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Synthesis of thermal tolerances of the common freshwater fish species in large Western Europe rivers

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ABSTRACT

Key-words:
*fish,
temperature,
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The effects of industrial cooling water on fish communities were widely debated at the end of the seventies, when large thermal power plants were being developed. This led to numerous research programs on thermal tolerance in fish. The recent warming climatic period and especially the 2003 heat wave have brought thermal biology back to center stage. The work presented here has consisted in analyzing historical and contemporary literature to update basic knowledge on thermal tolerances of 19 riverine fish species. These data were then validated and completed by European fish specialists. We finally proposed a synthesis, based on more than 300 references, which details thermal tolerances for the entire life cycle: reproduction, embryonic, larval, juvenile and adult life stages. This updated material is of great importance to an understanding of the trends observed in fish communities or for forecasting future behavior in climate change scenarios.

RÉSUMÉ

Synthèse des tolérances thermiques des espèces de poissons communes des rivières et fleuves de plaine de l'ouest européen

Mots-clés :
*poissons,
température,
tolérance
thermique,
réchauffement
climatique*

L'effet de l'élévation de température des cours d'eau a été largement débattu à la fin des années 70 qui ont connu le développement des centrales thermiques de grande puissance. Ces études ont généré alors de nombreux programmes de recherche sur la tolérance thermique des poissons, dont les résultats sont parfois oubliés ou difficiles à rassembler. Le réchauffement climatique actuel et en particulier l'épisode caniculaire de 2003 a mis de nouveau ce thème sur le devant de la scène. Le travail de synthèse présenté a consisté à analyser des données historiques et contemporaines de la littérature, afin de mettre à jour les connaissances de base sur les tolérances thermiques de 19 espèces de poissons d'eau douce. Cette synthèse a ensuite été validée et complétée par des spécialistes européens. Elle s'est appuyée sur plus de 300 références qui détaillent les tolérances thermiques de chacun des stades du cycle de vie des espèces étudiées : reproduction et stades embryonnaire, larvaire, juvénile et adulte. Cette mise à jour est essentielle pour comprendre les tendances d'évolution déjà constatées des communautés de poissons et prévoir les futures évolutions en fonction de différents scénarios de changement climatique.

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INTRODUCTION

The effect of water temperature on aquatic organisms was a central theme of research in aquatic ecology in the Seventies, in response to concerns among the public of the impact of industrial installations dependent on cooling water in their processes, with this water then being restituted at higher temperature to rivers (Leynaud, 1967; Talmage, 1977). Subsequent to the installation of atmospheric cooling towers, this topic ceased to draw as much attention for close to three decades, but returned to center stage on a major scale following the European heat wave of 2003 (De Bono *et al.*, 2004) and particularly in light of data on global warming (in the 20th century, a mean rise of air temperature each decade of +0.10 °C to 0.16 °C, according to the Intergovernmental Panel on Climate Change, 2007) and in view of GIEC forecasts (predicted temperature in 2090–2099 in comparison with 1980–1999: +1.8 °C to 4.0 °C depending on the scenario, GIEC, 2007). On a more local scale, more insidious disruptions in thermal regimes have also been noted in recent years: the effects of urbanization and heating of water by water treatment stations (Kinouchi, 2007: +0.11 °C to 0.22 °C per year on sites affected by releases from large agglomerations like Tokyo) or by the increase of impermeabilized surfaces (Leblanc *et al.*, 1997), the effects of dams which can result in a rise or a drop of the downstream temperature (Quinn and Adams, 1996 in Petersen and Kitchell, 2001; Olden and Naiman, 2010: threshold of 15.5 °C reached 1 month earlier in spring and 15 days later in fall, Columbia River, Bonneville Dam, USA) or the effects of diminishing riparian cover on rivers, leaving larger surfaces of water open to direct solar radiation (Bartholow, 2000: +3 °C to 6 °C for the mean daily temperature and +3 °C to 8 °C for the maximum temperature averaged over a number of cases; Burton and Likens, 1973 in Kaushal *et al.*, 2010 and Moore *et al.*, 2005: daily maximum of 4 °C to 5 °C higher following a wooded riparian area clear cut).

In ecology, temperature is a key abiotic factor, more difficult to interpret than in physics given that one must take into consideration not only instantaneous values but also their annual, seasonal and daily variation. Cumulative temperatures in a range favorable for organisms impact their physiology (the sum of degree days or of daily means above 0 °C or above a known threshold for a target species, Allan, 1995). From a functional perspective, temperature acts on physico-chemical variables (e.g. the solubility of oxygen), on the speed of recycling of nutrients or of decomposition of organic matter, and on the metabolic dynamics of living organisms (e.g. primary production). Critical periods for aquatic organisms may, for example, occur in the case of simultaneity of a hydric stress like a low-water episode and a high temperature in the aquatic environment (Miller *et al.*, 2007). On the scale of biota, particularly poikilothermic organisms, the temperature of the surrounding environment influences the metabolism (Gillooly *et al.*, 2001; Brown *et al.*, 2004), the rate of ingestion and digestion (Brett and Higgs, 1970; Tseitlin, 1980), and reproductive cycles (De Vlaming, 1972), with demands that vary during ontogenesis (Lapkin *et al.*, 1983 in Raat, 1988). Swimming behavior (Mann and Bass, 1997; Ojanguren and Brana, 2000) and speed of growth (Wieser *et al.*, 1988; Wolter, 2007) are also temperature-dependent. Consequently, the dynamics of populations and communities, their relative composition (Kishi *et al.*, 2005) and their size distribution (Daufresne *et al.*, 2009) are in large proportion governed by ambient thermal regimes. Depending on their requirements and their thermal tolerances, ectothermic species will or will not cope with new environmental conditions: some will decline, and even disappear from some geographical zones (Webb, 1996; ex. certain mollusks in the Saône River, France, Mouthon and Daufresne, 2006), while others, on the contrary, will expand their area of distribution (Hickling *et al.*, 2006). To fully understand the changes observed or to anticipate the future state of species distribution, it is essential to know their thermal preferences; interpretation of temperature should, however, be nuanced given that certain behaviors (Davey *et al.*, 2006; aptitude to dispersion, ability to find thermal shelters, Torgersen *et al.*, 1999) and certain phenotypic aptitudes (plasticity in the period of development, Schaefer and Ryan, 2006) enable some species to survive critical thermal episodes.

Recent syntheses on the thermal requirements of temperate fish species have focused on temperatures in the embryonic and reproduction phases (Teletchea *et al.*, 2007, 2009b), for species interesting from a zootechnical perspective. Partial syntheses were also published earlier (Hokanson, 1977; Alabaster and Lloyd, 1982; Mann, 1996; Küttel *et al.*, 2002; Teletchea *et al.*, 2009a), but to our knowledge, there has been no recent synthesis available to all stages of fish species commonly found in medium-size and large rivers.

This article meets that need for understanding the thermal profiles of nineteen species which constitute the core of the fish communities, not including salmonids, found in streams of river class 5 or larger in Western Europe (Keith *et al.*, 2011; Teletchea, 2011).

When they were available, we give the requirements for all developmental stages (adult, embryo, larval, juvenile) or specific critical period (reproduction), based on observations in both natural and controlled. We follow common definitions of the literature for these life stages (Balon, 1975), e.g. “embryo” corresponds to the incubation period from fertilization up to the hatching of larvae. The literature available via digital documentary databases does not always include some interesting, though sometimes quite dated, texts, which may even be unscientific or poorly referenced texts in native languages (German, French). We made a significant effort to exploit all those we could access; we completed our work by directly questioning European authors (23 contacted) likely to have this type of information. For the 19 species studied (Table I), the compilation bears on more than 300 references. The complete bibliographical information is provided in Appendix.

Table I

Latin code, Family, English name, Latin name and French code of the 19 studied species.

Code Latin	Family	English name	Latin name	Code French
Alb	Cyprinidae	Bleak	<i>Alburnus alburnus</i>	ABL
Bar	Cyprinidae	Barbel	<i>Barbus barbus</i>	BAF
Tel	Cyprinidae	Vairone	<i>Telestes souffia</i>	BLN
Rho	Cyprinidae	Bitterling	<i>Rhodeus sericeus</i>	BOU
Bli	Cyprinidae	White bream	<i>Blicca bjoerkna</i>	BRB
Abr	Cyprinidae	Common bream	<i>Abramis brama</i>	BRE
Eso	Esocidae	Northern pike	<i>Esox lucius</i>	BRO
Lec	Cyprinidae	Chub	<i>Leuciscus cephalus</i>	CHE
Rut	Cyprinidae	Roach	<i>Rutilus rutilus</i>	GAR
Gob	Cyprinidae	Gudgeon	<i>Gobio gobio</i>	GOU
Gym	Percidae	Ruffe	<i>Gymnocephalus cernuus</i>	GRE
Chn	Cyprinidae	French nase	<i>Chondrostoma nasus</i>	HOT
Per	Percidae	Eurasian perch	<i>Perca fluviatilis</i>	PER
Lep	Centrarchidae	Pumpkinseed	<i>Lepomis gibbosus</i>	PES
San	Percidae	Pike perch	<i>Sander lucioperca</i>	SAN
Sil	Siluridae	Catfish	<i>Silurus glanis</i>	SIL
Abb	Cyprinidae	Spiralin	<i>Alburnoides bipunctatus</i>	SPI
Cht	Cyprinidae	Sofie	<i>Chondrostoma toxostoma</i>	TOX
Lel	Cyprinidae	Dace	<i>Leuciscus leuciscus</i>	VAN

Given the intrinsic disparity in sources and methods for calculating the important thermal variables (Beitinger and Bennett, 2000, list 450 tolerance values for 116 species), we begin by explaining the definitions retained. We then comment on the data for each species analyzed. Lastly, we propose a synthesis of the thermal ranges tolerated, grouping species with similar requirements.

