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Changes in fish communities in a context of climate change

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Introduction

Lakes, rivers and marshes cover only 0.01% of the surface of the planet. But in spite of their small surface area, they are home to a vast diversity of species (Mc Allister, 1997). Approximately 9% of all animal species identified to date (approximately 1.4 million) live in continental aquatic environments (Balian *et al.*, 2008). Some 40% of the 30 000 fish species worldwide and over 100 000 invertebrate species live in fresh water[7]. However, that richness notwithstanding, freshwater environments have shown relative and absolute extinction rates much higher than those for marine and terrestrial environments (Dudgeon *et al.*, 2006; Heino *et al.*, 2009). In continental France, of the 69 species[8] assessed, four species of freshwater fish have disappeared and four others are critically endangered (IUCN France red list; MNHN; SFI; Onema, 2010). Worldwide, over a dozen species would appear to have become extinct (see *http://creo.amnh.org*). This decline may be explained primarily by overfishing, water pollution, modifications to hydrological regimes, the destruction, fragmentation and uniformity of habitats and the increased numbers of invasive species (Dudgeon *et al.*, 2006).

Climate change will most likely worsen this phenomenon by increasing water temperatures, reducing precipitation and contributing indirectly to the emergence of greater conflict concerning the use of water resources (Xenopoulos *et al.*, 2005). Empirical observations over the 1900s showed that climate change has already affected many species and communities of species in different parts of the world (Hughes, 2000; McCarty, 2001; Walther *et al.*, 2002; Parmesan and Yohe, 2003; Root *et al.*, 2003).

It has therefore become essential to understand the precise effects of climate change on fish communities in order to implement adaptation measures that are consistent with the measures designed to mitigate the other anthropogenic pressures weighing on the environment (Heino *et al.*, 2009).

For a number of decades, numerous projects to determine the current effects of climate change on the environment have been undertaken. Various approaches have been proposed, including experiments under (semi-)controlled conditions and analysis of past and present fish-monitoring data (see Box 3). The results of this work have enhanced understanding of the current impact of climate change on different spatial and temporal scales.

The purpose of this chapter is to present the most recent results on observed changes in freshwater fish, ranging from individual fish to the entire community, in response to climate change.

7. Data presented during the Eawag annual information day in June 2010 (http://www.eawag.ch/index_EN).
8. The total number of freshwater fish species inventoried in continental France is 95. The characterisation report produced by IUCN dealt with 69 species among the 95 (source: IUCN France; MNHN; SFI; Onema, 2010).

What data is required to study the long-term evolution of aquatic communities?

Decades-long data series on the targeted species and, ideally, the environmental conditions (temperatures, physical-chemical characteristics, hydrology, etc.) are required to study the long-term evolution of aquatic communities. In France, data have been gathered at the monitoring points of the hydrobiological fish network (RHP) since 1995 and those established at nuclear power plants (CNPE) since 1977. Note that many of the RHP monitoring points were transferred to the new WFD monitoring networks in 2007.

The hydrobiological fish network (RHP)

Launched nationwide in 1995, the RHP network was initially made up of approximately 650 monitoring sites where annual electrofishing campaigns were carried out. This project was part of two water-quality monitoring programmes, namely the national basin network (RNB) and the additional basin network (RCB). In 2007, RNB and RCB were replaced by the surveillance-monitoring network (RCS) and the operational-monitoring network (RCO) respectively.

Within these two new networks, the number of sites where fish monitoring takes place is 1 506 out of the total of 1 569 monitoring points in the RCS (see Figure 22). Work is carried out at each monitoring point once every two years and the resulting data serve to assess the status of fish communities and to detect trends on the river-basin level. However, the shift in the objectives set for the new RCS network (checks on good status using bioassessment tools) led to changes in the sampling strategy (methods, tools used, etc.) that has not simplified the analysis of the data series.

Monitoring at nuclear power plants

EDF, the French electricity company, has a total of 19 nuclear power plants in France, including 14 on major rivers (Loire-Vienne, Rhône, Seine, Garonne, Rhine-Meuse-Moselle), four on sea coasts and one on an estuary (Gironde). Since its commissioning, each nuclear power plant has been subjected to environmental (including hydrobiological) monitoring by a scientific team. A public report is drafted annually for each plant and delivered to the State services. The purpose of the physical-chemical and biological programme is to monitor the concentration in water of the chemical substances released by the plant to the environment, to observe the natural evolution of the surrounding environment and to detect any abnormal trends caused by the plant. These monitoring programmes are an outstanding source of data for the assessment of fish communities.

Figure 22

Position of surface-water qualitative monitoring points (RCS) in the river-basin districts.

General trends in observed impacts of climate change

In going through its life cycle, each species has a number of more or less strict requirements in terms of water quality (e.g. oxygen content) and habitat (e.g. flow velocity in rivers). These parameters are conditioned by two key factors:

- temperature, which influences the productivity of the ecosystem;
- hydrology, which influences sediment transport and consequently the habitat.

The interaction between these two factors has an influence on the level of dissolved oxygen.

Given that these two factors shift from the source of a river to the estuary, it is possible to establish guilds[9] of species that have their successive (or cumulative) habitats along the longitudinal gradient. Huet (1949) proposed a classification system for fish species based on the width and slope of a river, factors that are correlated with the river morphology, hydrology and water temperature.

Generally speaking (see Figure 23), it may be said that:

- the cold-water rheophilic[10] and stenothermal[11] species are found in the upstream sections of rivers (trout zone). These species include brown trout (*Salmo trutta*), bullheads (*Cottus* spp.), brook lamprey (*Lampetra planeri*) and minnows (*Phoxinus* spp.);
- the rheophilic cyprinids, e.g. barbel (*Barbus barbus*), daces (*Leuciscus* spp.), schneider (*Alburnoides bipunctatus*), gudgeons (*Gobio* spp.), chub (*Squalius cephalus*) and nase (*Chondrostoma nasus*), are found in the intermediate sections of rivers (grayling and barbel zones);
- finally, the limnophilic[12] and thermophilic[13] species are generally found in downstream sections with slight slopes (bream zone), e.g. bitterling (*Rhodeus amarus*), white bream (*Blicca bjoerkna*), rudd (*Scardinius erythrophthalmus*), bleak (*Alburnus alburnus*), roach (*Rutilus rutilus*), pikeperch (*Sander lucioperca*), perch (*Perca fluviatilis*), common carp (*Cyprinus carpio*).

Given that the life cycles of fish and their distribution are determined primarily by the temperature and hydrological regime, global warming is potentially a major cause of change in fish populations and communities. Whether gradual or sudden, effects are produced on many levels, for example by modifying certain processes such as growth and reproduction, or by modifying the phenology[14] of populations and consequently the relations within food webs. Climate change can also induce changes in the ranges of species and consequently in the structure of communities (see Figure 24). In the following pages, examples illustrating the diversity and impact of these effects will be presented.

9. Group of taxonomically similar species (fish in this case) that have comparable requirements in terms of one or more ecological factors (temperature, hydrology, etc.).
10. Species that spend their entire lives in running waters.
11. Species capable of tolerating only very slight variations in temperature above or below mean values.
12. Species that live in calm sections of rivers or in stagnant waters (e.g. marshes).
13. Species that prefer warm waters.

