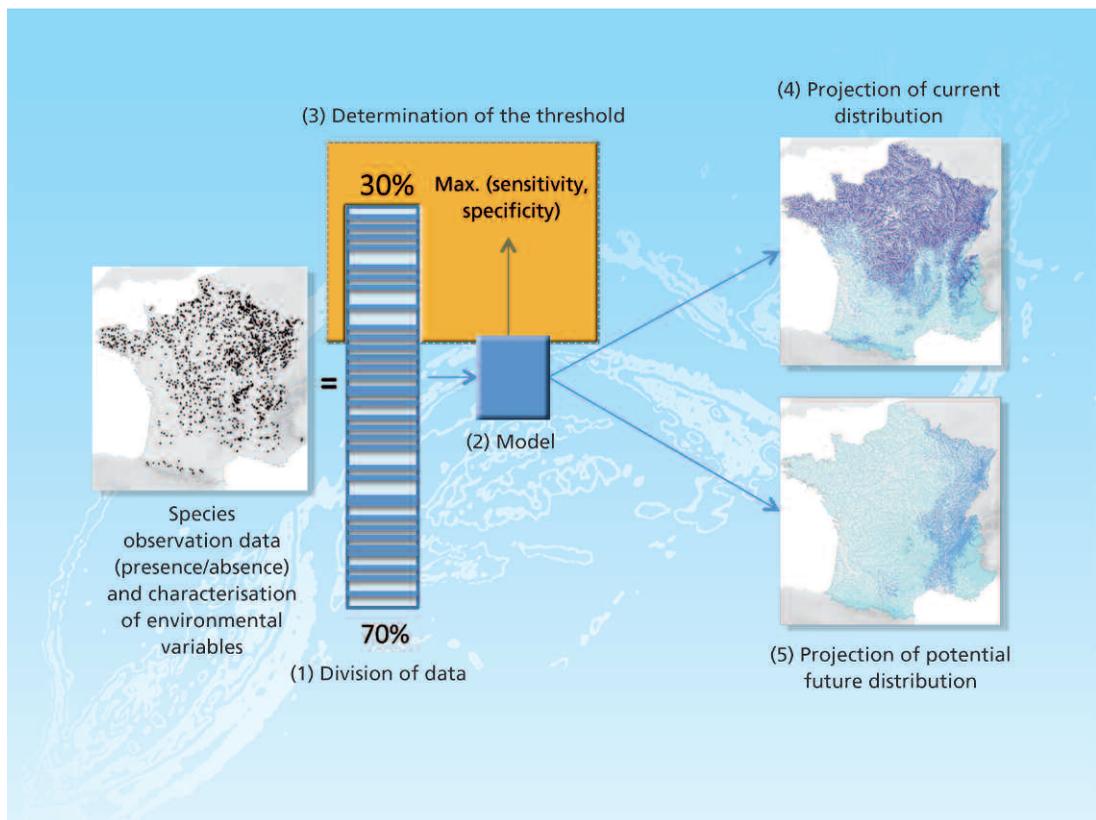


Diagram showing the various steps in statistical modelling (diagrams modified, originally from Nenzén and Araújo, 2011).

(1) The observation data on the species are randomly divided into two batches for the model calibration and assessment phases (see below).

(2) 70% of the data are used for the calibration phase.

(3) The resulting model is applied to the remaining 30% of data to test model performance (sensitivity, specificity). The results serve to determine a probability threshold between presence and absence of the species. The model is used to project the probability of occurrence to the current environment (4) and the future environment (5).

The formulation of species distribution models involves the following steps:

- selection of the statistical methods;
- description and selection of the data used to build the models;
- the main steps involved, e.g. calibration, validation and projection of the favourable or unfavourable habitats (see Figure 15) in a suitable context, for example the French hydrographic network (Vogt *et al.*, 2007);
- production of results, i.e. indices for species and communities.

These different steps are discussed in detail below.

## Selection of the statistical methods

The different approaches to statistical modelling are traditionally grouped into six major types:

- geographic envelopes;
- climate envelopes;
- multivariate methods;
- regression methods;
- classification methods;
- learning methods (Guisan and Zimmermann, 2000).

These approaches differ in terms of the required types of data, the underlying hypotheses, the mathematical algorithms and/or the complexity of the model.

Three types of models are commonly used (Elith *et al.*, 2006; Lawler *et al.*, 2006; Pearson *et al.*, 2006; Buisson, 2009) (see Box 7). However, none have achieved true consensus because they all have a number of advantages and disadvantages. For this reason, some researchers have suggested that all the approaches be considered simultaneously with a comparison of the output variables (Thuiller *et al.*, 2009). Others favour using a single statistical approach (Logez *et al.*, 2012).

Box 7

### Presentation of the statistical methods

The most commonly used types of statistical methods are presented below.

■ **Generalised linear models (GLM)** (McCullagh and Nelder, 1989) can model relations more complex than simple linear regressions. **Generalised additive models (GAM)** (Hastie and Tibshirani, 1990), a non-parametric extension of GLMs, produce smoothed response curves on the basis of the observation data. **Multivariate adaptive regression splines (MARS)** (Friedman, 1991) are an adaptive adjustment method using non-linear regression, based on data divided into subgroups for which local adjustment (smoothing) is carried out.

■ **Classification methods such as Linear discriminant analysis (LDA)**, which builds synthetic variables using linear combinations of explanatory variables to enhance discrimination of presence/absence data and **Classification and regression tree methods (CART)** (Breiman *et al.*, 1984), based on building a decision tree in order to rank data according to the explanatory variables.

■ **Learning methods such as Artificial neural networks** (Rumelhart and McClelland, 1986) are based on weighted non-linear combinations of the explanatory variables that are optimised to improve predictions. **Random forest methods (RF)** (Breiman, 2001) build hundreds to thousands of decision trees (similar to CART). **Aggregated Boosted Trees (ABT)** (Friedman, 2001) are based on building sequences of decision trees combining a boosting algorithm and a regression-tree algorithm.

## Description and selection of the data used to build the models

### ■ Presence (and absence) data

The presence data<sup>20</sup> constitute the basic input for distribution models. These data are generally drawn from inventories using standardised and systematic protocols (electrofishing sampling strategies), but also local observations (sport fishing) and museum collections. Presence can thus be documented on various spatial scales depending on the source of information (monitoring point, river reach, river basin).

Data representativeness is a decisive factor. For each species, the data must be capable of describing the most complete range of favourable and unfavourable conditions possible, in order to model as accurately as possible the effective distribution of the species (Stockwell and Peterson, 2002; Barry and Elith, 2006). Distribution modelling implies that the data must cover all or almost all of the range, i.e. on the European scale for most taxa (with the exception of certain exotic species, such as catfish and topmouth gudgeon). Practically speaking, the species that have not undergone extensive study or are relatively rare are generally not included in assessments.

### ■ Environmental variables

To produce robust projections, selection of the environmental data (called the explanatory variables) is an important step because it implies selecting the parameters that best describe the realised niche of the species (Pearson and Dawson, 2003; Dormann, 2007; Broennimann *et al.*, 2007).

The environmental data may be drawn directly from data-collection campaigns in the field on the local scale or from geographic databases providing information on, for example, the climate conditions, relief or land use. Specifically concerning climate data, national data on the current and future situation are available from Météo-France as well as from international organisations (Worldclim<sup>21</sup>). However, the spatial resolution is limited (maximum resolution = a raster<sup>22</sup> with cells of 1 km x 1 km, in general). Downscaling<sup>23</sup> can subsequently be used to link the presence data obtained on the scale of a monitoring point or a river reach with the available climate data (see the first chapter).