DEFINITIONS AND METHODOLOGY

> RANGE OF OPTIMUM TEMPERATURES

Within their range of optimum temperatures, fish feed and show no signs of abnormal behavior; they are not in a state of stress (Elliott, 1981). Within this temperature range, physiological adjustments come effectively into play to enable the fish to withstand relatively high temperatures: induction of thermal stress proteins, modification of fatty acids in membranes (Iwama *et al.*, 1998). The lower limit of this range is the minimum optimum temperature and the upper limit, the maximum optimum temperature.

> EFFECT ON THE PERIOD OF DEVELOPMENT

In fish, gametogenesis and egg-laying take place within well-defined temperature ranges. As for other physiological functions, there is a range of optimum temperatures for reproduction and upper and lower thermal thresholds above and below which gametogenesis and spawning are no longer possible.

The number of degree days is the unit by which we can determine the period of embryonic development as a function of the mean daily water temperature: for example, the period between two specific stages in development. The number of degree days is obtained by adding the mean temperature on each day between the two development stages in question. Most of the time, this number is measured in the laboratory at a given temperature which remains constant throughout the experiment, and is then calculated by multiplying this temperature by the period of embryonic development (in number of days).

> EXPERIMENTALLY ESTABLISHED CRITICAL TEMPERATURE AND LETHAL TEMPERATURE

Definitions

Thermal stress causes reactions which follow three successive phases in fish. These were identified in the laboratory and well described by Elliott (1981). The first phase is characterized by reluctance to feed, sudden sequences of activity during which the fish bump against the wall of the aquarium, momentary loss of balance, defecation and rapid respiratory movements. In the second phase, the fish becomes immobile but shows brusque though feeble swimming motions; most of the time it floats on its side or back; it may rapidly change color and ventilation movements speed up. The last phase is characterized by restricted movements which can only be seen around the operculum, the pectoral fins and the eyes; this continues until the fish is dead. If the fish are placed in cooler and better oxygenated water, those which have reached the last stress phase do not recover but die (experiments conducted by Cocking, 1959 on roach (*Rutilus rutilus*) and by Elliott, 1981 on trout (*Salmo trutta*)).

Range of resistance to temperature

During episodes of thermal stress, physiological protection mechanisms are overwhelmed by the rapid appearance of the effects; fish can, however, “resist” for a certain time without suffering serious damage or at least with a high survival rate. This range of temperatures within which the fish suffer from thermal stress is called the “zone of resistance”.

Range of tolerance to temperature

Within the “zone of resistance”, there is a “zone of tolerance” within which stress behavior does not occur and survival of the fish is, in theory, certain. In this zone, the fish survive the thermal shock but their physiological functions (feeding, respiration, growth) can be affected. Thermal tolerance therefore only has meaning in the short term (from one to a few days maximum). This zone is most often delimited by the lethal temperatures determined in the 24- to 48-hour range. The data collected over longer periods (7 days) begin to integrate physiological effects other than merely thermal stress.

Lethal temperature: instantaneous mortality

In the zone of resistance, the temperature at which all fish die in less than ten minutes corresponds to the temperature of instantaneous mortality (Cocking, 1959).

Experimental methods for determining these temperatures

Two experimental methods were developed to characterize thermal stress, essentially in the 60s and 70s: the Critical Thermal Method – CTM, and the method based on the temperature causing the first mortalities, Incipient Lethal Temperature – ILT.

These two methods for determining thermal tolerance in fish species do not arrive at the same boundary temperatures because of the different experimental conditions, even though in both cases, they correlate positively with the acclimation temperature.

Acclimation temperature

The acclimation temperature is the temperature to which batches of fish are experimentally exposed for several days (at least a week, according to Fry, 1971) prior to a thermal tolerance test (Armour, 1991). The acclimation temperature is within the zone of tolerance of the fish.

Determination of critical temperatures

CTM is a technique for determining thermal tolerance of fish in the laboratory. It was initially fine-tuned in order to study amphibians, then extended to fish (Cowles and Bogert, 1944).

A sample of fish acclimated to a given temperature is subjected to a linear rise (or drop) in temperature up/down to a predefined sublethal threshold (which is nonetheless close to the lethal temperature). This threshold, which corresponds to the Critical Temperature (CT) maximum or CT minimum value, is the point at which movement of the fish becomes uncoordinated and they are no longer able to flee the conditions which may ultimately result in death (Houston, 1982). According to this methodology, the “lethal temperature” thermal variable is estimated without killing any individuals; the damage observed is reversible and there is no lethal effect. The choice of the sublethal criterion can vary with the author: Beitinger *et al.* (2000), for example, cite the onset of violent muscular spasms (Matthews and Maness, 1979), the loss of balance (Watenpaugh *et al.*, 1985) or opening of the opercula (Middaugh *et al.*, 1975).

The boundary temperatures obtained with this type of experiment are often higher than those found with the ILT method, due to the generally shorter period of exposure to the tested temperatures (Todd *et al.*, 2008).

Determination of lethal temperatures

ILT is the oldest and most common laboratory method for investigating lethal temperature. It was developed by Fry *et al.* (1942) on the basis of studies of the relationship between thermal dose/response (Bliss, 1937).

Batches of fish acclimated to a given temperature are suddenly transferred into water which is warmer or cooler than the temperature of acclimation and left for a variable period of time. The proportion of dead fish is then measured in each batch. The data are then statistically processed to determine the lethal temperature.

The lethal temperature ($LT_{x,y}$) is the temperature which causes the death of a fraction of a batch of fish (x) after a given period of exposure (y). The periods in question generally vary from 100 min to 24 h, and sometimes up to 96 h. For example, 24-hour LT_{50} is the lethal temperature for 50% of the test batch after 24 h. When the rate of mortality is not given, it is assumed to be LT_{50} , which is the variable determined with the least uncertainty in experiments. By analogy, LC_{50} for dioxygen corresponds to the dioxygen concentration which is lethal for half of the individuals tested at a given acclimation temperature.

Practical tests in water warmer or cooler than the acclimation temperature provide respectively higher and lower lethal temperatures.

For a given biological stage (eggs, larvae, juveniles, adults), the lethal temperature depends on the acclimation temperature and the period of exposure to warming or cooling; it rises when the acclimation temperature increases, then reaches a threshold value. This threshold value is generally termed the Ultimate Incipient Lethal Temperature (UILT) while the lethal temperatures in the phase of dependence on acclimation temperature are called the Incipient Lethal Temperature (ILT). We must recall that these thermal variables are LT_{50} values.

Significance of critical and lethal temperatures

Depending on the experimental way in which they are determined, these variables represent a thermal stress which is lethal (lethal temperature) or sublethal (critical temperature). In one case, the thermal stress causes irreversible damage resulting in death; in the other, warming causes uncoordinated movements which cease when the fish is returned to water at the acclimation temperature. In both cases, therefore, it is a question not of physiological effects over the long term due to an oxygen deficit or to degradation of the global energy balance, but rather of rapid reactions to the variation in temperature, leading in the short term to a physiological disorder.

Figure 1a shows three regions:

- the zone of thermal tolerance, compatible with survival of the fish;
- the zone of thermal resistance;
- the zone of instantaneous mortality.

> METHODOLOGY ADOPTED BY THE AUTHORS

We opted to synthesize all data collected on thermal tolerances of the species, proposing two temperature ranges characteristic of each life stage when sufficient data was available (Figure 1b):

- a range of optimum temperatures corresponding to the range in which most data mentioned in the literature under this name fall;
- an expanded range of optimum temperatures corresponding to the extreme minimum and maximum temperatures tolerated, whose limits correspond to those of the range of resistance defined above. This range is limited by CT max values established in the laboratory when they exist. For the embryo stage, it is often the lethal temperature (the boundary temperatures between the optimum and lethal temperature are difficult to measure).