Figure 23

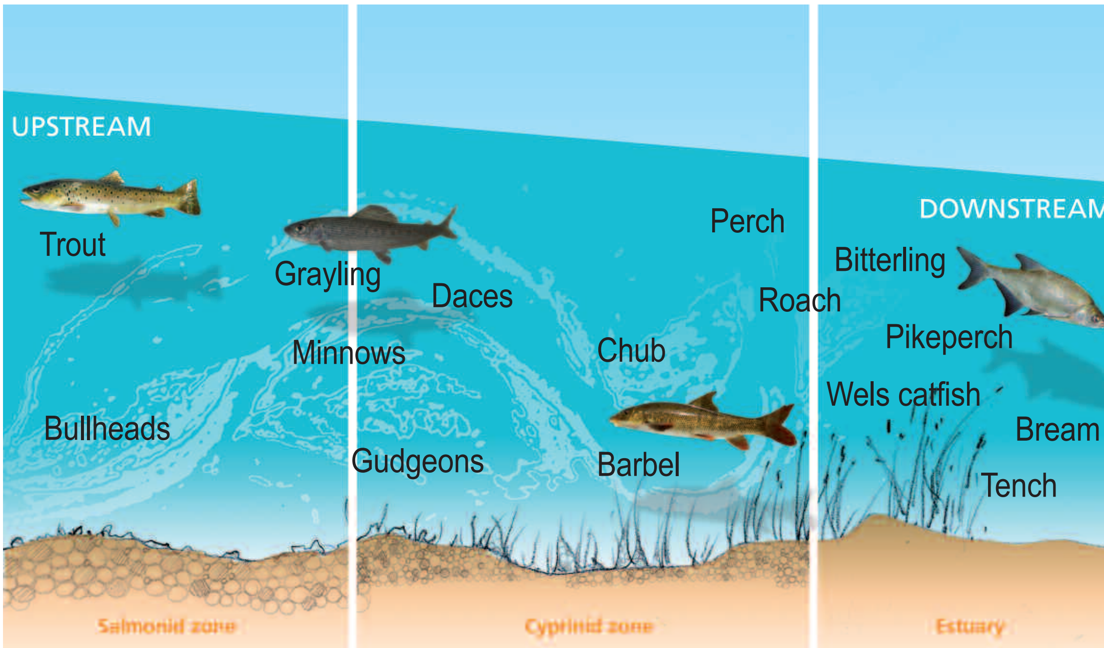
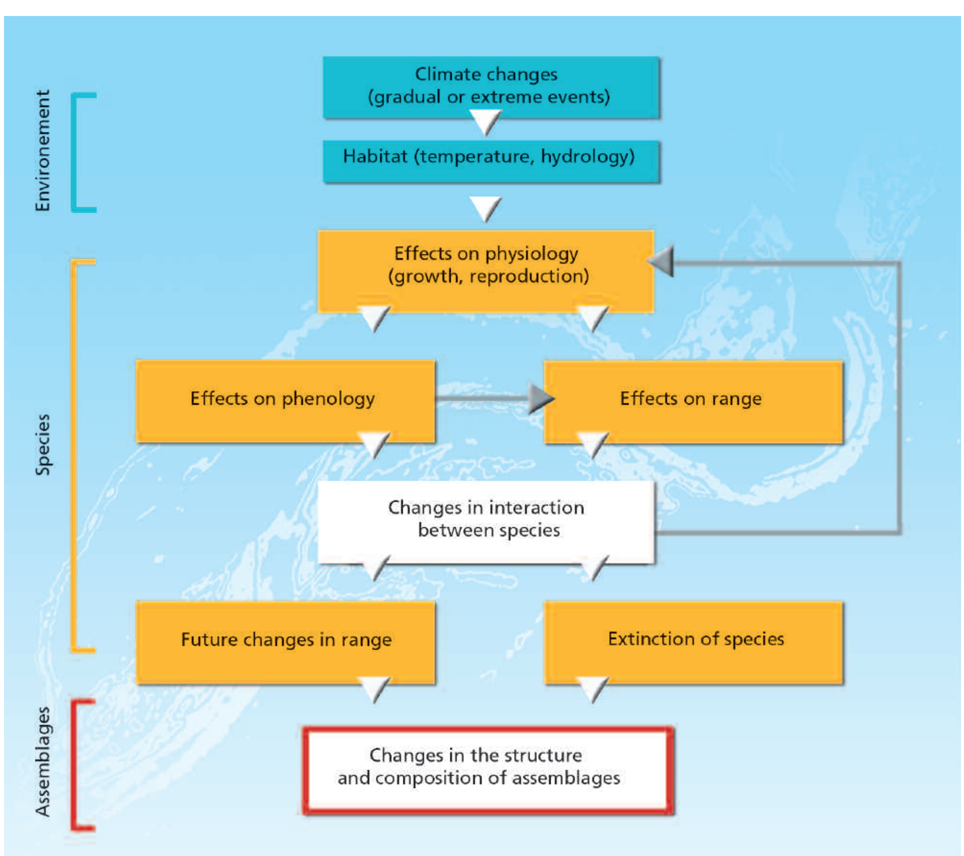


Diagram showing the changes in fish communities along the longitudinal (upstream-downstream) gradient.

Figure 24



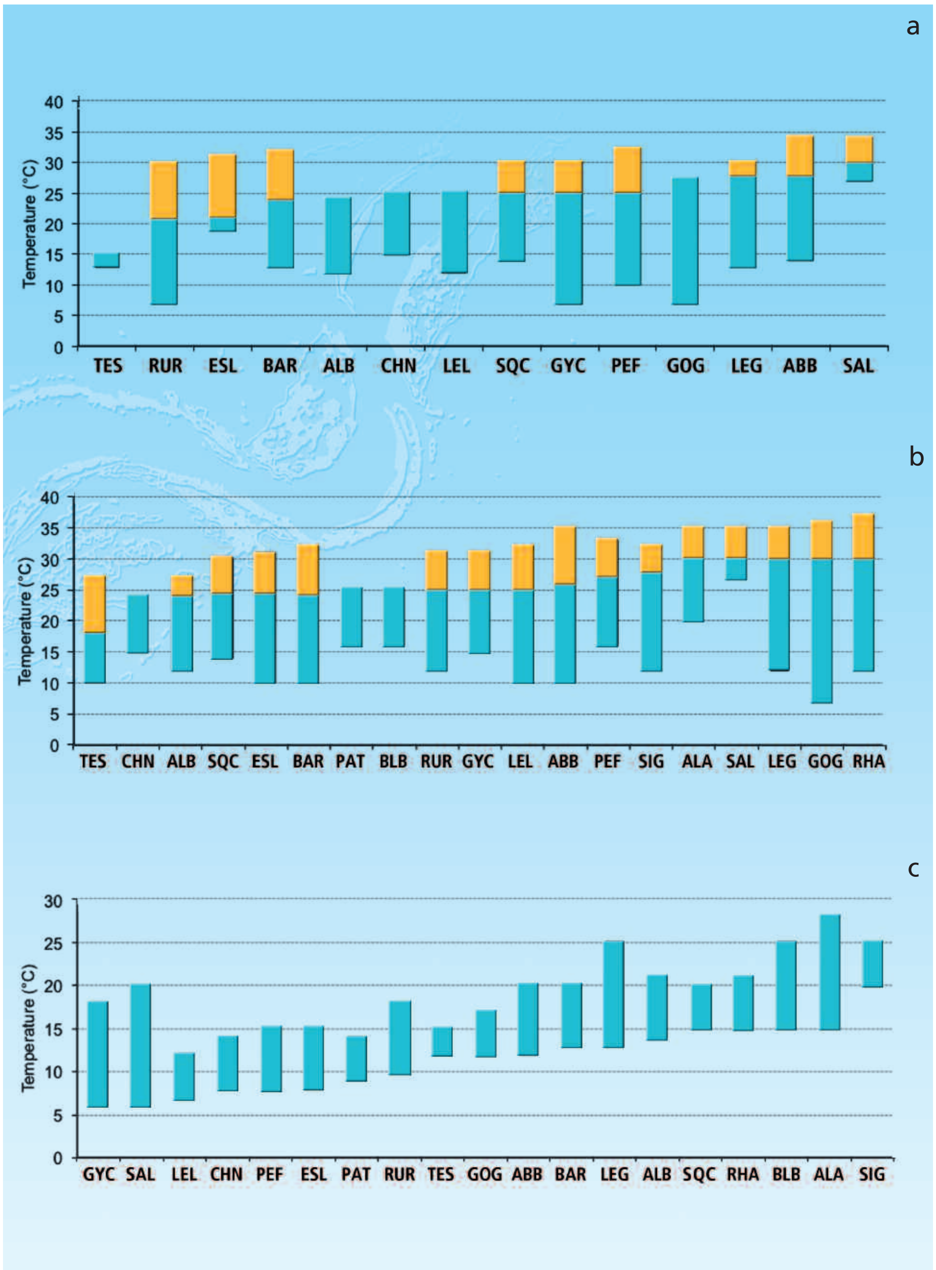
Potential consequences of climate change on assemblages of fish species (diagrams modified, originally from Hughes, 2000 and Buisson, 2009).