Selection of the explanatory variables is subject to a certain number of constraints. For example, selection of a limited number of explanatory variables, based where possible on confirmed biological mechanisms, produces results that are easier to interpret and more robust. The variables should also limit as much as possible any redundancy in the information they provide (correlation) in order to avoid bias caused by collinearity phenomena. Conversely, when useful variables, e.g. water temperature, are not available but are nonetheless fundamental in explaining species distribution, it is possible to use another highly correlated variable as a proxy, for example the air temperature (Buisson *et al.*, 2008; Sharma *et al.*, 2007; Lassalle and Rochard, 2009a).

## Main modelling steps

The steps in statistical modelling are presented below.

The first step, called the calibration step, corresponds to a learning phase in which the model is designed to produce predictions that correspond as closely as possible to the observed presence-absence data. The output data of a calibrated model generally corresponds to presence probabilities ranging from 0 to 1.

20. Ideally, absence data could also be used. However, it is much more difficult to prove the absence of a species than its presence due to constraints inherent in sampling techniques.

21. <http://www.worldclim.org/>.

22. Image data divided into a matrix of squares.

23. A technique used to obtain information on the local or regional scale from larger-scale climate projection models or data analyses (see the first chapter).

The second, validation step is an assessment phase to determine the predictive performance of the model. A number of approaches exist and are generally based on confronting the projections with a set of observed data that were not used for the calibration phase. To judge the predictive performance of a model, various indices are used (Liu *et al.*, 2005; Nenzén and Araújo, 2011). Examples are the sensitivity (the percentage of correctly predicted presences) and the specificity (the percentage of correctly predicted absences). The currently most widely used coefficients are True skill statistic (TSS) (Allouche *et al.*, 2006) and Area under the receiver operating characteristic curve (AUC) (Hanley and McNeil, 1982). The capacity of a model to make correct predictions may differ for the presence and absence of a species, which means it is necessary to use the different indices during the assessment phase to quantify the level of confidence that may be vested in the model.

Note that in both cases, the presence probabilities calculated by the model (between 0 and 1) can be converted into a binary variable (presence = 1, absence = 0) for comparison purposes with the input data (presence-absence). To that end, a threshold must be set<sup>24</sup>. Above the threshold, the probability of occurrence for the species is assumed to be a presence, below the threshold an absence. This technique simplifies model interpretation, however it masks a part of the uncertainty affecting the model.

## Determining the favourability of current and future habitats

At the end of the calibration and validation steps, the calibrated models are used to project the current distribution of each fish species. Using the results and in view of anticipating the impact of climate change on fish communities, the probabilities of future occurrence under the new climate conditions are then calculated in order to project the potentially favourable, future habitats for each of the studied fish species.

## Results

### ■ Results on the species level

By comparing the current and future ranges (presence-absence) for each species, it is possible to calculate the gains and losses of potentially favourable habitats and the changes (expansion, displacement, shifts, contraction) in the range, and then to estimate the vulnerability and the risks of local extinction for a species in a given context. The change in the distribution of a species is generally expressed using indices, notably:

- the variation in prevalence, i.e. the change (between the current and future climates) in the number of spatial entities where the presence of the species is predicted (expressed as a percentage of favourable sites);
- the Species range change (SRC) (Thuiller *et al.*, 2009), i.e. the difference in the future between the number of "newly favourable" spatial entities and the number of "no longer favourable" spatial entities, divided by the number of currently favourable spatial entities for the species.

These indices<sup>25</sup> may be accompanied by an expert-knowledge-based index indicating the degree of relevance of the projections taking into account the biology of the studied species (see Box 8).

### ■ Results on the community level

The individual responses for each species present in each assemblage are then combined to assess the effects of climate change on the structure of communities. A number of indices are produced:

- the first is species richness, i.e. the total number of species present in each spatial entity (current and future richness, and the difference between the two). This index is calculated by adding together all the presence-absence maps of the studied species for both the present and the future;

24. A threshold above which the habitat is considered favourable for the species must be set, taking into account a specific combination of environmental data. Traditionally, a threshold of 0.5 has been used, but other approaches have been suggested. They are based on the capacity of models to correctly reproduce presence and absence in order to optimise the threshold probability of occurrence value (Liu *et al.*, 2005; Nenzén and Araújo, 2011).

25. Note that other indices may be formulated on the basis of the results obtained, e.g. length of river reaches gained or lost by a species.

- it is also possible to qualify the change in the composition of communities using a renewal index estimated on the basis of loss or gain of species at a given point (Peterson *et al.*, 2002; Buisson and Grenouillet, 2009);
- finally, a "similarity" index (e.g. the Jaccard index) compares the number of species found in both communities and the number of species found in only one or the other of the communities. It can vary between zero (no common species) and one (identical communities). Generally speaking, an increase in similarity suggests greater uniformity of communities whereas a reduction indicates differentiation (Olden and Rooney, 2006; Buisson and Grenouillet, 2009).

### Qualitative assessment of projections based on expert knowledge

In addition to statistical indices, the predictive performance of the models can be assessed by experts (ichthyologists) on the basis of current knowledge on species ecology. For example, for the Explore 2070 project (MEDDE/Biotope, 2013), the results were assessed in light of the intrinsic capabilities of the species to disperse. The dispersal capability was assessed using three criteria:

- the intrinsic capability of the species to disperse under favourable conditions (Keith and Allardi, 2001; Jenkins *et al.*, 2007);
- the capability of the species to overcome obstacles to flow, whether natural or anthropogenic;
- the degree to which the species is manipulated by humans, either voluntary (stocking) or involuntary manipulation (e.g. escape from a fish farm).

The resulting index is expressed on a scale of three, i.e. the probability of the species being able to colonise a new habitat is low, medium or high.

For a species for which the probability of colonisation is low, it is assumed that its future favourable habitat will not differ significantly from the habitat projected using the "zero dispersal" hypothesis (see Box 11). If the projection foresees a major reduction in the favourable habitat, the species is considered highly vulnerable. Conversely, when the probability of colonisation for a species is high and the future favourable habitat increases significantly under the "unlimited dispersal" hypothesis, the species is considered less vulnerable to climate change.

### The limits of modelling

Multiple sources of uncertainty are inherent in the use of models. Uncertainty may arise from the hypotheses on the GHG emission scenarios (see the first chapter) or from the design itself of the models due to the equations used or the processing of the equations (climate models, species distribution models, downscaling models). It may also be caused by the quality of the biological and/or environmental variables or the lack of representativeness of certain processes. The sources of uncertainty are listed below.

#### Quality of the biological and environmental variables

The capacity of models to correctly project the ecological niche of species depends directly on the quality and relevance of the ecological input variables. However, numerous constraints and uncertainties weigh on the collection of biological and environmental data.



### **Biological variables**

The capacity to detect the fish of a given species can vary widely from one site to another, depending on the behaviour and abundance of the species, the type of environment, the sampling method, and can also vary according to the season of the year (meteorological and hydrological conditions). For example, adult carp live in areas that are too deep for electrofishing and their reproductive success (presence of juveniles) varies widely over time. Consequently, the absence of a species in a sample does not mean that the species is necessarily absent on the site. Anthropogenic pressures can also skew modelling of realised niches for many species (see the section below).

### **Environmental variables**

Integration of all the environmental variables informing on the ecological requirements of species is relatively difficult for reasons having to do with data availability and with statistical issues. Environmental variables fluctuate over both time and space. In general, model inputs consist of averaged data that mask extreme events that may occur more often in the future.