Generally speaking, data from observations described in original paper were preferred over compilations in the literature. Particular attention was also given to consistency in data, to establish the ranges for a given life stage and between different stages for a single species. When the data were sufficiently robust for the other life stages and insufficient for the juveniles

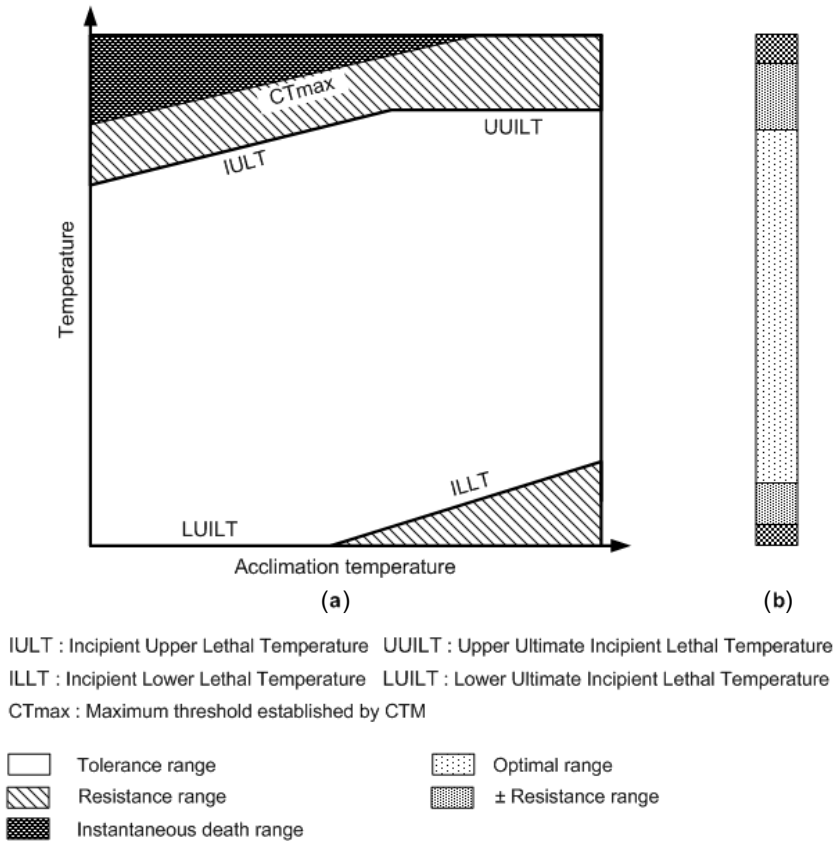


Figure 1
 Different thermal variables (adapted from Beitinger et al., 2000b; Todd et al., 2008). (a) Different temperature variables versus acclimation temperature, (b) synthetic range of temperature tolerance.

or adults of a single species, certain range boundaries were transposed from one stage to another, according to the following rules:

- juvenile range = adult range;
- optimum juvenile range = extended larva range.

> **TEMPERATURE-RELATED PARAMETERS**

Fish species have habitat preferences which differ notably from one life stage to another. Because thermal preferences also differ according to the life stage, the parameters retained vary for each one. Each period in the life cycle of the fish is therefore examined independently. For the adult and juvenile stages, the temperatures optimum for life are inventoried. Boundary temperatures obtained in the laboratory (CTM or ILT experiments) are also generally available for these stages. Lastly, when mortality temperatures for individuals are observed in the field, they are mentioned.

For the embryo and the larva, we added the period in number of degree days for each of the two stages, with the associated water temperature when it was known.

The threshold temperatures for the beginning and end of reproduction are also useful parameters.

For each temperature datum found, some information about the corresponding study is systematically provided when it was given (location of the study, temperature recorded *in situ*

or obtained from laboratory experiments, references to other studies). This information will later make it possible to compare values of a similar nature.

Among the different parameters found, some were given preference due to their ecological significance.

Within the range of optimum temperatures, the fish experiences no stress and lives without constraint. This datum is therefore essential to a good synthesis of thermal tolerances.

Among the experimental data found, the IULT for 24 h was preferred over data obtained with shorter periods of exposure. This is because the boundary temperatures obtained with shorter periods of exposure (for example 100 or 1000 min) have consequences: the final phase of thermal stress described by Elliott (1981) is reached.

> FISH SPECIES

This synthesis bears on 19 fish species: those most commonly found in medium- to large streams (river order 5 or higher) in Western Europe. In-depth bibliographical research was conducted on their thermal tolerances. These 19 species of non-migratory fish are: vairone, sofie, nase, gudgeon, chub, dace, spirlin, barbel, bitterling, roach, bleak, bream, white bream, perch, ruffe, pike-perch, northern pike, pumpkinseed and catfish (Table I with scientific name).

> OVERVIEW OF DATA COLLECTED

Among the 390 references consulted and inventoried giving thermal tolerance data for the target fish species, close to 300 are quoted in this paper. Around one-quarter of those references are compilations of data (works on a general nature on freshwater fish or bibliographical summaries of studies of the temperature factor), and three-quarters are observations. Only 35% of the temperatures found were obtained from laboratory experiments (65% come from field studies).

Table II summarizes the number of data collected (of all types) for the different life stages of the 19 target species in this paper. An optimum temperature range is considered as a single datum when it appears in a single reference.

Generally speaking, the thermal tolerances of the different life stages of a fish are not studied in uniform fashion: the larval and juvenile stages are very little documented in comparison with the others. Data on the embryo stage is extremely heterogeneous depending on the species, while the adult and reproduction stages are the most studied in the life cycle, in terms of temperature. Despite the efforts of researchers, there are four species, each characterized by fewer than ten data, for which information is very limited in terms of thermal tolerance: these are the vairone, sofie, bitterling and white bream (Table II, in gray).

RESULTS

The thermal tolerance data collected for each stage in the life cycle of each species are commented on below and presented in full in Appendix. The species are classified by family in accordance with their theoretical longitudinal zonation in streams (Verneaux, 1981). Optimum temperature ranges and broader ranges whose extreme limits correspond to those of the zone of resistance are proposed for each life stage when the data exist or can reasonably be estimated (see the methodology adopted by the authors in paragraph 1.4).

> CYPRINIDAE FAMILY

Western Vairone (*Telestes souffia*)

The embryo stage of the western vairone is estimated at 7 days at 13.9 °C by Bohl *et al.* (2004). These same authors (Bohl *et al.*, 2004) keep western vairone embryos in an aquarium at between 13.9 °C and 18.5 °C.

Table II

Summary of the number of data for each species life stage (classified according to Verneaux typology, 1981).

Species	Embryo	Larva	Juvenile	Adult	Spawning (+gametogenesis)	TOTAL
Vairone	1	0	2	2	3	8
Sofie	1	1	0	2	5	9
French nase	12	6	1	2	14	35
Gudgeon	3	1	1	11	7	23
Chub	12	8	1	5	5	31
Dace	21	4	1	1	17	44
Spirilin	3	2	0	2	7	14
Barbel	15	3	4	3	9	34
Bitterling	0	0	0	3	4 (+1)	3
Roach	5	2	10	12	15	44
Bleak	1	1	0	4	7	13
Common bream	8	2	1	9	13	33
White bream	2	0	0	2	5	9
Eurasian perch	11	8	6	18	16	59
Ruffe	6	2	3	2	8 (+1)	13
Pike perch	10	4	2	5	13	34
Northern perch	10	3	3	11	14	41
Pumpkinseed	1	2	3	18	4	28
Catfish	4	2	0	9	8	23
TOTAL	126	51	38	121	162	498

In grey: Species for which less than 10 data were found.

The optimum temperature for the juvenile stage appears to lie between 13 °C and 15 °C with an extreme minimum temperature of 10 °C (Bohl *et al.*, 2004).

For the adult stage, the optimum is between 10 °C and 18 °C (Ginot *et al.*, 1996; Fishbase), with extremes of 1.9 °C to 4 °C for the minimum temperature (Bohl *et al.*, 2004) and 27 °C for the maximum (Stankovitch, 1921; Ginot *et al.*, 1996).

Lastly, reproduction occurs between 12 °C (Natura 2000) and 15 °C (Bohl *et al.*, 2004), with an extreme maximum temperature estimated at 19 °C (Bohl *et al.*, 2004). Spillmann (1962 in Schwarz, 1996) mentions a lower maximum between 11 °C and 13 °C.

Sofie (*Chondrostoma toxostoma*)

Spillmann (1961) estimates that the sofie embryo hatches between 12 and 15 days after egg-laying (but specifies no temperature). Gozlan *et al.* (1999) mention breeding sofie in an aquarium at 6 °C with an incubation period of 8 days.

The latter authors (Gozlan *et al.*, 1999) observed larval growth in the natural environment at temperatures ranging between 14 °C and 18 °C.

The range of optimum temperatures for the adult stage falls between 16 °C and 25 °C (Gozlan, 1998).

Bruslé and Quignard (2001) estimate the reproduction optimum between 9 °C and 11 °C while Perche (1948 in the Doubs basin, France, in Spillmann, 1961) and Lelek (1987) mention an onset of reproduction at 13 °C. The Natura 2000 data sheet on the species places reproduction at temperatures between these two values, between 11 °C and 13 °C, on the lower stretch of the Verdon, south-east France. It appears to be accepted by ichthyologists that the temperature preferenda for the sofie are close to those of the French nase, *i.e.* between 8 °C and 14 °C. However, Chappaz *et al.* (1989 in Maier *et al.*, 1995) observed spawning in the Verdon one month later than for the French nase, *i.e.* between the end of May and the beginning of June. Optimum temperatures for reproduction appear therefore to lie between 9 °C and 14 °C for the sofie.

Nase (*Chondrostoma nasus*)

Optimum temperatures for development of the nase embryo lie between 10 °C (Penáz, 1974b in the Czech Republic) and 17 °C (Müller, 1997 in Küttel *et al.*, 2002); four references give optima in this range (Penáz, 1974b; Lusk, 1995 in the Czech Republic; Herzig and Winkler, 1985 in Küttel *et al.*, 2002; Keckeis *et al.*, 2001 in Austria, in Schiemer *et al.*, 2003). The extreme temperatures tolerated are, for the most part, estimated between 8 °C (Prokes and Penáz, 1978; Kamler *et al.*, 1998) and 19 °C (Schiemer *et al.*, 2004) with one lethal temperature put by Kamler *et al.* (1998 in Kamler, 2002) at 20 °C.

Herzig and Winkler (1986) established an equation linking the period of incubation (D in days, 50% of hatches) to temperature (T in °C):

$$D = 1258/(T - 2.62)^{1.994}$$

or, 23.1 days at 10 °C and 5.8 days at 17 °C, the range of validity of the equation.