14. Phenology is the study of the timing of periodic events (generally annual) among life forms, determined by seasonal variations in the climate. In botany, periodic events are, among others, flowering, sprouting of leaves, fruition. In the animal kingdom, examples are the arrival of migratory birds, the return of salmon to spawning grounds, etc.

Potential and observed impacts of climate change on the physiology of organisms

All vital functions, such as metabolism, ingestion and digestion rates, swimming and reproduction, depend on the environmental conditions and notably the water temperature (Piffady, 2010; Souchon and Tissot, 2012; see Figure 25). For example, sexual maturation and gamete formation are generally triggered by a change in temperature at which the future reproducers begin to mature. The trigger may be a rise or fall in temperature, a threshold or phenomena linked to the day-night cycle. The same is true for each step in the reproductive process including migration, spawning, egg development (see for example Migaud *et al.*, 2002).

Figure 25

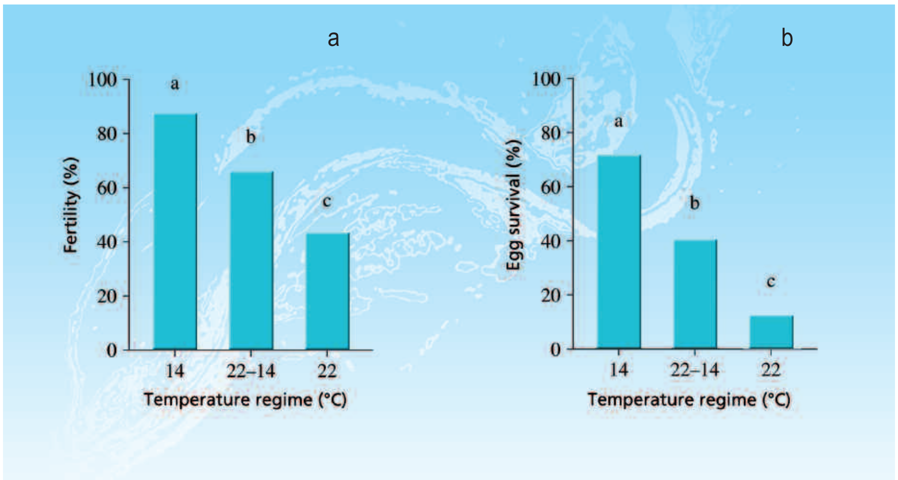


(a) Optimum temperature range (blue) and resistance zone (orange) of juvenile fish, (b) of adults, (c) optimum temperature range for reproduction (Souchon and Tissot, 2012).

ABB
Common bream
(*Abramis brama*)
ALA
Bleak
(*Alburnus alburnus*)
ALB
Schneider
(*Alburnoides bipunctatus*)
BAR
Barbel
(*Barbus barbus*)
BLB
White bream
(*Blicca bjoerkna*)
CHN
Nase
(*Chondrostoma nasus*)
ESL
Pike
(*Esox lucius*)
GOG
Gudgeon
(*Gobio gobio*)
GYC
Eurasian ruffe
(*Gymnocephalus cernuus*)
LEG
Pumpkinseed
(*Lepomis gibbosus*)
LEL
Dace
(*Leuciscus leuciscus*)
PAT
South-west European nase
(*Parachondrostoma toxostoma*)
PEF
Perch
(*Perca fluviatilis*)
RHA
Bitterling
(*Rhodeus amarus*)
RUR
Roach
(*Rutilus rutilus*)
SAL
Pikeperch
(*Sander lucioperca*)
SIG
Wels catfish
(*Silurus glanis*)
SQC
Chub
(*Squalius cephalus*)
TES
Blageon
(*Telestes souffia*)

Experiments under controlled conditions have attempted to assess the impact of the temperature regime on the physiology of certain fish, notably cyrophilic[15] and stenothermal species. For example, it has been shown that an increase in average temperature from 14 to 22°C during vitellogenesis[16] in Atlantic salmon (*Salmo salar*) significantly reduced the fertility and survival rate of eggs (King *et al.*, 2007, see Figure 26).

Figure 26



(a) Mean fertility rate and (b) mean survival rate of eggs under different temperature regimes. Regime 1) constant 14°C, regime 2) first 22°C for six weeks, then 14°C for six weeks, regime 3) constant 22°C. Different letters (a, b, c) above the bars indicate significant differences in the results (diagrams modified, originally from King et al.*, 2007).*

Comparable results have been noted for rainbow trout (*Oncorhynchus mykiss*), coho salmon (*Oncorhynchus kisutch*), European bullhead (*Cottus gobio*) and for roach (*Rutilus rutilus*) (Flett *et al.*, 1996; Pankhurst *et al.*, 1996; Brodersen *et al.*, 2011; Dorts *et al.*, 2012), which highlights the great sensitivity of certain species to modifications in the temperature regime (threshold temperatures, amplitude, duration, repetition over time) and the importance of environmental factors such as the availability of food (Brodersen *et al.*, 2011). It should also be noted that modifications in the temperature regime can affect the capacity of species to withstand exposure to toxic substances (see Box 6, page 55).

These results, obtained under controlled conditions, have also been observed *in natura*. For example, just downstream of the Tihange nuclear power plant in Belgium, the increase in water temperature would seem to accelerate the maturation and development of ovaries in roach (Mattheeuws *et al.*, 1981). Similar results have been noted in the European bullhead. Higher temperatures in certain parts of the Bez river basin in France would seem to increase the growth of juveniles, accelerate maturation and reproductive efforts, and reduce life spans (Abdoli *et al.*, 2005, 2007). A consequence of the acceleration during maturation, a stage during which growth slows, might be a reduction in the final size of the fish (Abdoli *et al.*, 2005, 2007). This phenomenon has been observed on a much larger scale in both marine and freshwater environments for other fish species and is thought to be linked to climate change (Daufresne *et al.*, 2009; Jeppesen *et al.*, 2010; Sheridan *et al.*, 2011; Cheung *et al.*, 2012). Over the past 20 years, the average size of entire communities of fish would seem to have decreased. One of the mechanisms proposed to explain this phenomenon is a classic application of Bergmann's rule, which stipulates that warm-blooded animals tend to be smaller in warmer environments. However, given that fish are ectothermic, another underlying mechanism has been suggested to explain this phenomenon. According to Edeline *et al.* (2013), accumulated energy, i.e. the difference between the energy ingested and that expended to maintain life, increases faster in small animals than in larger animals when temperatures rise. This mechanism would make them more competitive in using resources than large animals, thus resulting over the long term in a reduction in sizes and a reorganisation of ecosystems (see Figure 27).

15. Species that prefer cold environments.
16. The process by which the vitellus develops. It contains the endogenous and exogenous reserves of the egg.

No conclusions may yet be drawn, but the increase in water temperatures caused by climate change would already seem to have affected the growth and perhaps the reproduction of certain organisms. The experiments and analyses presented below provide a rough idea of the magnitude of the changes that could occur in response to a more significant increase in temperatures.

Figure 27

Climate change could prove favourable for smaller species and lead to a reduction in the size of animals from larger species.

Effects on phenology

Seasonal variations in the climate determine the timing of an array of periodic events in fish, such as reproduction and migration. Phenology, the study of when seasonal activities occur, reveals the temporal responses of fish to environmental changes.