In addition, when certain fundamental variables are not available, proxies are used. That is notably the case for water temperature or river discharges, which are proxied by the use of air temperature and precipitation respectively (however, see Box 9). The use of proxies can lead to errors in some cases, for example when the water temperature is not linked to air temperature because the water is supplied by the water table or in the case of mountain streams supplied primarily with snow melt.

Other data, such as certain physical-chemical variables, e.g. oxygen content of water, are generally not input directly into models because standardised, large-scale measurements are technically difficult to obtain.

Finally, if the given range of environmental variables is too narrow, only partial characterisation of the niche for a species will be possible. In this case, favourable environmental conditions will not be taken into account, which will skew the calculated relation between species occurrence and the environmental variables.

All these factors result in approximations that, for certain species, reduce the capacity of models to produce robust projections on their ecological niche.

## **Box 9**

### **Inclusion of hydrological data in distribution models**

A line of research currently being explored attempts to integrate hydrological variables in distribution models by connecting a hydrological model to the climate models and then inputting the resulting hydrological data in the distribution models (Jähnig *et al.*, 2013).

This development work is currently under way, but is confronted with numerous technical difficulties. Even though the links between river discharge and ecological characteristics have been studied at length (see for example Bergerot, 2013; Anderson *et al.*, 2006; Lancaster et Downes, 2010; Poff and Zimmerman, 2010), the impact of modified hydrological regimes on biological behaviour is still poorly understood due to the large number of factors (hydrological factors and their interaction with other environmental factors) affecting the response of individual organisms.

### ■ Projections exceeding the data available for models

Extrapolation is a statistical term pertaining to the projections of a model using sets of data that are not those for which the model was designed (see Figure 39).

Figure 39

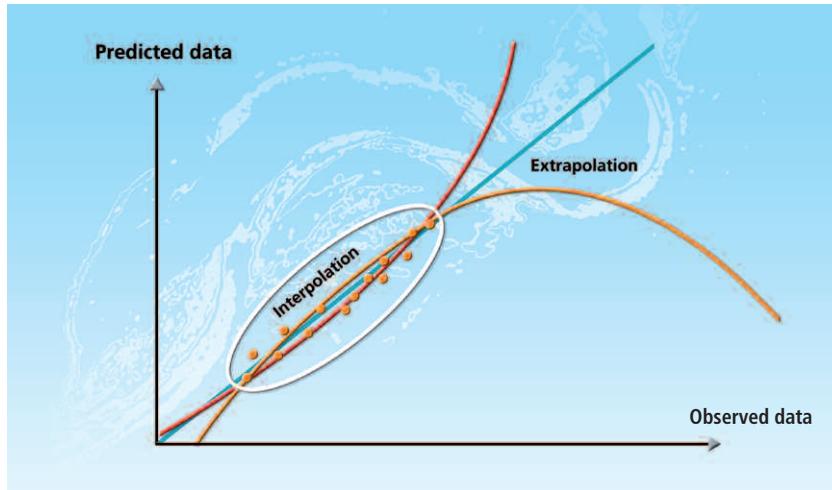


Diagram showing the limits of interpolation in describing data and the risks of extrapolation.

That is notably the case when models are used to predict distribution changes according to climate scenarios in which the climate variables exceed the ranges of values encountered under current conditions. The underlying hypothesis is to assume that the statistical relations established for the current data (during the calibration phase of the models) will continue to hold for values lying outside the current ranges of values. If this hypothesis turns out not to be true, the result for the projections is additional errors the degree of which it is fundamentally impossible to ascertain.

### ■ Non-inclusion of certain biological processes

To date, a large number of biological mechanisms have not been taken into account in species distribution models. That is notably the case for the dispersal capabilities of each species and the speed at which they can colonise a habitat. A Swedish exploratory study on pike revealed that the non-inclusion of dispersal capabilities led to overestimation of habitat gains for fish located downstream and underestimation of habitat losses for fish located upstream (Hein *et al.*, 2011).

Similarly, projections do not take into account biotic interactions (competition, predation, pathogens, etc.). This may have consequences for the results. Even though the importance of the biotic interactions is implicitly taken into account in the sampling data (Davis *et al.*, 1998; Sinclair *et al.*, 2010), the interactions are highly likely to change, notably due to the influence of climate change:

- exotic species introduced voluntarily or accidentally into rivers in continental France, such as the largemouth bass (*Micropterus salmoides*), could benefit from climate change and become invasive, thus potentially entering into competition (or even predation) with native species (Leprieur and Rubin, 2011; Lauzeral, 2012);
- in addition, climate change could encourage certain pathogens or indirectly modify host-parasite relations, thus making certain fish species more vulnerable to the diseases (Kocan *et al.*, 2009; Marcogliese, 2008) (see Box 4 in Chapter 2);

■ finally, certain species could encounter difficulties under the new climate conditions and disappear from some sites, which could work in favour of other species that were limited by the earlier presence of the first species.

Certain specific aspects such as needs in terms of food are also neglected, notably because the carrying capacity of the environment (assumed to be unlimited) is not taken into account. Similarly, distribution modelling of certain species is based exclusively on one part of their life cycle, consequently the definition of the ecological niche does not include all the environmental requirements of the species during the various stages of its life cycle, e.g. the part of the life cycle in the ocean for diadromous species.

Finally, it is also assumed that the relations between fish and the environment, established on the basis of the observed distribution, do not change over time. Modelling does not take into account adaptation phenomena (genetic selection), acclimation phenomena or the phenotypic plasticity of species confronted with climate change. However, genetic, phenological, physiological and morphological adaptations are possible and have been observed, e.g. in amphibians in the form of earlier reproduction (Beebee, 1995) and in the westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) (Drinan *et al.*, 2012). These simplifications, by not taking into account the potential changes in these relations over time, may limit the capacity of models to correctly project the impact of climate change.

Other types of models are currently being developed in order to take into account some of the ecological processes mentioned above (see Box 10).

#### Box 10

### The impact of climate change on species distribution in hybrid models and mechanistic models

Distribution models are impaired by significant limits. In that ecological processes are not explicitly included, dispersal capabilities are generally not taken into account and difficulties arise in determining the real habitat gains and losses of the studied species. In addition, the population dynamics of the species (growth, reproduction, mortality, migratory processes) are neglected, meaning the effects of climate change on the phenology<sup>26</sup> of the species are absent as well, thus making it difficult to make a reasonable estimate of their speed of expansion (or disappearance) and of the effective changes in their range (Guisan and Thuiller, 2005; Franklin, 2010). In light of this situation, the shift to more mechanistic models capable of integrating the thermal requirements, population dynamics and dispersal capabilities of species has become a major issue (Thuiller *et al.*, 2008; Huntley *et al.*, 2010).

Mechanistic approaches, based on the use of individual-based models, would seem to offer promising results. Contrary to statistical models, mechanistic approaches are robust because they address generic mechanisms and are not based correlations which do not necessarily imply any causal links. In addition, they can integrate individual variability, interaction between individuals as well as between individuals and their environment (a useful feature to take directly into account the effects of climate change on population dynamics), and an explicit representation of the environment (Tyler and Rose, 1994; Wiegand *et al.*, 2004; Jongejans *et al.*, 2008). In recent years, these models have been developed notably to study the large-scale impact of climate change on diadromous fish (Rougier *et al.*, 2014) and specifically on Atlantic salmon (Piou and Prévost, 2012, 2013).

26. Phenology is the study of the timing of periodic events (generally annual) among life forms, determined by seasonal variations in the climate.