For the larvae, the optimum temperature lies between 15 °C (Kamler *et al.*, 1998; Penáz, 1974a in Schiemer *et al.*, 2003 on the Danube) and 25 °C (Keckeis *et al.*, 2001; Schiemer *et al.*, 2004). The maximum tolerated is on the order of 28 °C (Penáz, 1974a in Schiemer *et al.*, 2003 on the Danube; Schiemer *et al.*, 2003; Spurny *et al.*, 2004 in Wolnicki and Gorni, 1994), a datum found in two articles (Wolnicki and Gorni, 1994; Schiemer *et al.*, 2003). The larvae also appears to tolerate temperatures up to 10 °C (Schiemer *et al.*, 2004).

In view of fishing results on the Rhône, Ginot *et al.* (1996) establish optimum temperatures for nase juveniles between 7 °C and 27 °C. It seems more realistic to put these temperatures within a more limited range, comparable to that for the embryo, between 15 °C and 25 °C (Kamler *et al.*, 1998; Penáz, 1974b in Schiemer *et al.*, 2003, 2004; Teletchea *et al.*, 2009b).

Bruslé and Quignard (2001) are the only authors to define thermal tolerance thresholds for the adult: they consider that the range of temperatures within which the adult feeds is between 4 °C and 24 °C. We believe, however, that the minimum optimum can reasonably be put higher, on a level with that for the juvenile, around 15 °C.

Most authors place the optimum temperature range for reproduction of the nase between 8 °C and 14 °C (Banarescu, 1964; Prokes and Penáz, 1978; Philippart, 1980; Penáz *et al.*, 1995; Poncin, 1996; Bruslé and Quignard, 2001; Keckeis *et al.*, 2001; Penáz, 1974b in Schiemer *et al.*, 2004; Teletchea *et al.*, 2009b). The extreme temperatures allowing for reproduction are on the order of 6 °C for the minimum (Filipi, 1962 in Albania; Lusk, 1967; Herzig and Winkler, 1985 in Küttel *et al.*, 2002) and 16 °C for the maximum (Alabaster and Lloyd, 1982; Herzig and Winkler, 1985 in Küttel *et al.*, 2002).

Gudgeon (*Gobio gobio*)

The period of embryonic development has been estimated in the laboratory at between 6.3 days at 20 °C (Brunet and Hoestlandt, 1972) and 6.9 days at 18.5 °C, or approximately 125 degree days, which is confirmed by Teletchea *et al.* (2009b). The optimum temperature range lies between 16 °C and 20 °C (Tocko, 1987 in Banarescu *et al.*, 2003b).

Teletchea *et al.* (2009b) estimate the optimum temperature for the larva at 20.5 °C.

Ginot *et al.* (1996) found optimum temperatures for the juvenile stage between 7 °C and 27 °C on the Rhône.

The most information available for the gudgeon bears on the adult stage: its lower optimum temperature has been put at 7 °C (Ginot *et al.*, 1996 on the Rhône) and its upper boundary temperature at 30 °C (Kryzhanovskii, 1949 in Alabaster and Lloyd, 1982; Elliott, 1981 in Küttel *et al.*, 2002). Three other references suggest a more restricted range (Bernet, 1960 on the Nivelle, France in Hynes, 1970; Bruslé and Quignard, 2001; Banarescu *et al.*, 2003a). Horoszewicz (1973 in Alabaster and Lloyd, 1982) found a lethal temperature of 36.7 °C in field experiments in Poland, in a dammed reservoir at 25.5 °C (sublethal threshold reached at 30.8–30.9 °C). Kryzhanovskii (1949 in Alabaster and Lloyd, 1982) gives the same lethal temperature. The authors therefore chose 36 °C as being the upper maximum temperature tolerated by this stage. The extreme lower temperature appears to be around 5 °C (Banarescu, 1964). Four authors conducted laboratory tests to identify the boundary temperatures. The IULT temperatures mentioned fall between 27.2 °C (Alabaster, 1964) and 30 °C (Varley, 1967 in Küttel *et al.*, 2002) depending on the author and the acclimation temperature. Kraiem and Pattee (1980) also recorded a LC50 for dioxygen of 1.8 mg·L⁻¹ at 20 °C (LC over 24 h of 1.9 mg·L⁻¹) and a CT max of 30 °C at 20 °C. This boundary temperature appears low in view of the optima mentioned in other references, and it was therefore not retained as the extreme temperature tolerated.

A few data on the temperatures at the beginning of reproduction are given, particularly in summaries of the literature (Kennedy and Fitzmaurice, 1972; Alabaster and Lloyd, 1982): the minimum optimum stands at 12 °C (Elliott, 1981; Kryzhanovskii, 1949 in Alabaster and Lloyd, 1982; Mann, 1996) and the maximum at around 17 °C (Bourgeois, 1964 in Kennedy and Fitzmaurice, 1972; Mann, 1996). Banarescu (2003b) mentions an extreme maximum temperature for reproduction of 24 °C.

Chub (*Leuciscus cephalus*)

For the chub embryo, Elliott (1981 in Küttel *et al.*, 2002) and Alabaster and Lloyd (1982) find a lower optimum temperature of 16 °C, the higher optimum being 24 °C for Alabaster and Lloyd (1982) in a heated lake. Both authors agree on a maximum tolerated temperature of 30 °C (Alabaster and Lloyd, 1982 find this value *in situ*), which is consistent with the 29 °C found by Mamcarz *et al.* (2005) in the laboratory. The lower lethal temperature in the laboratory is 9.5 °C for Mamcarz *et al.* (2005). Ten data provided by seven authors refer to the period between egg-laying and hatching; they range between 1.5 days at 27.5 °C (Kupren *et al.*, 2008) and 9 days at 12.3 °C (Mamcarz *et al.*, 2005).

The optimum temperature range for the larva lies between 14 °C (Penáz and Sterba, 1969) and 25 °C (Wolnicki and Myszkowski, 1999; Kwiatkowski *et al.*, 2008), according to three references (Shiri Harzevili *et al.*, 2003; Teletchea *et al.*, 2009b; Fishbase). All data used to establish this range come from laboratory experiments. Philippart *et al.* (1989) evaluate the time between egg-laying and hatching of the larval stage at 150 degree days, a value much lower than the 21 days at 25 °C proposed by two authors (Kwiatkowski *et al.*, 2008; Zarski *et al.*, 2008).

The optimum range for the juvenile is considered to be the same as for the larva, which corresponds well to the tolerances found on the Rhône (Ginot *et al.*, 1996). The maximum upper boundary is taken as identical to that for the adult (30 °C).

The optimum range of temperatures for the adult stage is estimated between 14 °C and 24 °C (Ginot *et al.*, 1996 on the Rhône; Cowx and Welcomme, 1998). The extreme minimum temperature is around 8 °C and the extreme maximum, 30 °C (Elliott, 1981; Alabaster and Lloyd, 1982). On the basis of two findings of Horoszewicz (1973 in Alabaster and Lloyd, 1982) in Polish dammed lakes which warmed by 6 °C per hour, the lethal temperature has been established at 37.9 °C (acclimation at 25.7 °C) and 38.8 °C (acclimation at 30.8 °C).

The optimum temperatures for reproduction lie between 15 °C and 20 °C (Kucharczyk *et al.*, 2008 in laboratory).

Dace (*Leuciscus leuciscus*)

There is abundant data available for the embryo stage of the dace (Wurtz-Arlet, 1950; Mills, 1980; Kennedy, 1969 in Wüstemann and Kammerad, 1995; Herzig and Winkler, 1985 in Küttel *et al.*, 2002; Cowx and Welcomme, 1998; Bruslé and Quignard, 2001; Mamcarz *et al.*, 2005; Kupren *et al.*, 2008; Teletchea *et al.*, 2009b). In the laboratory, the dace embryo does not appear able to survive below 4 °C (Herzig and Winkler, 1985 in Küttel *et al.*, 2002; Mamcarz *et al.*, 2005; Mills, 1980), the optimum temperature range being 7–15 °C (Mills, 1991 in Küttel *et al.*, 2002; Mamcarz *et al.*, 2005), with a maximum optimum of 23 °C and a lethal temperature estimated experimentally by Mamcarz *et al.* (2005) at 25 °C. We should nonetheless note that Mills (1980) finds that growth stops at 16.5 °C in the laboratory.

The period of incubation is summed up in Mills' equation (1980), based on laboratory experiments: $D = 96.59 - 9.3T + 0.254T^2$

or, 46 days at 6.75 °C, 32 days at 8.8 °C, 30 days at 10 °C, 12 days at 16.5 °C.

For the larva, the optimum temperature range appears to fall between 16 °C (Lepičová *et al.*, 2002) and 25 °C (Herzig and Winkler, 1985; Kwiatkowski *et al.*, 2008). Teletchea *et al.* (2009b) propose a maximum temperature of 12 °C.

For the juvenile and adult, Wüstemann and Kammerad (1995) give tolerated temperatures between 4 °C and 22 °C, an optimum range between 10 °C and 20 °C and a lethal temperature of 32 °C. This lethal temperature depends on the dissolved oxygen concentration. The same authors (Wüstemann and Kammerad, 1995) measured a dioxygen LC for the adult dace of 3.2 mg·L⁻¹ for 24 h at 20 °C (dace do not survive long with this concentration). The range of optimum temperatures for the juvenile is considered identical to the extended range for the larva (12–25 °C). The maximum optimum for the adult is also set at 25 °C.