Over the past decades, phenological changes have been observed in many parts of the world and in a wide variety of taxonomic groups, including butterflies, amphibians, birds, mammals and many ligneous and herbaceous plants (Parmesan and Yohe, 2003; Root *et al.*, 2003).

There are fewer studies on fish due to the lesser number of data series spanning long time frames (see Box 3). However, the work by Wedekind *et al.* (2010) revealed that over a 62-year period, the spawning period of the grayling (*Thymallus thymallus*) occurred three weeks earlier in response to the increase in water temperature. Schneider *et al.* (2010) noted a similar phenomenon in the Walleye (*Sander vitreus*) over a period of 69 years. Gillet *et al.* (2006) observed that gonade development in the roach would seem to have accelerated due to the increase in average temperatures in Lake Geneva (over a 7-year monitoring period). Similar results were found at the Tihange nuclear power plant in Belgium where the increase in water temperature downstream would seem to accelerate the reproduction cycle (spawning three weeks earlier) in roach (Mattheeuws *et al.*, 1981).

Concerning diadromous salmonids and even though a link with climate change has not been established, a shortening of the biological cycle of Atlantic salmon has been observed in rivers in the Bretagne and Basse-Normandie regions (30-year monitoring period) and in the U.K. (60-year monitoring period, leading to a more rapid renewal rate of populations (Baglinière *et al.*, 2004; Aprahamian *et al.*, 2008). A 30-year monitoring programme of diadromous salmonids migrating up the Bresle River (Somme and Seine-Maritime departments) has shown that migration of sea trout now occurs primarily in the summer to the detriment of the fall migratory wave. Migration of salmon now occurs almost 45 days later than was previously the case, in mid September

(Euzenat, Fournel, Fagard and Delmotte, data not published). Similar results have been registered for the Atlantic salmon (see Figure 28) in the Nivelle River (Basque country), the Scorff (Bretagne region) and the Oir, a tributary of the Sélune River (Basse-Normandie region) (Bal, 2011).

Figure 28

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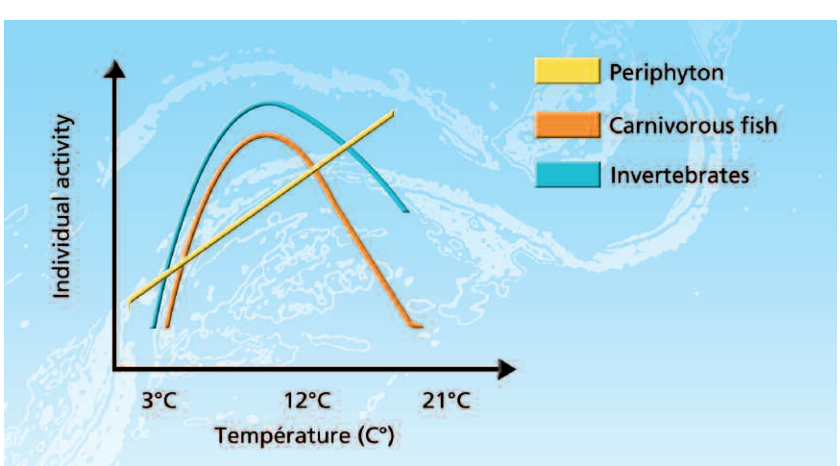
The reproductive period of the grayling may occur earlier in the year due to higher water temperatures.

Changes in phenology due to climate forcing may result in a loss of trophic synchronisation between species and consequently a restructuring of food webs (Beebee, 1995; Martin, 2007; Saino *et al.*, 2009; Helland *et al.*, 2009; Shutter *et al.*, 2012). For example, the increase in spring temperatures since the beginning of the 1960s provoked a temporal shift between the algal bloom of diatoms in a temperate North-American lake and the Daphnia populations that consume them (Winder and Schindler, 2004). Various studies have also shown the importance of:

- temperature in the predator-prey relations between the Dolly-Varden trout (*Salvelinus malma*), *Glossosoma* caddisfly larvae and the periphyton (Kishi *et al.*, 2005; see Figure 29);
- the period of abundant snow (frozen lake) in the interaction between brown trout and Arctic charr (*Salvelinus alpinus*) (Helland *et al.*, 2009).

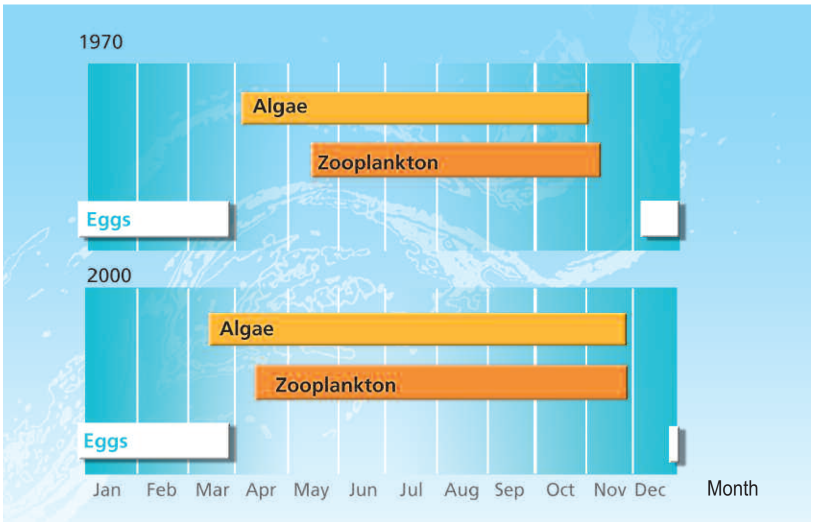
Figure 29



Interaction between temperature and predation, according to a lab experiment by Kishi et al. *(2005). In the optimum thermal zone for the fish (12°C), the top-down control over the invertebrates encourages periphyton productivity. At low temperature (3°C), no effects are observed. At 21°C, periphyton productivity is controlled primarily by invertebrate activity, which is still fairly high compared to the carnivorous fish.*

Finally, in Lake Geneva, the earlier development of phyto- and zooplankton in response to the increase in water temperature is thought to have increased the numbers and accelerated the development of whitefish larvae (*Coregonus lavaretus*), a species consuming plankton (*Gerdeaux*, 2004; see Figure 30).

Figure 30



*Improved synchronisation between whitefish (*Coregonus lavaretus*) populations and the productivity of phyto- and zooplankton in Lake Geneva (www.cipel.org).*

In light of the above data and in spite of the relatively limited duration of the data series, it would seem that the phenology of some fish species has already been modified in step with the climate change currently under way, with as a result in certain lakes a modification in the relations between predators and preys.

Changes in species distribution

Species inhabit zones where the environmental conditions are favourable to their biological cycle. When climate change occurs, they can:

- either adapt their physiological functions and in effect their life-history traits (individual adaptation or selection on the population level);
- or migrate, thus modifying their distribution in order to survive the climate change, on the condition that the dispersal capabilities of the species and the available resources are sufficient to enable such movements (Walther *et al.*, 2002).

A very large number of studies has shown that changes in distribution toward higher latitudes and/or altitudes have taken place over the past decades in response to rapid warming of the climate (Parmesan and Yohe, 2003; Chen *et al.*, 2011). A large number of taxonomic groups and particularly fish have made such changes in their ranges. A meta-analysis (review of 77 articles published between 1980 and 2011) attempted to assess the amplitude and direction of the changes observed over the past years (Comte *et al.*, 2013). Though most of the studies focussed primarily on a small number of families (*Salmonidae*, *Cyprinidae*, *Centrarchidae* and *Percidae*), the overall results are consistent and apply to both contraction and extension of ranges. For each of the families studied and depending on the species and its geographic location, either an increase or decrease in favourable habitat ranges was observed. However, it would seem that the species located upstream (trout zone, barbel zone) are those that more often suffer a reduction in their habitat range. Conversely, the limnophilic and thermophilic species (bream zone) would tend to benefit from an extension of their habitat range.