The formulation of hybrid models combining large-scale statistical relations and biological processes is another possible solution to improve projections (Brook *et al.*, 2009), notably for invasive species (Gallien *et al.*, 2010; Poulet *et al.*, 2012). The most commonly used hybrid models use the predictions of statistical models to delimit the parameters in mechanistic models (survival rate, dispersal rate, etc.) (Gallien *et al.*, 2010). They may include data on environmental fragmentation, an estimate of colonisation capabilities (Dullinger *et al.*, 2004; Engler and Guisan, 2009; Midgley *et al.*, 2010) and an analysis of the risks of local extinction (Anderson *et al.*, 2009).

These different approaches illustrate the complexity of the mechanisms involved and the consequences of that complexity in terms of the responses of species to climate change. They also place our capacity to predict the consequences of climate change for species and populations in a rather critical light. They require considerable knowledge on the processes related to population survival and demographics, as well as on the effects of the environment (temperature, discharge, etc.) on those processes (Helmuth *et al.*, 2005; Porter and Kearney, 2009; Buckley, 2010; Piou *et al.*, 2010). As a result, they are difficult to implement and can be used for only a limited number of species that have undergone extensive study (Lauzeral, 2012).

#### ■ Non-inclusion of anthropogenic pressures

In general, only climate forcing is taken into account in distribution models for future projections (but see Lassalle *et al.*, 2009b). Yet many other anthropogenic pressures, such as water abstractions, pollution, dams and weirs, loss of ecological continuity, fishing, stocking, etc. constitute important factors in the local presence of species (see for example Pont *et al.*, 2006).

These pressures can skew the modelling results for the realised niches of many species, for example certain favourable environments are not or no longer occupied by a species due to dams, abstractions, etc. That is the case for Atlantic salmon in the Seine basin. In the wake of various anthropogenic pressures, its range has been drastically reduced since the end of the 1800s (Belliard *et al.*, 2009). Conversely, certain modifications made to the environment can encourage the presence of a species, e.g. the slowing of the current by an obstacle is favourable for limnophilic species. Finally, stocking of commercial species (brown trout, pike, etc.) occasionally occurs in environments seen as less favourable, which distorts the modelling of the realised niche. It would be difficult to integrate these parameters in the models given the lack of available data and the lack of knowledge concerning how they will evolve in the future (see Box 11).

In addition, during the formulation of distribution models, it is assumed that these pressures will not change in the future and that their interactions with the environment will not change either, which does not seem very likely. Certain anthropogenic pressures increase the vulnerability of aquatic environments, notably through greater abstractions or degradation of water quality. That is why it is necessary, when interpreting modelling results, to assess the dynamics of fish populations assuming greater anthropogenic pressures. In addition, if the results are used locally, *ex post* analysis should be carried out to check that the habitats considered favourable by the models are in fact favourable in spite of any local pressures (hydromorphological alterations, eutrophication, etc.).

## Accounting for obstacles to river flow

To date, very few studies include in models the presence of obstacles to river flow, in spite of their significant impact on the effective distribution of aquatic species and on their future evolution.

For the Explore 2070 project (MEDDE/Biotope, 2013) and in work by Buisson *et al.* (2008), this variable was taken into account by projecting future distributions **assuming that dispersal is either equal to zero or unlimited**<sup>27</sup>.

- In the first case, only those zones currently considered favourable will be favourable in the future. The favourable area for a species can therefore either remain stable or decrease in size.
- In the second case, a species is deemed capable of dispersing throughout the entire hydrographic network. No obstacles block its dispersal.

The projections produced by these two scenarios indicate the range of possible outcomes. Depending on the ecology of each species (e.g. inherent dispersal capability), hypotheses can be drawn up to zero in on the most probable projections.

Explicit inclusion of obstacles to river flow in models has been proposed by Lassalle *et al.* (2009b) for migratory species (see also Hein *et al.*, 2011, in Sweden). However, only very large obstacles (dams) were taken into account in that study.

Today, the data on obstacles in French rivers (ROE-Onema<sup>28</sup> database on river obstacles) should help in devising models including the obstacles to dispersal for all freshwater species in continental France. For further progress, it will be necessary to obtain more complete and precise data on all obstacles (i.e. head-drop, existence of fish passes, etc.).



27. In Buisson *et al.* (2008), only the hypothesis of unlimited dispersal was taken into account.  
28. See <http://www.Onema.fr/REFERENTIEL-DES-OBSTACLES-A-L>.



## Main changes expected for fish in France in response to climate change

Studies based on species distribution models have increased rapidly in number over the past few years. Even though this type of study has been run far less often for fish than for terrestrial organisms, a recent bibliographical review nonetheless inventoried 66 scientific publications from 1980 to 2011 on the expected effects<sup>29</sup> of climate change on the distribution of freshwater fish around the world (Comte *et al.*, 2013). The study highlighted the heavy taxonomic preference in favour of salmonids, which represent 54% of the articles published. In France, there are only five native salmonid species out of the 69 species assessed (IUCN France; MNHN; SFI; Onema, 2010). What is more, less than 10% of the inventoried articles address species considered vulnerable by the IUCN (2009). The most studied groups are, in decreasing order, salmonids, cyprinids, centrarchids and percids (see Figure 40).

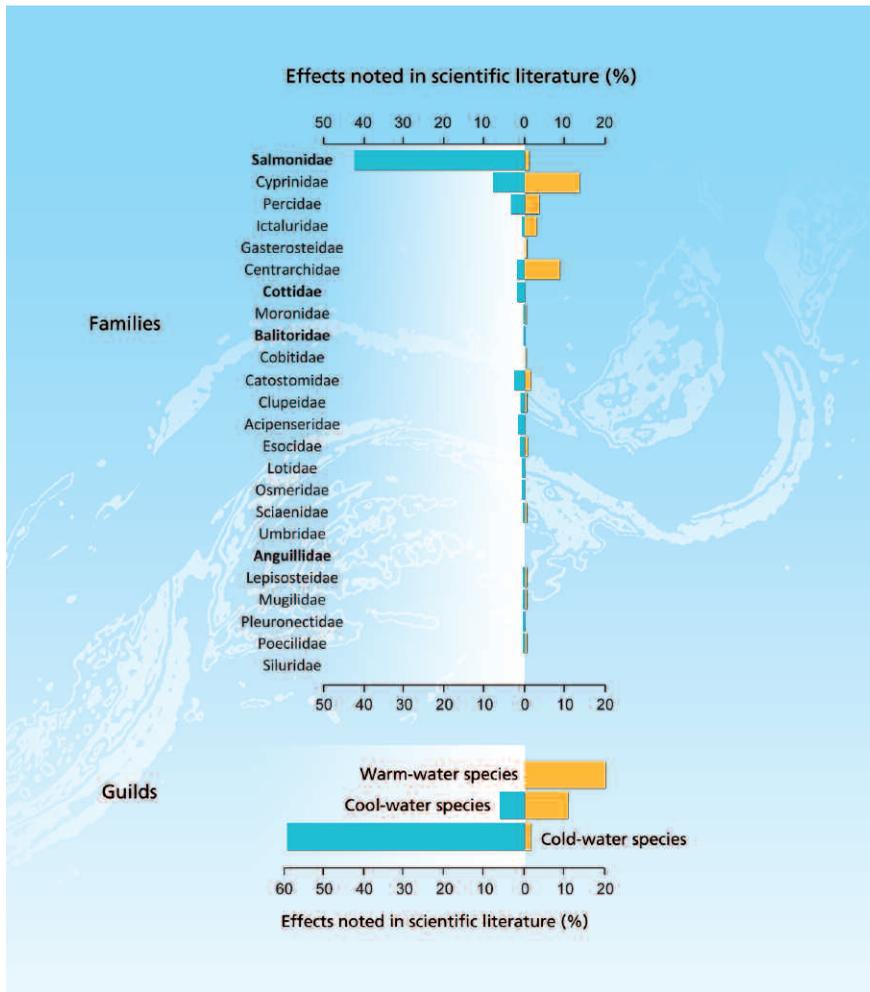
Among the species covered, some have specific characteristics that make them more difficult to model. For example, studies carried out on numerous taxonomic groups have shown that species inhabiting areas with a limited range of environmental conditions (specialist species) were more precisely modelled than species occupying wider ranges (generalist species), however, see also Jimenez-Valverde *et al.*, 2008. On the national level, projections concerning fish species that are more tolerant in terms of the thermal and altitudinal conditions are less precise than those for other species (Grenouillet *et al.*, 2011). In addition, rare species are particularly difficult to model due to the small quantities of occurrence data available (Lomba *et al.*, 2010). This lack of data in turn limits assessment possibilities concerning the response of the species to changes in its environment. However, certain modelling approaches specifically target the rare species, thus making it possible to provide at least a minimal description of their realised niches (Engler *et al.*, 2004; Hernandez *et al.*, 2006; Hayer *et al.*, 2008; Wisz *et al.*, 2008; Lomba *et al.*, 2010).