For dace, reproduction is preferentially at temperatures between 7 °C (Mann, 1974; Philippart, 1981; Millet, 1989) and 12 °C (Mann, 1996; Kucharczyk *et al.*, 2008); seven references give optimum temperatures between these limits (Kennedy, 1969; Lelek, 1987; Philippart *et al.*, 1989; Bourgeois, 1963 in France, in Wüstemann and Kammerad, 1995; Poncin, 1996 on the Meuse, Belgium; Herzig and Winkler, 1985 in the laboratory, in Küttel *et al.*, 2002; Teletchea *et al.*, 2009b). It apparently remains possible between 5 °C (Alabaster and Lloyd, 1982; Mann, 1996; Kucharczyk *et al.*, 1998) and 16.5 °C (Mills, 1980 in Millet, 1989 in the laboratory).

Spirlin (*Alburnoides bipunctatus*)

The period of incubation for the spirlin is around 100 degree days (Spillmann, 1961; Bless, 1996 who recorded 5.2 days at 19.3 °C; Bohl *et al.*, 2004).

The optimum temperature range for the larval stage is between 19 °C and 24 °C (Alabaster and Lloyd, 1982), 12 °C being the lower value (Bless, 1996).

The optimum for the juvenile (12–24 °C) is taken as the extended optimum temperature range for the larva.

Only extreme temperatures are given for the adult spirlin: they fall between 1.9 °C and 24 °C (Bohl *et al.*, 2004), with a lethal temperature of around 27 °C *in situ* in Switzerland (Breitenstein and Kirchhofer, 1999). The range of optimum temperatures would appear then, as for the larva and juvenile, to lie between 12 °C (minimum optimum adopted for the juvenile on the basis of the extreme minimum for the larva) and 24 °C.

Some references give optimum temperatures for reproduction: they fall between 14 °C (Pelz, 1986 in Breitenstein and Kirchhofer, 1999; Mann, 1996 in Breitenstein and Kirchhofer, 1999) and 21 °C (Bohl *et al.*, 2004), with two references that give optima within this range (Holcik and Hensel, 1971 in Papadopol and Cristofor, 1980; Philippart *et al.*, 1989). The extreme temperatures allowing for reproduction were observed to be between 12 °C (Bless, 1996 in the laboratory; Keith and Allardi, 2001) and 25 °C (Yildirim *et al.*, 1999 in Turkey). The spirlin is a fish with a staggered egg-laying period, which explains the temperature range during which reproduction is possible.

Barbel (*Barbus barbus*)

Thermal tolerances for the barbel embryo are widely documented (thanks in particular to syntheses by Krupka, 1988; Kamler, 2002; Küttel *et al.*, 2002). The optimum temperature according to most authors falls between 16 °C and 21 °C (Kraiem and Pattee, 1980; Penáz, 1973 in Kamler, 2002; Herzig and Winkler, 1985 in Küttel *et al.*, 2002). Only Baras (1995 in Bruslé and Quignard, 2001) notes a lower optimum of 13 °C. Penáz (1973 in Kamler, 2002) found that growth stopped below 12 °C and Elliott (1981 in Küttel *et al.*, 2002), above 20 °C. Krupka (1988) lists six periods between egg-laying and hatching, observed in different studies (Gyurko *et al.*, 1957 in Romania; Penáz, 1973; Krupka, 1988): they range between 3.7 days (Krupka, 1988) and 8 days (Penáz, 1973) at temperatures of 20.2 °C and 16 °C respectively. These values correspond relatively well to those given by Cowx and Welcomme (1998) (11 days at 14 °C and 5–6 days at 19 °C), by Poncin (1996) on the Belgian Meuse (3–4 days at 20 °C) and by Teletchea *et al.* (2009b) in the laboratory (5.6 days at 17.5 °C).

The various authors who have studied the larval stage in the laboratory bred barbel at temperatures between 14.8 °C and 18.9 °C (Vladimirov and Bodareu, 1975 in Banarescu, 2003a; Teletchea *et al.*, 2009b). The extreme temperature tolerated in the laboratory can reach 24.5 °C (Bodareu and Karlov, 1984 in Banarescu, 2003a). Krupka (1988) estimates the duration of the larval stage at 12.6 days at 20.2 °C.

Baras and Philippart (1999) have shown that growth in juvenile barbel ceases below a temperature of 13.5 °C on the Ourthe in Belgium. Ginot *et al.* (1996) sampled active barbel between 7 °C and 27 °C on the Rhône. The range of optimum temperatures therefore appears to fall between 13 °C and 24 °C (24 °C corresponding to the upper boundary for the larva). Kraiem and Pattee (1980) conducted several experiments in the laboratory on barbel juveniles, allowing them to estimate a CT maximum of 31.5 °C (chosen as the upper boundary temperature tolerated by this stage) and an IULT over 24 h of 30 °C for acclimation for 10 days at 20 °C (at this temperature, they found a LC for dioxygen of 2.1 mg·L⁻¹ for 24 h, with an LC50 of 2 mg·L⁻¹) and an IULT over 24 h of 29.7 °C for acclimation at 16 °C.

Optimum temperatures for the adult stage range between 10 °C and 24 °C (Leynaud and Allardi, 1974 on the Seine; Ginot *et al.*, 1996 on the Rhône; Fishbase). The maximum temperature tolerated was set at 32 °C, by analogy with the juvenile (Kraiem and Pattee, 1980).

Barbel reproduces preferentially at temperatures between 13.5 °C (Prignon *et al.*, 1988; Baras and Philippart, 1999; Elliott, 1981 in Küttel *et al.*, 2002) and 20 °C (Mann, 1996; Elliott, 1981 in Küttel *et al.*, 2002), though reproduction can begin at 8 °C (1985 in Küttel *et al.*, 2002) and continue up to 25 °C (Banarescu *et al.*, 2003a) and even 29 °C (Alabaster and Lloyd, 1982).

Bitterling (*Rhodeus sericeus*)

Wohlgemuth (1981) estimates the optimum temperature range for the adult bitterling at between 12 °C and 24.3 °C and Zahn (1963 in Jobling, 1981) extended it up to 30 °C. The lethal temperature in a warmed lake in Poland was put at 37 °C (Horosewicz, 1971 in Jobling, 1981).

In different summaries listed by Duyvené de Wit (1955), the optimum for reproduction in bitterling lies between 15 °C and 21 °C (Holcik, 2003; Natura 2000), with extremes of 12 °C and 26.2 °C (Tarkan *et al.*, 2005; Konečná *et al.*, 2009). Bruslé and Quignard (2001), however, find that the water temperature must be between 13–22 °C for gametogenesis to occur.

Roach (*Rutilus rutilus*)

For the roach embryo stage, Gulidov and Popova (1981 in Gillet, 1989) found a range of optimum temperatures between 12 °C and 24 °C; as for the lethal temperature, Horosewicz (1971 in Nzau Matondo *et al.*, 2007) estimates it at 26 °C in a warmed lake in Poland. Teletchea *et al.* (2009b) give a period between egg-laying and hatching of 7.4 days at 15.5 °C and Cowx and Welcomme (1998) put it at 11 to 12 days at 12.9 °C and 30 days at 7 °C.

The Fishbase website and Teletchea *et al.* (2009b) give an identical optimum temperature for the roach larval stage: 17.5 °C.

Ginot *et al.* (1996) found optimum temperatures for juveniles between 7 °C and 21 °C on the Rhône. Barbier and Pascal (1976) conducted experiments on roach juveniles, at nine acclimation temperatures (from 14.2 °C to 34 °C). They found IULT values over 24 h ranging between 26.9 °C and 34.7 °C, with most falling around 30 °C, which is considered to be the maximum upper boundary tolerated.

For the adult roach, Elliott (1994) finds optimum temperatures over an extremely wide range: 12 °C for the minimum and 25 °C for the maximum. Two authors added to these optimum temperatures with experiments conducted in the laboratory in England. For acclimation temperatures of 15 °C, 20 °C and 25 °C, Alabaster (1964) recorded respective IULT values after 1000 min of 27.3 °C, 29.4 °C and 31.5 °C. Cocking (1959) found upper lethal temperatures between 30.1 °C and 35.2 °C in the course of seven experiments (acclimation varying from 17 °C to 33 °C) and the lowest ILLT, at 7 °C, for acclimation at 23 °C. The upper boundary tolerated is 31 °C according to Cocking (1959) (IULT maximum of 20 °C).

The optimum temperature for roach reproduction lies between 10 °C (L'Abbée-Lund and Vøllestad, 1985 in Gillet, 1989 in Scandinavia; Easton and Dolben, 1980 in Gillet and Quétin, 2006) and 18 °C (Spillmann, 1961; Holcik and Hruska, 1966 in Gillet and Quétin, 2006); this range is confirmed by seven references to optimum temperatures (Easton and Dolben, 1980 in Gillet, 1989; Mills, 1981 in Gillet, 1989; Elliott, 1994; Poncin, 1996; Diamond, 1985 in the UK in Gillet and Quétin, 2006; Teletchea *et al.*, 2009b). The lower boundary temperature given is around 7 °C (Mann, 1996; Noges and Jarvet, 2005 in Estonia) and the upper boundary temperature around 22 °C (Gillet and Quétin, 2006 on Lake Geneva).

Bleak (*Alburnus alburnus*)

Only Alabaster and Lloyd (1982) have studied the embryo stage of the bleak, calculating a minimum CT of 14 °C and a maximum CT of 31 °C (the limits of the extended range of maximum and minimum temperatures tolerated) for a range of optimum temperatures between 21 °C and 27 °C. Spillmann (1961) estimates the period required between egg-laying and hatching of larvae between 14 and 21 days.