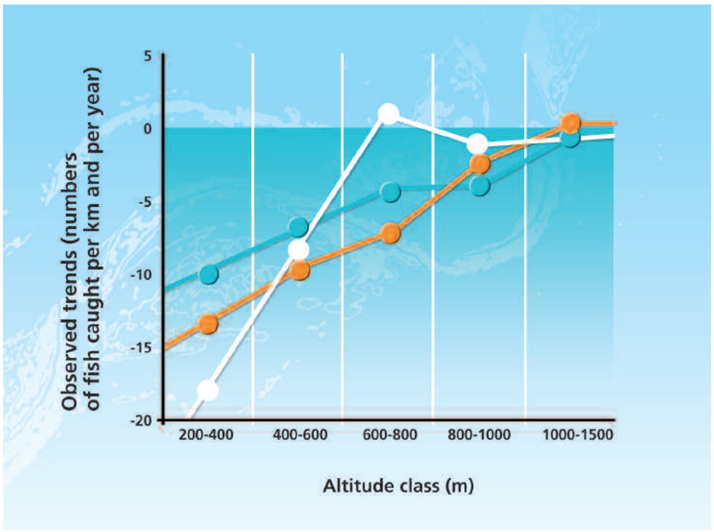
Figure 31

Trout have been confronted with a considerable reduction in favourable habitats since the 1980s.

These results have been confirmed for France as a whole. Comte and Grenouillet (2013) compared the modelled spatial distribution in the French hydrographic network between an "old" period (1980-1992) and a more "recent" period (2003-2008). Their results revealed that most species moved to higher altitudes (13.7 m per decade on average) and further upstream (600 m per decade on average). In a manner consistent with the changes in annual isotherms, fish species have moved along altitudinal gradients and extended their upper limit, while significant reductions in the lower limits of habitat ranges along the upstream-downstream gradient have also been observed, notably for species inhabiting the intermediate and upstream sections of rivers (see Figure 31). However, the speed at which most species move along the altitudinal and upstream-downstream gradients is insufficient to compensate for climate change (temperature change). Species are thought to have accumulated considerable delays (altitude = 46.8 m per decade, movement upstream = 15 km per decade) in responding to climate change.

A Swiss study has confirmed these trend data for brown trout (Hari *et al.*, 2006; see Figure 32). Over the past three decades, the reduction in size of thermally favourable habitats and the increased frequency of proliferative kidney disease (PKD) (see Box 4) have led to a massive loss in the numbers of fish from an average of 907 per kilometre before 1987-1988 to an average of 484 per kilometre afterwards.

Figure 32



Trends in trout angling catches in Swiss rivers (per km and per year) as a function of the altitude (an indication of population sizes in each altitude class). The white circles correspond to trends observed over the period 1978 to 1987, the blue and orange circles (two separate data series) correspond to trends observed over the period 1988 to 2001. The first observation is that the decline in numbers decreases as the altitude increases. Secondly, prior to 1988, numbers were stable above 600 metres, but since then the dividing line is closer to 1 000 metres, which suggests that the drop in numbers is no longer observable exclusively in the lower sections of rivers (diagrams modified, originally from Hari et al.*, 2006).*

Changes in the distribution of other aquatic organisms

Fish are not the only aquatic organisms whose geographic distribution is likely to be modified by climate change. The geographic range of some cyanobacteria capable of producing toxins, e.g. *Cylindrospermopsis raciborskii*, has recently undergone modifications, due notably to the influence of climate change (Gugger *et al.*, 2005a; Gugger *et al.*, 2005b), with serious consequences in health and ecological terms (food webs, ecological functioning). Similarly, certain tropical diatom species, e.g. *Hydrosera triquetra* and *Diadesmis confervacea*, have over the past few years become permanent inhabitants in most rivers in southern France, probably in response to the observed rise in temperatures (Coste, 2006).

Macroinvertebrates are also affected. For example, Floury (2013) showed that warming and, to a lesser degree, the reduction in the discharge of the Loire River were involved in the disappearance or the progressive decline of rheophilic and cryophilic macroinvertebrates, e.g. *Chloroperlidae* spp. Conversely, it would appear that limnophilic and thermophilic taxa benefited, including certain invasive species, e.g. *Corbicula* spp. Taxa that are sensitive to pollution (*Brachycentridae, Philopotamidae*) have also made a comeback over the past few years due to the improvement in water quality.

Finally, it is not impossible that global warming has had an influence on spatial trends in the proliferative kidney disease (PKD) noted in trout, grayling and salmon (Hari, 2006). Warming is thought to have extended the seasonal activity of the pathogenic agent which can propagate only when water temperatures exceed 9°C. In addition, the disease manifests itself only when temperatures exceed 15°C (Gay *et al.*, 2001; Chilmonczyk *et al.*, 2002; Wahli *et al.*, 2002). The increase in water temperatures could boost the propagation of the disease, even if to date the primary cause would seem to be linked to practices in commercial fishing (release of fish from infected fish farms). The same is true for fish pathogens such as *Ichthyophonus* spp. and *Argulus coregoni*, whose propagation and virulence could be modified by climate change, e.g. an increase in pathogen growth rates, physiological or immune-system changes in hosts, etc. (Marcogliese, 2008; Kocan *et al.*, 2009).

The studies presented above indicate that changes in distributions have already been observed in some rivers, on both local and larger scales. These changes may result in smaller ranges or even the local extinction of species. This is because the climatically favourable habitat of a species may become too small or too isolated from the initial geographic zone due to natural (divisions caused by river basins, relief, the continent itself) and/or anthropogenic fragmentation (dams, weirs, hydromorphological alterations) that exceeds the capacity of the fish to disperse in step with the current rapid rate of climate change (Devictor *et al.*, 2008; Isaak *et al.*, 2013; Comte and Grenouillet, 2013). Note that certain studies suggest that in addition to climate change seen as a gradual change in water temperatures, it is also important to take into account the impact of extreme events (see Box 5). On the other hand, some species may benefit from climate change and also be in a position to take advantage of breaks in biogeographic boundaries caused by human activities, e.g. canals between river basins, global trade, voluntary introduction of species, thus gaining access to numerous new habitats and potentially becoming invasive (Walther *et al.*, 2002; Rahel and Olden, 2008). Similar to changes in phenology, these changes in the distribution of species modify community structures. For example, a study by Daufresne and Boët (2007) revealed an increase in species richness and a decrease in equitability[17] in fish communities in response to an increase in water temperatures in certain French rivers (Loire, Rhône, Seine). The drop in equitability is thought to be due primarily to the low number of species benefiting from climate change. Other studies have also

17. Equitability is an indicator for the relative presence of species within a community. The more the numbers of each species tend to be equal, i.e. equitable or even, the higher the level of equitability. On the other hand, if a majority of the individuals in a community belong to the same species, equitability is low.

highlighted an increase in the species richness of fish communities in French rivers (Poulet *et al.*, 2011; Alonso *et al.*, 2013). Three potential causes for the local increase in species richness have been mentioned:

- the introduction of non-native species;
- the reduction in organic pollution, which has encouraged recolonisation by certain species;
- climate change, which has encouraged colonisation further upstream by thermophilic species.

However, a number of researchers think that this increase could be temporary because the speed at which a species appears is generally faster (a single individual is sufficient) than that at which a species disappears (Wilson, 1990).

Encadré 5

What is the effect of extreme events on aquatic biodiversity?

The consequences of climate change are generally perceived as gradual changes in certain environmental variables (temperature, precipitation, etc.). However, the issue of extreme events has come increasingly to the fore as a decisive element in biodiversity, highlighting the need to take these phenomena into account in the study of climate change and its impacts.