### Potential effect of climate change on the distribution of freshwater fish

In spite of significant uncertainty, certain major trends would seem to emerge on the national level. Cold-water species, characterised by narrow thermal tolerances such as brook lamprey, brown trout and bullheads, would seem to be the species most systematically impacted by climate change (Pont and Rogers, 2003; Buisson *et al.*, 2008; Buisson *et al.*, 2010; Tisseuil *et al.*, 2012a; Explore 2070 – MEDDE/Biotope, 2013) (see Figure 41, Box 12).

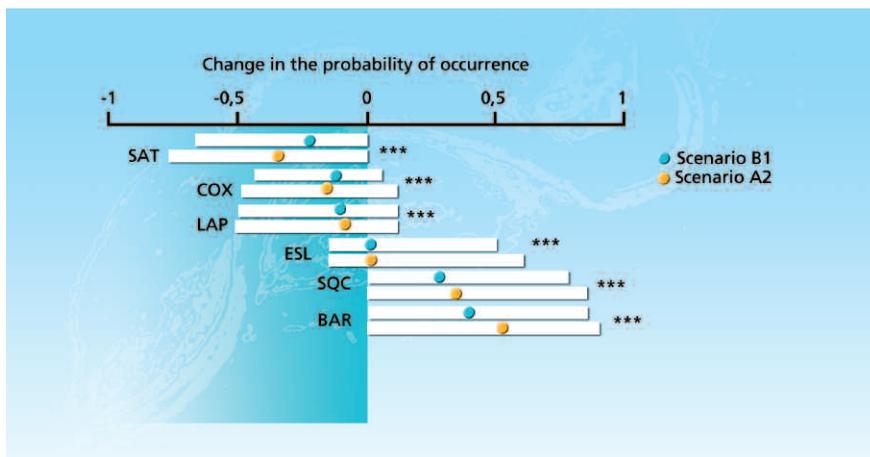
29. A total of 77 publications were analysed, of which 66 addressed expected effects and 11 observed effects.

Figure 40



Proportion of negative expected effects (blue bars, reduction in favourable habitats) and positive expected effects (orange bars, increase in favourable habitats) for freshwater fish species grouped in taxonomic families and/or thermal guilds (diagrams modified, originally from Comte et al., 2013).

Figure 41



Brown trout: SAT  
 Bullheads: COX  
 Brook lamprey: LAP  
 Pike: ESL  
 Chub: SQC  
 Barbel: BAR

Changes in the probabilities of occurrence according to the SRES B1 and A2 scenarios for the period 2051 to 2080, for six species of river fish (diagrams modified, originally from Buisson et al., 2008). The change is the difference between the current and future average probabilities of presence for all the sites studied in France. The median values (points) and the minimum-maximum values indicate the amplitude of the changes in the probability of presence. A significant difference between the two scenarios is signalled by \*\*\* ( $p < 0.01$ ).

## **Assessing the vulnerability of fish to climate change, the example of brown trout**

For the Explore 2070 project, the potential impact of climate change on the distribution of 38 fish species was assessed using scenario A1B for the period 2060 to 2089. The assessment included both quantitative analysis based on the projections of the distribution models and qualitative analysis based on expert knowledge. The precise method employed is presented in detail in the final report that may be downloaded from <http://www.developpement-durable.gouv.fr/-Explore-2070-.html>.

The vulnerability analysis is presented as a data sheet indicating the effective distribution of the species, its colonisation capability, an analysis of the projections for current and future favourable habitats, and a vulnerability assessment including quantitative and qualitative indices (colonisation capability and the level of uncertainty affecting the results) (see Boxes 8 and 11).

### **Current distribution and species biology**

Brown trout are now found primarily in mountainous regions (Alps, Pyrenees, Massif Central, Vosges, Jura), in rivers in Brittany, in coastal rivers in Normandy and in northern France, as well as in certain rivers in limestone plains. In the above rivers, the thermal requirements of the species are met (4 to 19°C).

### **Colonisation capability**

Brown trout have excellent colonisation capabilities. In addition to its proficiency in overcoming obstacles, humans intervene significantly to promote sport fishing (stocking). Consequently, the capability of the species to disperse to new habitats is high.

### **Projection of current distribution of favourable habitats**

The model indices for sensitivity (74% of presences are correctly projected) and specificity (78% of absences are correctly projected) are high in general. The projection of the current distribution of favourable habitats for trout corresponds on the whole with the observed distribution of the species in France (see Figure 42).

### **Projection of future distribution of favourable habitats**

In that trout have high colonisation capabilities, the unlimited-dispersal scenario was preferred for the analysis (see the definition in Box 11). According to that scenario, the favourable habitat for brown trout is projected to be reduced by one-third in 2070 (see Figure 42). The remaining habitat would consist of refuge zones at the heads of river basins.