According to Fishbase, the optimum temperature for the bleak larva is around 22.5 °C.

For the adult stage, the optimum is unsure: Elliott (1981 in Küttel *et al.*, 2002) gives a value of around 30 °C, whereas it is around 20 °C for Alabaster and Downing (1966 in Coutant, 1975). The lethal temperature was found by Horoszewicz (1973 in Alabaster and Lloyd, 1982) to be 37.7 °C for acclimation at 25.7–26.2 °C in a dammed lake whose temperature rises 6 °C per hour in Poland. The maximum tolerated is therefore probably slightly lower, no doubt around 35 °C.

Several references, both data compilations (Prokes and Penáz, 1978; Keith and Allardi, 2001) and field studies (Berg, 1949; Chappaz *et al.*, 1987 on Lake Sainte Croix, South East France), place the onset of reproduction at 15 °C and all authors agree on a maximum optimum temperature of 28 °C (Alabaster and Lloyd, 1982; Statova, 1973 in Gillet, 1989; Mann, 1996; Keith and Allardi, 2001). The minimum tolerated for reproduction is 14 °C (Alabaster and Lloyd, 1982).

Common bream (*Abramis brama*)

The range of optimum temperatures for the embryo of the common bream lies between 12 °C (Herzig and Winkler, 1986 in Küttel *et al.*, 2002) and 23 °C (Alabaster and Lloyd, 1982). The lower boundary found is around 8–9 °C (Alabaster and Lloyd, 1982; Elliott, 1981 in Küttel *et al.*, 2002) while the lower lethal temperature recorded in the laboratory is 5 °C (Herzig and Winkler, 1986 in Küttel *et al.*, 2002). The upper boundary is set at 28 °C (Elliott, 1981 in Küttel *et al.*, 2002) with a lethal temperature of 32 °C (Herzig and Winkler, 1986 in Küttel *et al.*, 2002). Bruslé and Quignard (2001) estimate the period between egg-laying and hatching at 9 days at

20 °C and 10 days at 18 °C, as against 5.8 days at 20 °C for Keith and Allardi (2001) and 7.5 days at 18 °C for Cowx and Welcomme (1998). At 16.5 °C, Teletchea *et al.* (2009b) estimate it at 6.4 days.

According to Fishbase, the optimum temperature for larvae is 17.5 °C. Teletchea *et al.* (2009b) place it rather at 19.5 °C.

For the juvenile stage, the extended optimum range is between 14 °C and 34 °C (Kucharczyk *et al.*, 1998 in Küttel *et al.*, 2002). We believe that the maximum optimum should be lower, around 28 °C.

The optimum range for the adult falls between 10 °C (Fishbase) and 26 °C (Müller, 1997 in Küttel *et al.*, 2002), with extreme temperatures tolerated between 5 °C (Holker, 2006) and 28 °C (EIFAC, 1969 in Küttel *et al.*, 2002). The upper lethal temperature was observed to be 35.7 °C for acclimation at 25.7 °C in a warmed lake in Poland (Horoszewicz, 1972). Several laboratory experiments also establish boundary temperatures. Alabaster (1964) recorded an IULT of 30.2 °C for 1000 minutes after acclimation at 20 °C. The synthesis drawn up by Küttel *et al.* (2002) lists maximum CT values of 35 °C (Müller, 1997), considered to be the extreme maximum tolerated, and 36 °C (EIFAC, 1969). Finally, Alabaster and Downing (1966) recorded a maximum CT of 30.2 °C for acclimation at 20 °C.

The optimum range for reproduction for the common bream lies between 12 °C (Löffler, 1982; Mann, 1996; Bruslé and Quignard, 2001) and 20 °C (Mann, 1996; Poncin, 1996 on the Meuse; Keith and Allardi, 2001; Herzig and Winkler, 1985 in Küttel *et al.*, 2002). The lower boundary temperature is estimated to be around 8 °C (EIFAC, 1969 in Küttel *et al.*, 2002) and the upper boundary 28 °C (Statova, 1973 in Gillet, 1989).

White bream (*Blicca bjoerkna*)

For the embryo stage of the white bream, the only datum collected comes from Cowx and Welcomme (1998), who estimate the time between egg-laying and hatching of larvae at 4 days at 20 °C (and 5 days at 15 °C).

Observations on the Rhône show evidence of activity of white bream juveniles between 4 °C and 27 °C (Ginot *et al.*, 1996).

Cowx and Welcomme (1998) estimate the optimum range for the adult stage at between 16 °C and 25 °C. Brylinska and Zbikowska (1997) also place the optimum for adults within this range. On the Rhône at Bugey, Ginot *et al.* (1996) found temperatures tolerated between 4 °C and 27 °C.

The optimum for reproduction is between 15 °C (Poncin, 1996 on the Meuse) and 25 °C (Mann, 1996), with two authors placing the optimum temperature for adults in this range (Peczalska, 1979 in Brylinska and Zbikowska, 1997; Brylinska and Zbikowska, 1997). Reproduction is nonetheless possible between 9.6 °C and 29 °C in Russia (Roenko, 1965 in Brylinska and Zbikowska, 1997).

> PERCIDAE FAMILY

Perch (*Perca fluviatilis*)

The perch embryo stage is well documented: the broad range of optimum temperatures found is between 7 °C (Gillet, 1989) and 21 °C (Hokanson and Kleiner, 1974; Wang and Eckmann, 1994 in Küttel *et al.*, 2002) and the more limited range between 12 °C (Alabaster and Lloyd, 1982; Wang and Eckmann, 1994 in Küttel *et al.*, 2002) and 18 °C (Alabaster and Lloyd, 1982; Saat and Veersalu, 1996). Five references give experimentally determined boundary temperatures (Alabaster and Lloyd, 1982; Hokanson, 1977 in Karas, 1996; Swift, 1965 in Küttel *et al.*, 2002; Elliott, 1981 in Küttel *et al.*, 2002; Wang and Eckmann, 1994 in Küttel *et al.*, 2002): the minimum ILLT value is 6 °C (Hokanson, 1977 in Karas, 1996; Elliott, 1981; Wang and Eckmann, 1994 in Küttel *et al.*, 2002) while the maximum is recorded at 26 °C (Alabaster

and Lloyd, 1982). Teletchea *et al.* (2009b) found a period of 13.2 days at 12.5 °C between egg-laying and hatching in the laboratory.

For the larva, the optimum temperature falls between 12 °C (EIFAC, 1969 in Küttel *et al.*, 2002) and 25 °C (Karas, 1996). The lower boundary temperature is estimated at around 5 °C, with another author giving optimum temperatures in this extended range (Karas, 1987 in Urho, 1996). Hokanson (1977 in Karas, 1996) found an IULT of 36 °C and a CT maximum of 34 °C, retained as the upper boundary temperature tolerated. Keith and Allardi (2001) put the duration of the larval stage between 120 and 200 degree days.

The juvenile stage has essentially been studied by means of experiments in the laboratory and only two references propose optimum temperatures: Karas (1990) found that growth ceases below temperatures of 8–10 °C and Hokanson and Kleiner (1974) put the optimum at 25 °C. The synthesis of Hokanson (1977) quotes CT maximum values around 35.5 °C (Weatherley, 1973) and 35.9 °C (Horoszewicz, 1973) as well as IULT values between 31.4 °C (Alabaster and Downing, 1966) and 33.5 °C (Willemsen, 1977) for an acclimation temperature between 25 °C and 30 °C. These IULT values appear more consistent with the optimum range chosen; the 32 °C value is therefore taken instead of 35 °C to represent the upper boundary temperature tolerated by this stage.

For the adult, many authors have inventoried boundary temperatures. The optimum range appears to fall between 16 °C and 27 °C (Horoszewicz, 1973 in Hokanson, 1977; Craig, 1978 in England). There is an extended range of optimum temperatures between 12 °C and 31 °C in North America and in Australia, where the species has been introduced (Thorpe, 1977b). Keith and Allardi (2001) report that growth ceases at around 10 °C. Finally, three authors give lethal temperatures *in situ* that are dependent on the acclimation temperature: Shkorbatov (1964 in Alabaster and Lloyd, 1982) found mortality at 30 °C and 33.5 °C in Russia; Filon (1972 in Alabaster and Lloyd, 1982), however, reports lethal temperatures of 23.2 °C (for acclimation at 0.1 °C) and 36.2 °C (for acclimation at 28.4 °C), also in Russia; these values are consistent with those found by Horoszewicz (1973 in Alabaster and Lloyd, 1982) in Poland. Boundary temperatures established in the laboratory (IULT and CT maximum) have been proposed by seven authors. Willemsen (1977 in Alabaster and Lloyd, 1982) and EIFAC (1969 in Küttel *et al.*, 2002) give CT maxima of 33 °C and 34 °C respectively (taken as the upper boundary temperature tolerated by this life stage). Varley (1967 in Küttel *et al.*, 2002), Colette *et al.* (1977) in Iran, Thorpe (1977b) and Müller (1997 in Küttel *et al.*, 2002), recorded IULT values over an unspecified period of time that range between 30 °C and 33.5 °C. Alabaster (1964) established IULT values of between 24 °C and 31.4 °C for 1000 minutes and for acclimation temperatures between 6 °C and 25 °C.