In France for example, the heat wave of 2003 would seem to have been a major event for biodiversity that resulted in high mortality levels in fish populations in certain rivers, notably among the species inhabiting the trout and grayling zones. In parallel, changes in the migratory rhythms of four diadromous species (Atlantic salmon - *Salmo salar*, Allis shad - *Alosa alosa*, eels - *Anguilla anguilla* and sea lampreys - *Petromyzon marinus*) and an increase in their mortality rates were observed in the Garonne and Dordogne Rivers and in the Loire basin (Conseil économique et social des Pays de la Loire, 2004; Travade and Carry, 2008).

In the Saône River, mollusc communities were also impacted (Mouthon and Daufresne, 2006). Certain bivalves (*Pisidium* genus) almost disappeared from samples taken in 2003 and did not show high levels of resilience in 2004. Only eight of the 24 species present in the Saône River, upstream of Lyon, would seem to have withstood the heat wave somewhat better.

These observations suggest that some species have limited resistance and resilience in the face of temporary increases in temperatures (Mouthon and Daufresne, 2006). Heightened frequencies of extreme events in the future could have more negative consequences than gradual changes in climatic conditions. However, only long-term monitoring will provide the data required to assess precisely the resilience of populations confronted with sudden changes in the climate (Matthews *et al.*, 2013).

Figure 33

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The increase in the frequency of extreme events due to climate change, e.g. dry periods, will have serious consequences for aquatic biodiversity.

Climate change is not the only factor involved in the modifications noted in the distribution and structure of communities. Other factors such as alterations in hydrological regimes and improvements or decreases in water quality also play a crucial role (see Box 6). The arrival of new species may also be explained by the development of waterways as well as voluntary (stocking) or accidental introductions. The drop in the numbers of certain species, notably diadromous fish, is due to various factors such as overfishing, development work in rivers (obstacles to migration), problems with water quality, etc. Grenouillet and Comte (2014) discovered that the estimated changes in distribution (colonisation or disappearance) for 32 freshwater species in continental France caused by non-climate factors were far greater than the changes caused by the climate. It would thus appear that the role of climate change in modifications to fish distribution (at least for a certain number of species) is often overestimated and that better assessment of other factors, both natural and anthropogenic, is required. In addition, the study revealed a certain latency to the effects of climate change concerning both colonisations and local extinctions, i.e. some populations persisted in areas subject to theoretically unfavourable climates and other areas (variable in size depending on the species) subject to theoretically favourable climates remained uninhabited. In the final analysis, climate change is simply one factor in global change. It is therefore very important to stress the fact that anthropogenic pressures and climate change act together and tend to increase the vulnerability of environments and species, an example being the greater increases in water temperatures due to reductions in river discharges.

Figure 34

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b © Y. Falatas - Onema

Climate change must not mask the many other pressures weighing on aquatic environments and that inhibit the adaptation of organisms to changes in the climate.

Impacts on aquatic organisms caused by the interaction between water quality and climate change

The health of aquatic organisms can be indirectly affected by a number of environmental parameters influenced by climate change, e.g. temperature, water pH and salinity, penetration of UV rays in the water column, etc. The effects of interactions between climate change and chemical stresses caused by certain potentially toxic aquatic pollutants are an example of the consequences that could turn out to be particularly harmful for certain species. There are a number of aspects to these effects.

Heightened sensitivity to modifications in temperature regimes

The capacity of species or populations to tolerate thermal stress may be reduced if there is simultaneous exposure to toxic chemical substances. The modifications caused by climate change in certain environmental parameters, such as water temperature, interact with other stress factors weighing on the environment, thus affecting the physiological functions in charge of maintaining homeostasis, i.e. the capacity of an organism to maintain its equilibrium in spite of external pressures (Noyes *et al.*, 2009). Ectothermic organisms such as fish, whose body heat is derived from the environment, are particularly sensitive to the interactions between temperature and contaminants. The tolerance of four species of freshwater fish to upper temperature limits is limited in fish exposed to sub-lethal concentrations of two insecticides (endosulfan and chlorpyrifos) (Patra *et al.*, 2007). Similarly, the acclimation potential of brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) to temperature rise is reduced by sub-lethal concentrations of DDT and exposure of a small cyprinid (*Pimephales promelas*) to low concentrations of cyfluthrine reduces its thermal-tolerance range by almost 30% (Noyes *et al.*, 2009). These effects would seem to be bidirectional because water temperature also influences the sensitivity of fish to toxic substances. In a context of climate change, exposure to toxic substances will represent a particularly difficult problem for aquatic species already living close to the limits of their "thermal tolerance". Stenothermal species, which can withstand only very small variations in temperature, will have greater difficulties in adapting to temperature rise and are likely to be confronted with high mortality rates resulting in local extinctions, notably where the environment is already disrupted (Kimberly and Salice, 2012).

Increased toxicity for certain fish species

Numerous studies have revealed a direct relation between water temperature and the toxicity of a wide range of contaminants for several fish species (Noyes *et al.*, 2009). For example, for channel catfish (*Ictalurus punctatus*), the toxicity of atrazine, a widely used herbicide that was banned ten years ago, increases with a rise in water temperature and a drop in the level of dissolved oxygen. Similarly, the mortality of juvenile rainbow trout (*Oncorhynchus mykiss*) exposed to endosulfan, an insecticide, increases when the water temperature rises from 13°C to 16°C. Conversely, the toxicity of other insecticides such as DDT and pyrethrenoide-based products increases at lower water temperatures. Even though the underlying mechanisms are not yet fully understood, it would seem that the relation between temperature and toxicity is in part due to a temperature-controlled modification of the metabolism of the organisms, which influences the biotransformation of the bioaccumulated contaminants. That is the case for certain persistent organic pollutants such as PCBs (polychlorinated biphenyls) where the biotransformation by rainbow trout into toxic active metabolites (i.e. hydroxylated PCBs) increases when the water temperature rises from 8 to 16°C (Noyes *et al.*, 2009; Hooper *et al.*, 2013).

■ Alteration of bioaccumulation processes

Climate change is also likely to cause certain modifications in the structure and type of trophic interactions, in migratory patterns and in the feeding behaviour of certain species, which could alter bioaccumulation and bioamplification processes for persistent organic pollutants (POP) in aquatic food webs (Noyes *et al.*, 2009). The experimental data acquired on fish indicate generally higher levels of contaminant bioaccumulation and of elimination rates when water temperatures rise (Noyes *et al.*, 2009; Sokolova and Lanning, 2008). These increased levels of contamination in organisms result notably from a modification in the ventilation rate in response to a reduction in oxygen solubility at higher temperatures.

Recent studies (e.g. Gouin *et al.*, 2013) attempted to estimate, on the global level, the impact of climate change on exposure and accumulation levels in aquatic food webs using the IPCC climate projections. Given constant levels of hydrophobic organic contaminants (HOC), the results of simulations carried out using "multimedia" models indicate that the projected levels of environmental exposure are at most two times as high as current levels. The direct effects of climate change on potential HOC bioaccumulation in aquatic food webs are extremely variable and highly dependent on the partition equilibrium properties of these substances between the various environmental compartments and on biotransformation constants. The study authors note, however, a number of residual uncertainties (i.e. potential effects on pollutant emissions, physical-chemical properties of substances and degradation constants) affecting the study results (Gouin *et al.*, 2013).

■ Indirect effects caused by ecosystem degradation

The number and size of "dead zones", i.e. aquatic environments with low levels of dissolved oxygen, have increased significantly over the past decades. This phenomenon is caused by excessive levels of nutrients (N and P) in water due to the use of fertilisers and made worse by the combustion of fossil fuels, the loss of wetlands and urbanisation (Diaz and Rosenberg, 2008). The frequency, duration and scale of hypoxic or anoxic zones are likely to increase because of climate change, notably due to greater run-off of nutrients in regions subjected to more frequent extreme rainfall and to greater stratification of water columns. Recent studies would seem to indicate that fish subjected to repeated and/or prolonged hypoxia may suffer alterations in reproductive functions controlled by the endocrine system, to the point of producing detrimental effects on populations (Thomas *et al.*, 2007). This phenomenon is likely to occur in addition to the effects produced by the many pollutants in aquatic environments that can cause endocrine disruptions, including natural hormones, synthetic hormonal compounds, certain medicines for human and veterinary use, and a vast array of chemical substances (brominated flame retardants, plasticisers, detergents, herbicides, pesticides, etc.).