### **Assessment of species vulnerability**

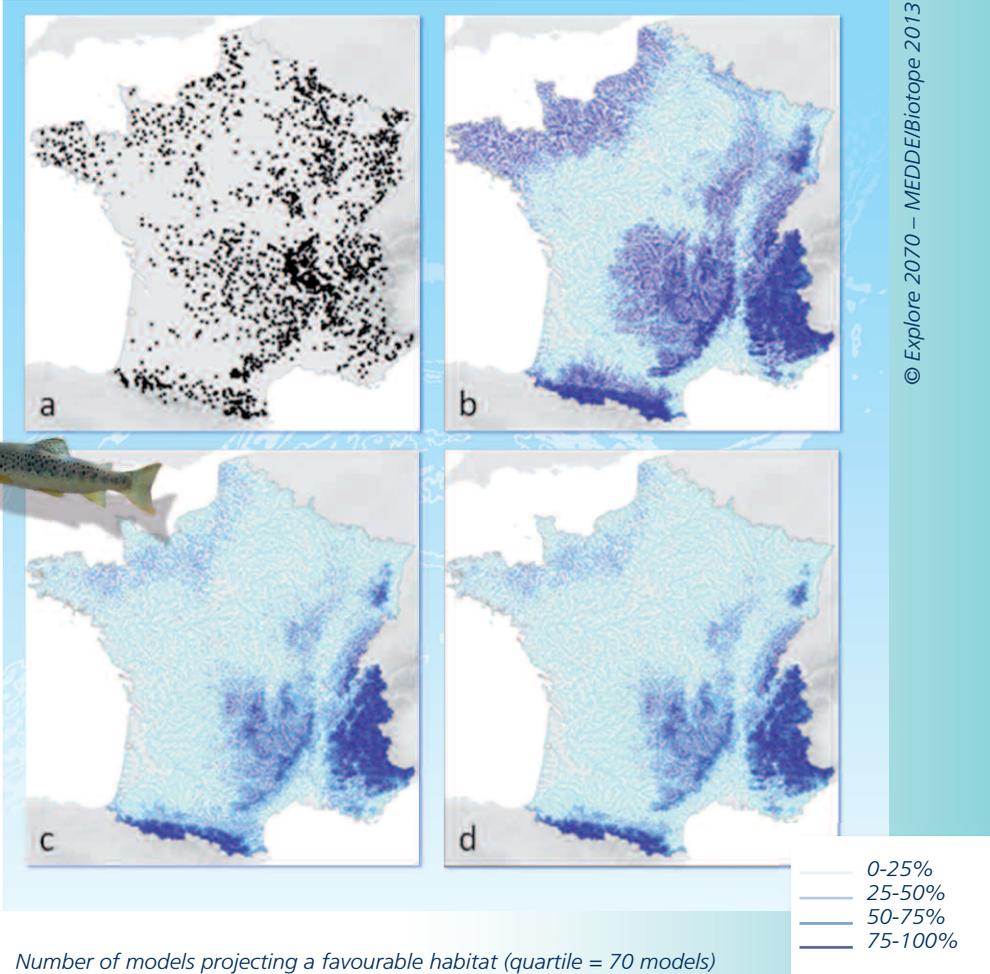
For France as a whole and on the basis of the results, brown trout would appear to be highly sensitive to climate change.

They are therefore very vulnerable. The confidence index assigned by the experts to these results is 3 (on a scale of 1 to 3, where 3 is the highest level of confidence).

Figure 42



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Number of models projecting a favourable habitat (quartile = 70 models)

- Examples of favourable-habitat projections for a species (brown trout) that reacts negatively to climate change.
- (a) Presence observed (n=2 703 out of 4 381 sampling stations, source Onema, 2000-2008, using electrofishing).
  - (b) Habitats projected as currently favourable.
  - (c) Habitats potentially favourable in the future according to the zero-dispersal scenario.
  - (d) Habitats potentially favourable in the future according to the unlimited-dispersal scenario (scenario A1B for the period 2060 to 2089). The higher the number of models projecting a favourable habitat, the greater the probability that the river reach is in fact favourable for the species (Explore 2070 - MEDDE/Biotope, 2013).

Other species, essentially those inhabiting the bream and barbel zones (see Chapter 2), systematically respond positively to climate change. For example, that is the case of chub and barbel (Pont and Rogers, 2003; Buisson *et al.*, 2008; Buisson *et al.*, 2010; Explore 2070 - MEDDE/Biotope, 2013) (see Box 13). However, greater uncertainty weighs on these projections than on those for cold-water species. Because these species have very large ranges, the predictive capacity of models is reduced in light of the variables taken into account. As a result, only partial knowledge is available on their realised niche (Grenouillet *et al.*, 2011; Logez *et al.*, 2012). Concerning their distribution, the modelling results generally indicate an extension of their ranges to sections further upstream. The ranges of species living exclusively at the heads of river basins would be reduced to high-altitude refuge zones and the risks of their local extinction would be increased in certain lower-lying basins. The ranges of species in downstream zones would be modified with upper limits farther upstream, whereas changes in the downstream limits would depend more or less on the species. For some species, new river basins could become favourable. However, there is uncertainty concerning the capability of these species to colonise the new habitats and hydraulic constraints could limit their movement upstream.

It is also important to note that modelling of the realised niche for certain species, notably those located downstream, remains highly uncertain in spite of a major effort to improve processes (due to less effective sampling in large environments, less precise data due to greater heterogeneity and increased anthropogenic pressures).

Worldwide, the effects of climate change on the distribution of fish point in the same direction as the projections carried out in France. Cold-water species such as salmonids will likely be subjected to primarily negative effects whereas species located in the intermediate and downstream sections, such as cyprinids and centrarchids should benefit (Comte *et al.*, 2013).

### **Assessing the vulnerability of fish to climate change, the example of chub**

For the Explore 2070 project, the potential impact of climate change on the distribution of 38 fish species was assessed using scenario A1B for the period 2060 to 2089. The assessment included both quantitative analysis based on the projections of the distribution models and qualitative analysis based on expert knowledge. The precise method employed is presented in detail in the final report that may be downloaded from <http://www.developpement-durable.gouv.fr/-Explore-2070-.html>.

The vulnerability analysis is presented as a data sheet indicating the observed distribution of the species, its colonisation capability, an analysis of the projections for current and future favourable habitats, and a vulnerability assessment including quantitative and qualitative indices (colonisation capability and the level of uncertainty affecting the results) (see Boxes 8 and 11).

#### **Current distribution and species biology**

Chub are present in all French rivers with the exception of Brittany, a small number of coastal rivers and in the extreme northern section of the country. They are not present in rivers at mid and high altitudes. The species is fairly ubiquitous and tolerant.

#### **Colonisation capability**

The species has not been extensively manipulated by humans (except as bait) and has good colonisation capabilities. It is therefore likely that it can rapidly colonise favourable habitats.

#### **Projection of current distribution of favourable habitats**

The projection of the current distribution of favourable habitats for chub corresponds well to the observed distribution of the species in France, but would seem to be slightly underestimated. The sensitivity index is 76% (proportion of presences correctly projected) and the specificity index is 74% (proportion of absences correctly projected).