In his synthesis, Hokanson (1977) proposes a range of optimum temperatures for reproduction between 5 °C and 19 °C depending on the region (EIFAC, 1968; Bastl, 1969; Kovalev, 1973), which is consistent with the broad range found in the literature (Thorpe, 1977a; Alabaster and Lloyd, 1982; Poncin, 1996 on the Meuse; Elliott, 1981 in Küttel *et al.*, 2002). The limited range lies between 8 °C and 15 °C (Lam, 1983; Gillet, 1989; Philippart *et al.*, 1989; Mann, 1996; Gillet and Dubois, 2007 on Lake Geneva; Teletchea *et al.*, 2009b; Fishbase).

Ruffe (*Gymnocephalus cernuus*)

The thermal optimum for the ruffe embryo has been recorded between 9 °C and 21 °C in the laboratory (Saat and Veersalu, 1996) and the maxima tolerated are between 6 °C and 24 °C, also in the laboratory (Saat and Veersalu, 1996). The periods of incubation given by Ogle (1998), Bruslé and Quignard (2001) and Teletchea *et al.* (2009b) are consistent: 10 days at 12.5 °C, 8 days at 14.5 °C and between 5 and 12 days at 10–15 °C respectively. Fairchild and McCormick (1996), on the other hand, found much longer incubation periods for the ruffe: 9, 14 and 26 days at 11 °C, 16 °C and 21 °C respectively.

The optimum range for larvae falls between 25 °C and 30 °C (Kammerer, 1907), and the minimum temperature tolerated is 10 °C (Hokanson, 1977 in Ogle, 1998).

Ruffe juveniles grow between 7 °C and 24.8 °C, with an optimum at 21 °C (Edsall *et al.*, 1993 in Ogle, 1998). Hokanson (1977) reports two boundary temperatures recorded in the laboratory: one IULT for 1000 min of 30.4 °C after acclimation for 11 days at 20 °C (Alabaster and Downing, 1966) and a CT maximum of 34.5 °C after acclimation at 24.1–25.7 °C (Horoszewicz, 1973). The maximum temperature tolerated by the ruffe juvenile is taken as 30 °C, since the CT max was measured at an acclimation temperature at the extreme of the optimum range for this stage.

Alabaster (1964) conducted laboratory tests on adults at 15 °C and 20 °C: he found respective IULTs of 28.1 °C and 30.4 °C for 1000 min. The optimum range retained here is between 15 °C and 25 °C (the maximum optimum temperature retained for the juvenile), with a maximum of 31 °C (Alabaster, 1964).

Reproduction occurs for ruffe between 6 °C and 18 °C (Kolomin, 1977; Ogle, 1998; Keith and Allardi, 2001). The University of Minnesota website states that spermatogenesis occurs between 2 °C and 18 °C (Butskaya, 1985).

Pike-perch (*Sander lucioperca*)

Many articles have reported on the thermal tolerances of the pike-perch embryo (Hokanson, 1977; Gillet, 1989; Lappalainen, 2001; Küttel *et al.*, 2002; Lappalainen *et al.*, 2003). The range of optimum temperatures for this stage falls between 12 °C and 20 °C (Alabaster and Lloyd, 1982; Elliott, 1981 in Küttel *et al.*, 2002; Muntyan, 1967 in Lappalainen *et al.*, 2003; Kokurewicz, 1969 in Lappalainen *et al.*, 2003). There is a more extended range whose lower boundary lies between 3 °C (Hassler, 1982 in Gillet, 1989) and 8 °C (Muntyan, 1967 in Lappalainen, 2001) with the upper boundary at 24 °C (Elliott, 1981 in Küttel *et al.*, 2002). Deelder and Willemsen (1964 in Hokanson, 1977) and Muntyan (1967 in Hokanson, 1977) give ILLT and IULT values between 9 °C and 24 °C, which corresponds to this broad range of tolerated temperatures. Alabaster and Lloyd (1982) also report a CT minimum of 7 °C and a CT max of 25 °C. This CT max was chosen as the upper boundary temperature tolerated by this stage. Gillet (1989) reported a period of 120 degree-days between egg-laying and hatching, consistent with the 8 days at 14.5 °C quoted by Teletchea *et al.* (2009b).

The various authors who have studied the larval stage of the pike-perch propose optimum temperatures between 14 °C and 23 °C (Hokanson, 1977; Teletchea *et al.*, 2009b; Fishbase), and even 26 °C (Zhdanova, 1966 in Hokanson, 1977 in Russia and in Finland). There are also two boundary temperature values established in the laboratory for the larval stage: an IULT of 31 °C and an ILLT of 6 °C (Hokanson, 1977).

Two authors have proposed a thermal profile for the juvenile stage (Horoszewicz, 1973 in Hokanson, 1977; Hokanson, 1977). The optimum temperature falls between 27.3 °C and 30 °C (Hokanson, 1977). The upper boundary temperatures determined in the laboratory are between 34.3 °C (IULT for 1000 min) and 37 °C (CT maximum) for acclimation at 25.6 °C (Horoszewicz, 1973 in Hokanson, 1977). For the sake of consistency, the temperature retained as the upper boundary temperature is 34 °C.

For the adult stage, all available data has been provided by Alabaster and Lloyd (1982). Two field studies of mortality in Eastern Europe report lethal temperatures between 31.5 °C and 37 °C (Poltavchuk, 1965 in Russia; Horoszewicz, 1973 in Poland) for acclimation between 21 °C and 25.6 °C, with maximum tolerated temperatures of 33.3 °C in Poland (Horoszewicz, 1973). Lastly, Willemsen (1977) reports a CT maximum of 35.4 °C in the Netherlands (acclimation at 25 °C), which has been retained as the upper boundary temperature. The range of optimum temperatures is taken as identical to that of the juveniles (optimum between 27 °C and 30 °C).

The temperatures for the beginning and end of reproduction have been reported by seven authors, with boundary values of 3 °C in Eastern Europe and 26 °C in Finland (Zhdanova, 1966; Alabaster and Lloyd, 1982; Raikova-Petrova and Divkov, 1998). All other references place the lower boundary temperature at around 6–8 °C (Fishbase; Hokanson, 1977; Deelder and Willemsen, 1964 in Gillet, 1989; Gillet, 1989; Mann, 1996; Raikova-Petrova and Divkov,

1998 in Bulgaria; EIFAC, 1969 in Küttel *et al.*, 2002; Fontell *et al.*, 2004 in Finland; Teletchea *et al.*, 2009b) and the upper boundary value at 20 °C (Hokanson, 1977; Gillet, 1989; Mann, 1996; EIFAC, 1969 in Küttel *et al.*, 2002; Fontell *et al.*, 2004 in Finland).

> *ESOCIDAE* FAMILY

Northern pike (*Esox lucius*)

The optimum temperature for the northern pike embryo ranges between 8 °C and 14 °C (Willemsen, 1959), with extremes tolerated of 4 °C and 23 °C in the laboratory (Lindroth, 1946; Lillelund, 1966; Ignatieva and Kostomarova, 1966 in Saat and Versaluu, 1996). The minimum lethal temperature is 3 °C (Hassler, 1982), while Steffens (1976) places the maximum lethal temperature at 21 °C in Germany (a value lower than the extended optimum quoted). Hassler (1982) mentions tolerance on the part of northern pike embryos to diurnal temperature variations of 4 °C in the laboratory. The three data found in the literature referring to the duration of the embryo stage (Chimits, 1956; Braum, 1963; Teletchea *et al.*, 2009b) follow the equation established by Lindroth (1946):

$$D = 4 + 1.2619 - T$$

D: day of incubation and *T*: water temperature in °C, within the range of 10–14 °C.

Hokanson *et al.* (1973 in Hokanson, 1977) recorded an IULT of 28.4 °C for larva and estimate the maximum tolerated temperature at 28 °C. The optimum is more likely between 12 °C and 21 °C (Hokanson *et al.*, 1973; Teletchea *et al.*, 2009b).

Casselman (1978 in Jobling, 1981) places the optimum temperature for growth of northern pike juveniles in Canada between 19 °C and 21 °C. Cvancara *et al.* (1977) recorded an LD50 of 30.8 °C and an IULT of 29.4 °C in the Mississippi and Scott (1964 in Hokanson, 1977), an IULT of 33 °C in the laboratory. The LD50 found, equivalent to a CT max, is taken to be the upper boundary temperature tolerated by the northern pike juvenile.

The optimum temperature for the adult stage ranges between 10 °C and 24 °C (Mc Cauley and Casselman, 1981; Keith and Allardi, 2001), according to three references (Hokanson, 1977 in Jobling, 1981; Casselman, 1978 in Canada, in Jobling, 1981; Craig, 1996 in Bruslé and Quignard, 2001). The upper boundary temperature was found to be 26 °C in Ohio, USA (Bevelhimer *et al.*, 1985) and an extended range of 4–27 °C was observed on the Rhône (Ginot *et al.*, 1996). The upper lethal temperature was found in the laboratory to be 34 °C (Scott, 1964 in Jobling, 1981) while Casselman (1978) found a lower lethal temperature of 0.1 °C in Ontario (Canada). Hokanson *et al.* (1973 in Hokanson, 1977) and Casselman (1978) give an IULT of around 29 °C, comparable to the lethal temperature given by Huet (1962) in the natural environment. For the sake of consistency, the authors have retained 31 °C as the upper boundary, the same value as found for the preceding stage.