Case studies in continental France

The Rhône basin

The Rhône River has undergone development work to produce hydroelectric power and enable navigation. The work modified the original hydromorphological conditions and created new environments (canals, impoundments, short-circuited sections with regulated discharges). In addition to these more or less recent hydromorphological changes that structure the physical habitats of species, since the end of the 1970s the chemical quality of water has been modified (reduction of organic pollution and certain toxic substances) and non-native species have appeared and developed. These phenomena modify the biological structure and functioning of the Rhône ecosystem. Over the past three decades, the temperature regime of the Rhône has also undergone warming averaging 1.5°C in the upper reaches and 2.0°C in the lower reaches below the confluence with the Isère River (Daufresne *et al.*, 2004; Daufresne and Boët, 2007; Poirel *et al.*, 2008; see Table 2).

Tableau 2 *Average temperature per decade, monitored at 15 points along the Rhône and its tributaries (from the upstream sections on the left to the downstream sections on the right), and the differences between successive decades (according to Poirel* et al.*, 2008).*

Average / decade	SCX	LEM	ARV	POU	CRE	BUG	AIN	JON	SAO	SAL	SPE	RGL	ISE	SOY	CRU	TRI	DUR	ARA
1977-1986	-	11.3	-	10.4	11.0	11.4	10.6	12.5	13.0	12.8	-	-	10.1	12.0	12.1	12.1	13.1	13.2
1987-1996	-	11.9	-	11.3	11.9	12.1	11.6	13.3	13.4	13.7	14.7	14.7	10.7	13.2	13.5	13.4	13.5	14.7
1997-2007	7.4	12.3	8.4	11.4	12.2	12.4	12.1	13.9	14.0	14.0	15.1	15.4	10.8	14.1	14.1	14.0	13.5	15.2
Difference between successive decades	**SCX**	**LEM**	**ARV**	**POU**	**CRE**	**BUG**	**AIN**	**JON**	**SAO**	**SAL**	**SPE**	**RGL**	**ISE**	**SOY**	**CRU**	**TRI**	**DUR**	**ARA**
(87/96) - (77/86)	-	0.60	-	0.90	0.89	0.78	1.00	0.76	0.42	0.93	-	-	0.58	1.16	1.38	1.32	0.39	1.49
(97/06) - (87-96)	-	0.38	-	0.03	0.31	0.30	0.47	0.63	0.58	0.34	0.44	0.70	0.08	0.92	0.59	0.51	0.02	0.58

Pougny (POU), Creys-Malville (CRE), Bugey (BUG), Jons (JON), Loire sur Rhône (LSR), Saint Alban (SAL), Seuil de Peyraud (SPE), Roche de Glun (RGL), Soyons (SOY), Cruas (CRU), Tricastin (TRI), Aramon (ARA), Pont de Chazey (AIN), Couzon (SAO), Beaumont Monteux (ISE), Porte du Scex (SCX), Arve au Bout du Monde (ARV), the Rhône at Halle de l'Ile (LEM), Durance (DUR).

This rise in the average temperature and, more precisely, the earlier dates at which the various thresholds are reached, the reduced duration of the cold period and the lengthening of the warmest period are thought to explain in part the variations observed in macroinvertebrate and fish communities.

Since 1979, fish communities have come to be dominated by species preferring relatively warm waters (e.g. chub), whereas cold-water species (e.g. dace) have declined (Daufresne *et al.*, 2004; Daufresne and Boët, 2007). This phenomenon has also been noted for macroinvertebrates, with the *Athricops* and *Potamopyrgus* genera replacing *Chloroperla* and *Protoneumura* (Dolédec *et al.*, 1996; Daufresne *et al.*, 2007), except in the lower Rhône, where communities are already dominated by limnophilic and thermophilic taxa.

In the Rhône river basin as a whole, the effects of climate change can already be widely observed even though trends remain difficult to assess due to the existence of multiple confounding factors (human activities).

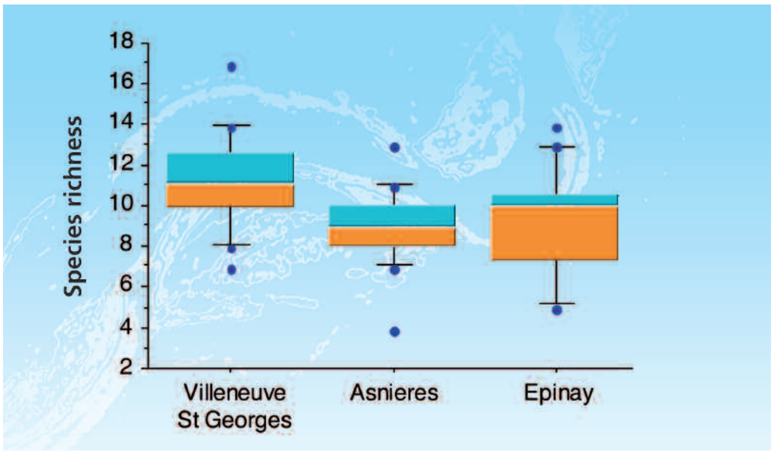
The Seine basin

Similar to the Rhône basin, the basin of the Seine River has undergone extensive anthropic development. Whereas the original fauna comprised some 30 species during the last glacial periods (between 24 and 33, depending on the hypotheses), human activities since the Middle Ages resulted at the end of the 1900s in the detection of 23 new species due to direct (voluntary introductions) or indirect (modifications made to aquatic environments) efforts (Belliard *et al.*, 1995, 2009). Over the same period, seven migratory species out of the ten original disappeared from the river basin, on the one hand because of the creation of obstacles in the main rivers and, on the other, the deterioration in water quality and the disappearance of perifluvial wetlands (Belliard *et al.*, 1995, 2009).

Since the 1970s, major efforts have been made to restore the quality of the river, thus enabling the return of certain migratory species (European smelt - *Osmerus eperlanus*, sea trout, shad, sea lampreys - *Petromyzon marinus*) and increases in the abundance of species particularly sensitive to the quality of the environment (barbel, dace). That being said, species richness continues to vary widely along the longitudinal gradient, with generally more diversified fish communities upstream of Paris (see Figure 35).

Within the Seine basin, fish communities have been considerably influenced by a vast array of factors producing effects on different spatial and temporal scales. This context makes it very difficult to determine the impact of climate change alone on fish populations. In addition, less information is available on changes in water temperature than for the Rhône. Preliminary studies covering the period 1998 to 2004 do not indicate a rise in water temperature in the Grande Bosse side channel between Montereau and Nogent sur Seine (Tales, 2008), however the data series is so short that it is difficult to draw any robust conclusions. The same authors also

Figure 35



Changes in species richness of fish communities along the longitudinal axis of the Seine River between 1990 and 2005 (diagrams modified, originally from Belliard et al.*, 2009). The bottom and top of the boxes represent the 25th and 75th percentiles (i.e. the box contains 50% of the observed values), and the ends of the whiskers represent the 10th and 90th percentiles (i.e. the interval between the whiskers contains 80% of the observed values). The median is represented by the border between the blue and orange sections.*