#### **Projection of future distribution of favourable habitats**

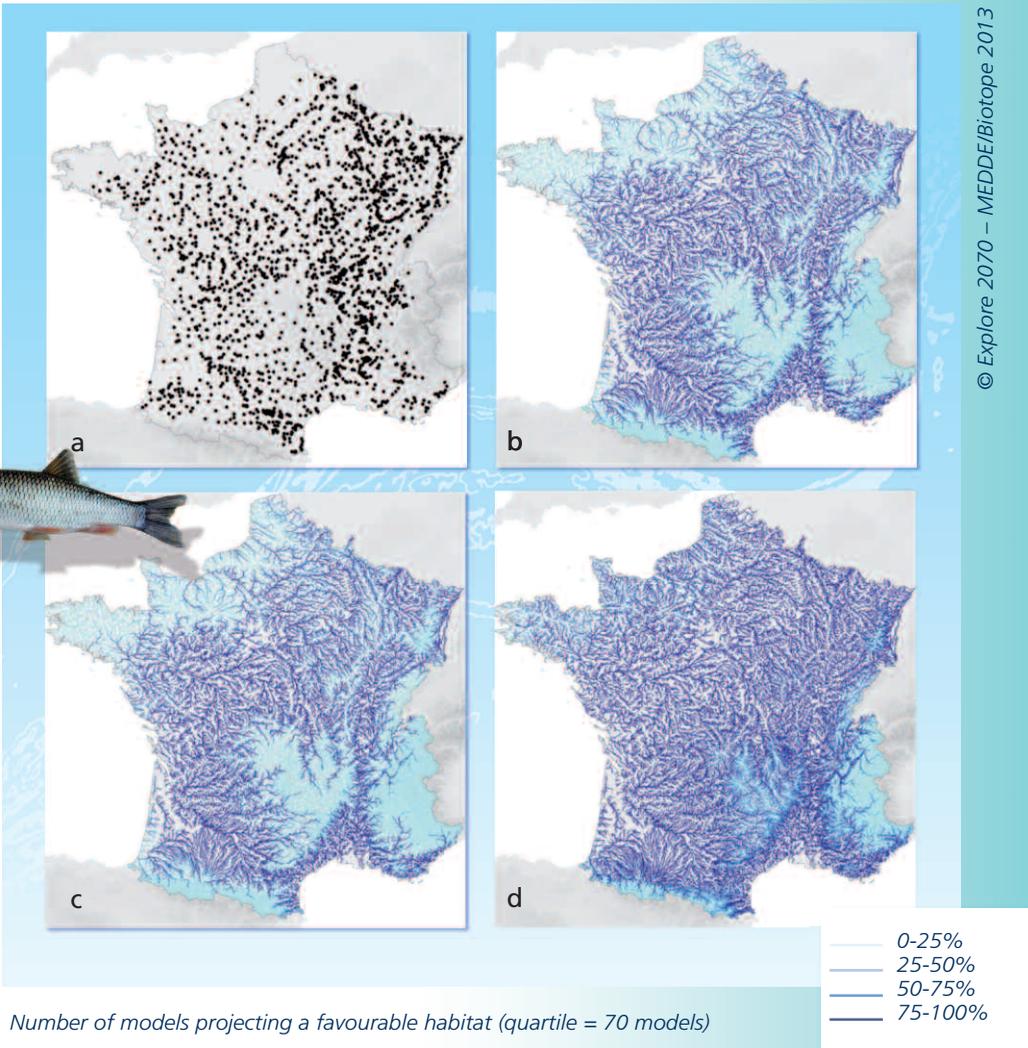
In that chub have non-negligible colonisation capabilities, the unlimited-dispersal scenario was preferred for the analysis (see the definition in Box 11).

According to the A1B climate-change scenario selected, by 2070 the species should benefit from a major increase in favourable habitats. With the exception of mountain regions and the coast in the north-western section of the country, the entire hydrographic network should become favourable (see Figure 43).

#### **Assessment of species vulnerability**

Chub should benefit strongly from climate change and colonise virtually all the river reaches in the basins where they are already present. The vulnerability of the species is low. The confidence index assigned by the experts to these results is 3 (on a scale of 1 to 3, where 3 is the highest level of confidence).

Figure 43



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Number of models projecting a favourable habitat (quartile = 70 models)

Examples of favourable-habitat projections for a species (chub) that reacts positively to climate change. (a) Presence observed (n=2 219 out of 4 381 sampling stations, source Onema, 2000-2008, using electrofishing). (b) Habitats projected as currently favourable. (c) Habitats potentially favourable in the future according to the zero-dispersal scenario. (d) Habitats potentially favourable in the future according to the unlimited-dispersal scenario (scenario A1B for the period 2060 to 2089). The higher the number of models projecting a favourable habitat, the greater the probability that the river reach is in fact favourable for the species (Explore 2070 - MEDDE/Biotopie, 2013).

Figure 44



a, b © N. Poulet - Onema

According to the statistical models, future climate change should be detrimental for brown trout (a) and beneficial for chub (b).

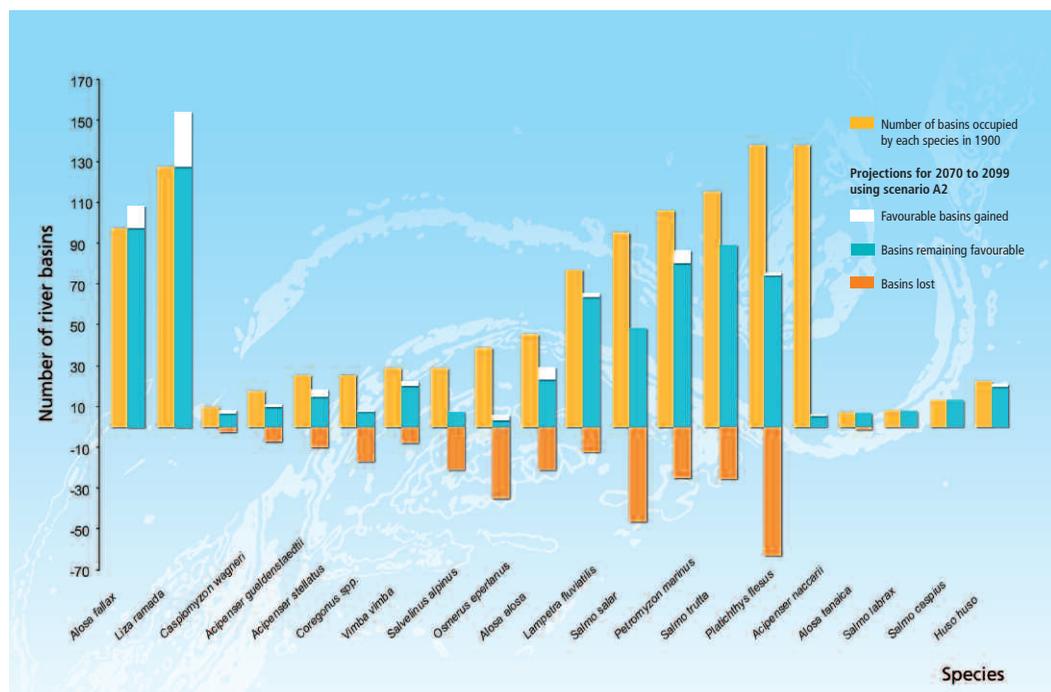


## Potential effects of climate change on diadromous fish in European and French river basins

The results of the projections run for diadromous fish differ depending on the species. For the European and North African basins, Lassalle *et al.* (2009ac) showed that among the 20 species studied using an intermediate GHG emissions scenario (scenario A2, see Figure 45), three long-term (2070 to 2099) trends stood out:

- species for which the number of favourable basins increased (10 to 30%), e.g. eels and Twaite shad - *Alosa fallax*;
- species for which the number of favourable basins decreased (16 to 92%), e.g. Atlantic salmon and Arctic charr;
- species for which distributions changed little or not at all, e.g. Caspian lamprey - *Caspiomyzon wagneri*.

Figure 45



Predicted changes in distribution for each diadromous<sup>30</sup> species (presence or absence in each river basin) for Europe and Northern Africa (Lassalle *et al.*, 2009c).

Concerning France, the results of the studies converge with those for Europe for Atlantic salmon and eels (scenarios A1B, A2 or B1, Buisson *et al.*, 2008; Explore 2070 - MEDDE/Biotopie, 2013). On the other hand, simulations produced by demogenetic<sup>31</sup> individual-based models indicate that strong variations in discharge between summer and winter could cause greater problems for the continued existence of salmon in small French coastal rivers than the increase in temperature (Piou *et al.*, 2010; Piou and Prévost, 2013). According to these authors, degradation of the conditions required for marine growth is thought to potentially be the factor having the greatest impact on the risks of local extinction (Piou *et al.* 2010; Piou and Prévost, 2013). These results are consistent with a study by Friedland (1998).