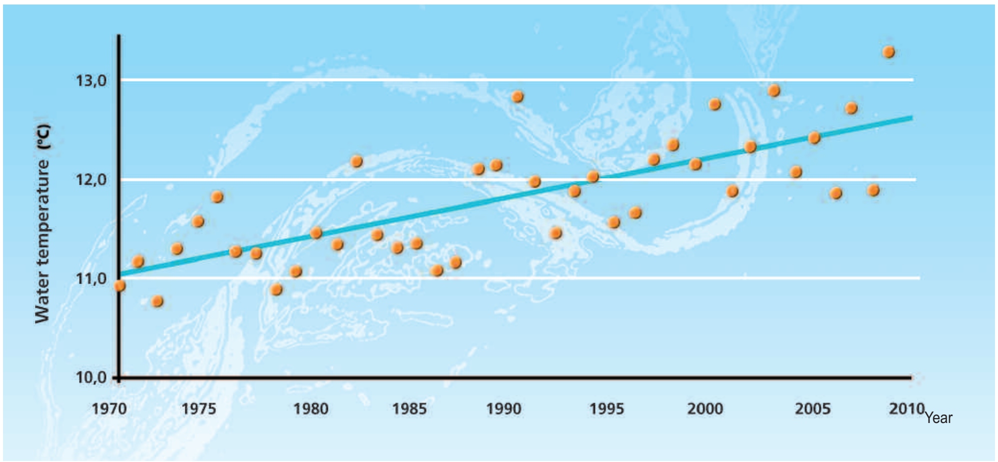
could not establish any significant correlation between fish communities and hydroclimatic variability. The work by Belliard *et al.* (2009) would nonetheless suggest an increase in the numbers of perch and a decrease in the numbers of cyprinids during the heat-wave years (2003-2004). The mechanisms involved could not be identified (direct effect of temperature or predation between species).

Lake Geneva

Lake Geneva lies at an altitude of 372 metres and covers 580 square kilometres. It receives inputs from various rivers in the Swiss cantons (Valais, Vaud, Fribourg and Geneva) and from the neighbouring French departments (Haute-Savoie, Ain). Among these numerous tributaries, the Rhône has by far the largest discharge and alone represents 75% of the inputs to Lake Geneva.

The creation of a systematic monitoring programme for lake waters in 1957, on behalf of CIPEL (International commission to protect Lake Geneva), produced data on water temperatures. The results reveal an increase in the annual average temperature of over 1°C at the bottom of the lake (309 metres) and of over 1.5°C at five metres below the surface over the past 40 years (CIPEL, 2009). The winter temperature of the lake rose from 4.5°C in 1963 to 5.1°C in 2006 and vertical thermal stratification due to the lower density of warm water now occurs one month earlier than 30 years ago (see Figure 36).

Figure 36



Change in annual average temperature at a depth of five metres in Lake Geneva (according to www.cipel.org).

These changes have had visible consequences for planktonic and fish communities, and generally speaking on ecosystem functioning. Due to the earlier occurrence of thermal stratification, maximum primary production of phytoplankton and of herbivorous zooplankton now takes place one month earlier in the spring (Anneville *et al.*, 2005). Massive consumption of the phytoplankton by the zooplankton provokes a sharp drop in algal biomass and results in the transparent-water phase[18] being brought forward from June to May. The phosphorous available in the upper water layer is more rapidly consumed by the primary production and quickly becomes a limiting factor, whereas sufficient concentrations remain in the deep, cold waters receiving less light. These conditions are favourable for the series of "autumn" algae that develop over the summer in the deep waters. These algae contribute very little or not at all to energy transfers to the higher levels of the feed web due to their lack of palatability for zooplankton, resulting in a significant restructuring of trophic transfers in the lake.

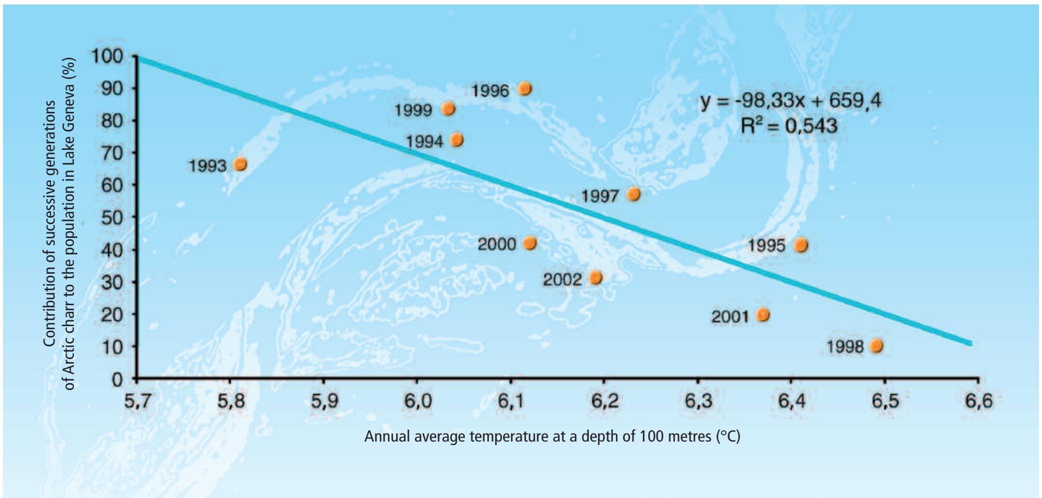
18. The transparent-water phase occurs following the spring development of phytoplankton, when the algae are eaten by the herbivorous zooplankton. This phenomenon has increased in frequency with the development of eutrophication.

A number of changes have also been noted concerning fish communities (Jeppesen *et al.*, 2012). The reproduction period for roach is now approximately one month earlier, whereas that of perch has remained virtually unchanged. Spawning by whitefish, a cold-water species, now occurs approximately two weeks later in December, in response to the rise in water temperature. Given that plankton cycles take place one month earlier, the whitefish larvae now inhabit waters that are warmer than 30 years ago and offer more abundant nutrients. These phenological changes have resulted in an increase in whitefish populations, a fact confirmed by catch data over the past 30 years (less than 50 tons in the 1970s and over 300 tons since 1997) (Gerdeaux *et al.*, 2004).

On the other hand, Arctic charr, a relic species from the glacial period, would appear to be particularly threatened because its oogenesis is blocked by temperatures exceeding 7°C (Danis *et al.*, 2004; see Figure 37). Over the long term, projections indicate that the Arctic charr will disappear and will be replaced initially by whitefish, subsequently by cyprinids.

Climate change thus impacts the composition of the communities inhabiting Lake Geneva and the overall functioning of the lake ecosystem. It should be noted however that major oligotrophication efforts have been made over the past decades and probably contributed to the observed effects.

Figure 37



Strength of Arctic charr cohorts[19] *as a function of the annual average water temperature at a depth of 100 metres in Lake Geneva. Ovulation in Arctic charr is blocked if the water temperature at a depth of 100 metres exceeds 7°C (*Gerdeaux, 2011*).*

19. Index indicating the relative importance of a cohort in the population.

Conclusion and outlook

The physiology, biological rhythms and distribution of fish depend on environmental factors such as temperature, hydromorphological conditions and water quality (dissolved oxygen, pollutant concentrations, etc.). Climatic disruptions impact these factors and thus constitute a major source of change for fish species.

Though it is very difficult in the freshwater context to distinguish between the effects of climate change and those of local anthropogenic pressures, a number of studies have revealed the impact of temperature increases on fish communities. Changes in certain physiological characteristics in response to an increase in water temperature have in turn resulted in changes in reproduction, growth and seasonal rhythms. In addition, some species have moved up river, extending their range when movement is not blocked by other factors such as weirs and dams. These movements have led to changes in the composition of communities with as a consequence modifications in species richness and in the number of dominant species.

Even though the signs are still not very clear in some rivers and interpretation is difficult due to anthropogenic pressures, the consequences of climate change are observable over France as a whole. They contribute to the impact of human activities in rivers (dams, reservoirs, sealing of banks, abstractions for various uses, release of polluted water, etc.) and can in certain cases reinforce the ecological modifications.

Unfortunately, the lack of long data series and the change in the sampling strategy for the surveillance-monitoring network limit the possibilities of studying current changes in communities in the context of climate forcing.