30. A diadromous fish spends part of its life in the sea and part in fresh waters.

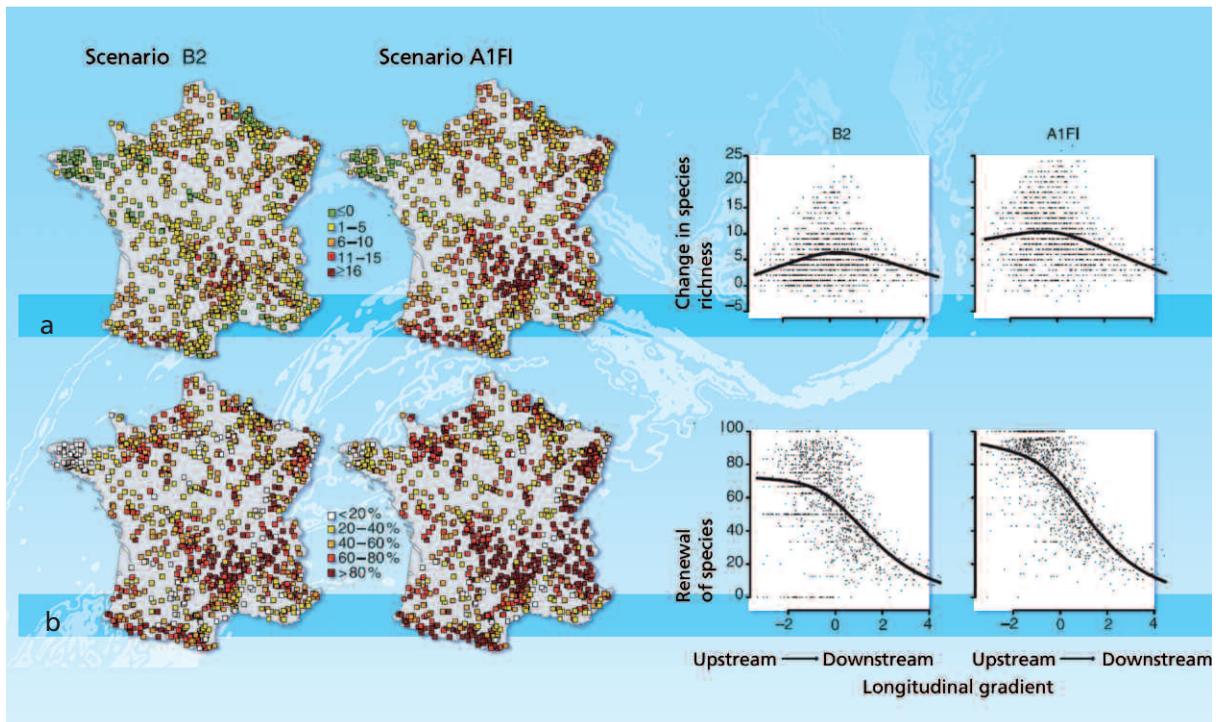
31. The key parameters determining the evolutionary potential and the continued existence of populations are 1) demographics, i.e. sufficient reproduction, and 2) conservation of a diverse gene pool, a factor in adaptive capacity. Demogenetic models look at these two parameters and their interaction with the environmental and demographic stochasticity resulting from global warming, for example.

## Potential effects of climate change on the community scale

Study of the potential response of communities to climate change consists of compiling the responses for each species and not on a direct approach addressing the community scale. This is because each species has a number of ecological specificities that distinguish its response to climate change, in terms of both the trend (positive or negative) and the amplitude of the response. For this reason, it was deemed preferable to proceed by first modelling the impacts on individual species before compiling all the results for the species in view of assessing the impact on the community level. However, it should be noted that this approach has a disadvantage in that it cannot take into account biotic interactions nor the capacity of environments to serve as habitats for species not included in the species modelling. In addition, not all the species present in France are taken into account. For this reason, the perception of communities remains partial.

Modelling to date concludes that species richness of fish should, on the whole, increase in all French rivers (Buisson *et al.*, 2008; Buisson and Grenouillet, 2009). This increase may be explained by the fact that habitats made favourable by climate change will likely be rapidly colonised by a large number of species from the downstream sections of rivers. According to Buisson (2009), the species richness in intermediate and upstream zones should increase more than in downstream sections where it should remain more or less constant (see Figure 46). These results are in line with a number of monitoring programmes carried out over the past decades on sea fish (e.g. Hiddink and ter Hofstede, 2008) and freshwater fish (e.g. Daufresne and Boët, 2007). The changes in species occurrence will probably result in greater uniformity of communities in rivers (Buisson and Grenouillet, 2009; Tisseuil *et al.*, 2012b). Finally, variations in diversity between communities (beta-diversity) will also change, due to two distinct underlying mechanisms. In the upstream and downstream sections, variations will be caused primarily by a modification in the species richness within communities (colonisation or local extinction), whereas in intermediate sections, the main mechanism will be a renewal of species, i.e. new species arriving from adjacent communities will replace species that have gone locally extinct (see Figure 46) (Tisseuil *et al.*, 2012b).

Figure 46



Projected change in (a) the species richness of fish communities and (b) taxonomic composition, according to scenarios B2 and A1FI. The changes are shown in map form (left) and along the upstream-downstream gradient (right) (Buisson and Grenouillet, 2009).



## Conclusion and outlook

Over the past few years, numerous tools have been developed to assess the impact of climate change on living organisms. Among those tools, statistical distribution models play an important role because they are relatively simple and can project the potential habitat changes of a given species in response to different climate-change scenarios. In that certain ecological processes are not taken into account in these models, other tools, namely mechanistic models, have been developed in parallel. They are more powerful, but require much more knowledge on species biology. That is why their application to a large number of species has remained limited.

Even though the many underlying assumptions limit the possibilities of transposing the results locally, the projections produced by the distribution models reveal trends that can be used to assess the vulnerability of each species and any changes in the richness and composition of communities along the upstream-downstream gradient.

Generally speaking, all the models foresee an upstream shift in the ranges of cold-water species. The ranges of species living exclusively at the heads of river basins would be reduced to high-altitude refuge zones and the risks of their local extinction would be increased in certain lower-lying basins (piedmonts, plains). Conversely, the conditions for species located in intermediate zones or downstream, such as cyprinids and centrarchids, would improve. On the community scale, an increase in species richness and greater uniformity of communities is expected in all rivers. In other words, the communities will probably be richer, but more similar to each other, resulting in a loss of diversity. It should however be noted that rare species are not taken into account due to a lack of sufficient data.

The vulnerability of species to climate change depends on the ecological requirements of each species and some of these requirements are currently not taken into account in the models for freshwater fish in continental France (dispersal capabilities, anthropogenic pressures, adaptive and evolutionary processes, etc.). A quantitative approach in conjunction with a critical analysis of the results based on expert knowledge would now appear to be a solution to refine the potential distribution maps for each species in the context of climate forcing.

In the future, the formulation of hybrid models combining both statistical and mechanistic models should make it possible to refine the projections produced by the distribution models, on the condition that the necessary data are available.

Figure 47



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*Bullheads, a group of small, benthic species inhabiting cold-water rivers, will likely be affected by climate change.*

The development of these models should proceed in parallel with the many research projects already under way to understand the pressure-impact relations (changes in thermal and hydrological regimes, sediment dynamics, invasive species, etc.) that are factors in defining adaptive measures. Use of data series spanning long time periods, for both biological and environmental data, e.g. discharges, water temperature, etc., is also essential. In addition, it would appear that knowledge on species' ecology, even that of the most common species, is far too fragmentary and insufficient for mechanistic models. Filling in the gaps is a further priority.

Finally, too few studies address time periods spanning the next decades, which are nonetheless an intermediate target of great importance for management. A great amount of work must be put into all the above topics.