Lastly, reproduction occurs optimally between 8 °C (Dubé and Gravel, 1978) and 15 °C (Machniak, 1975), with three references to optimum temperatures in this same range (Bryan, 1967 in the USA; Dubé and Gravel, 1978 in Canada; Teletchea *et al.*, 2009b). The extended range is between 6 °C (Machniak, 1975; Dumont *et al.*, 1980 in Canada) and 20 °C (Machniak, 1975), with two authors quoting upper boundary temperatures found in the laboratory between 15 °C and 20 °C (Franklin and Smith, 1963; Hokanson *et al.*, 1973 in Hokanson, 1977). Only two authors mention boundary temperatures below 4 °C (Machniak, 1975; Ovidio and Philippart, 2005 in Belgium).

> *CENTRARCHIDAE* FAMILY

Pumpkinseed (*Lepomis gibbosus*)

The duration of the embryo stage between egg-laying and hatching of the pumpkinseed larva is estimated at 3.1 days at 22.5 °C (Teletchea *et al.*, 2009b).

The optimum for the larva is 20.4 °C according to Fishbase, while Teletchea *et al.* (2009b) place it higher (23.5 °C).

The optimum temperature for juveniles is between 13 °C and 28 °C in Greece (Neophitou and Giapis, 1994 in Küttel *et al.*, 2002). An IULT of 30.2 °C was established by Black (1953 in EPRI, 1981) in Canada. Ferguson (1958 in Coutant, 1977) found a higher optimum temperature in the laboratory (31.5 °C).

In the EPRI summary (1981) of studies conducted in the United States, the adult appears to tolerate temperatures between 11.9 °C (Marcy, 1976) and 35 °C (Trembley, 1960; Neill, 1974). The optimum for growth, according to Brett (1979), is 30 °C and three data given by Coutant (1977) are below 28 °C (Neill, 1974 in Coutant, 1977; Reutter and Herdendorf, 1974 in Coutant, 1977), which argues for an upper boundary for the optimum range around this temperature. Four references (Trembley, 1960; Neill, 1974; Marcy and Jacobson, 1976; Wapora, 1977) listed by EPRI (1981) give higher maximum temperatures, more consistent with those found in the laboratory. CT maximum values have been established experimentally: Beitinger and Bennet (2000) give values between 30.1 °C and 35.1 °C (Becker and Genoway, 1979) depending on the acclimation temperature (10 °C and 20 °C respectively) in the United States. Hagen's synthesis (1973) mentions comparable CT maxima (25.5 °C to 34.5 °C) observed by Jones (1964). Burns (1973) and Reutter and Herdendorf (1976) report a slightly higher CT maximum (37.5 °C). A temperature of 35 °C has been retained by the authors as the upper boundary of the extreme range tolerated by this life stage. CT minima of 1.7 °C to 12.1 °C have also been recorded for acclimation temperatures of 15 °C to 30 °C (Becker *et al.*, 1977 in Beitinger *et al.*, 2000).

Temperatures during the reproduction are less well documented than for the other species studied. The upper boundary is 25 °C in Greece (Neophitou and Giapis, 1994 in Küttel *et al.*, 2002). The lower boundary temperature for reproduction may be around 13 °C. Three authors mention optima between these two boundary temperatures (Bruslé and Quignard, 2001; Williamson *et al.*, 1993 in Küttel *et al.*, 2002; Teletchea *et al.*, 2009b).

> SILURIDAE FAMILY

Wels catfish (*Silurus glanis*)

The period of incubation of the catfish embryo is between 2 and 3 days at 22–25 °C, or some 55 degree days (Lelek and Penáz, 1963; Bruslé and Quignard, 2001; Keith and Allardi, 2001; Teletchea *et al.*, 2009b).

The optimum temperature for the larval stage has been experimentally established at 24.5 °C (Teletchea *et al.*, 2009b). The minimum lethal temperature in the laboratory is estimated at 13 °C (Mihalik, 1982).

The range of optimum temperatures for the adult catfish falls between 12 °C and 28 °C (Berg, 1964; Abdullayev *et al.*, 1978; Hilge, 1985), but it can tolerate a broader range of temperatures, from 3 °C to 30 °C (Schlumberger *et al.*, 2001). Extreme temperatures below 12 °C are confirmed by three authors (Mihalik, 1982; Omarov and Popova, 1985; David, 2006). The only measurements of IULT are found in Vallod's synthesis (1987). These IULTs are between 30.2 °C for acclimation at 10 °C (lethal temperature of 30.5 °C) and 33 °C for acclimation at 20 °C (lethal temperature of 34.4 °C) (Toth *et al.*, 1982 in Vallod, 1987). The authors have chosen the intermediate temperature of 32 °C as the maximum upper boundary for the extended range of temperatures tolerated.

Finally, reproduction occurs optimally between 20 °C (Horvath, 1977; Bruslé and Quignard, 2001) and 25 °C (Woynarovich and Horvath, 1981; Bruslé and Quignard, 2001), and two authors mention optima determined in the laboratory within this temperature range (Horvath and Lucowicz, 1982 in Vallod, 1987; Teletchea *et al.*, 2009b). Lower tolerated temperatures have also been reported of at least 17 °C (Mohr, 1957; Mihalik, 1982 in the laboratory; Lelek, 1987).

Table III

Optimum temperature range and upper limit of the resistance temperature range for each species.

	Embryo			Larva			Juvenile			Adult			Spawning	
	Opt. min	Opt. max	MAX	Opt. min	Opt. max	MAX	Opt. min	Opt. max	MAX	Opt. min	Opt. max	MAX	Opt. min	MAX
Tel							13	15		10	18	27	12	15
Cht				14	18					16	25		9	14
Chn	10	17	20	15	25	28	15	25		15	24		8	14
Gob	16	20					7	27		7	30	36	12	17
Lec	16	24	30	14	25		14	25	30	14	24	30	15	20
Lel	7	15	25	16	25		12	25		10	25	32	7	12
Abb				19	24		12	24		12	24	27	14	21
Bar	16	21		15	19	24	13	24	32	10	24	32	13	20
Bit										12	30	37	15	21
Rut	12	24	26				7	21	30	12	25	31	10	18
Alb	21	27	31							20	30	35	15	28
Abr	12	23	28				14	28	34	10	26	35	12	20
Bli										16	25		15	25
Per	12	18	21	12	25	34	10	25	32	16	27	33	8	15
Gym	9	21	24	25	30		7	25	30	15	25	31	6	18
San	12	20	25	14	23	31	27	30	34	27	30	35	6	20
Eso	8	14	23	12	21	28	19	21	31	10	24	31	8	15
Lep							13	28	30	12	30	35	13	25
Sil										12	28	32	20	25

Italic and bold: data without associated reference (issued from precedent stage or estimated).

Opt. min and max: optimal range limits.

MAX: upper limit of the resistance range.

> SYNTHESIS OF RANGES OF TOLERANCE

The ranges of optimum temperatures together with the upper boundary of the range of resistance chosen for each stage of the species studied are found in Table III. All references on which our choices are based are listed in Appendix.

DISCUSSION

We have summarized the thermal tolerances of the target species on the basis of data with great geographical and temporal differences, obtained under diverse conditions, coming both from field observations and from controlled experiments in the laboratory. We provided a

detailed table listing all references used (Appendix). Above all, we reserve the possibility of reevaluating the interpretation of the values we propose.

Wherever possible, we have given priority to the use of source data. We also collected data from existing compilations (Hokanson, 1977; Alabaster and Lloyd, 1982; Mann, 1996; Küttel *et al.*, 2002; Teletchea *et al.*, 2009b).

In the case of observations in the field, different temperatures tolerated within a single species or by a given life stage may be found. This may be attributable to geographical differences in thermal regime (Kottelat and Freyhof, 2007, for example, say that the ruffe begins to reproduce at 6 °C in northern Europe and only above 10 °C in the south) or by the plasticity of the species. We know that there exists a natural phenotypic variation in thermal tolerance (Schaefer and Ryan, 2006), but the amplitude of variability and the point in ontogenesis at which it occurs are as yet poorly understood (Grünbaum *et al.*, 2007). The zebrafish (*Danio rerio*), for example, a thermophilic fish with a short life cycle, has an intrinsic plasticity with greater tolerance on the part of adults to high temperatures when the juveniles also have been exposed to high temperatures (Schaefer and Ryan, 2006). Another reference for muskellunge (*Esox masquinongy*), however, shows no difference in thermal tolerance among 2-year-old individuals from different populations (Wagner *et al.*, 2007). It is therefore a property difficult to generalize; we can note, however, that the truly reliable temperatures *in situ* are systematically around 1 °C to 4 °C lower than the lethal temperatures (Magnuson *et al.*, 1979; Eaton *et al.*, 1995); for this reason, we advise retaining as the benchmark the thermal tolerance maximum (7th column in the table in Appendix).

In addition to these considerations relating to variations among individuals or populations, further knowledge is needed for a good interpretation of thermal tolerance values:

- fish are extremely sensitive to temperatures in their environment; they can detect very minimal temperature changes on the order of 0.03 °C (Bull, 1936);
- they have a tendency to select thermal habitats which maximize their growth rate (Magnuson *et al.*, 1979);
- the lethal temperature may rise following progressive periods of acclimation, within a limit of 3 °C maximum for salmonids (e.g. Atlantic salmon, Garcia de Leaniz *et al.*, 2007). But we must remember that the periods of acclimation are long, on the order of 20 days for ectotherms (Lutterschmidt and Hutchison, 1998);
- at the highest tolerated temperatures, we must allow for the potential risks of a diminished food supply and heightened sensitivity to toxicity related to xenobiotics (Heugens *et al.*, 2001);
- adult fish subject to significant daily thermal amplitudes within their zone of maximum tolerated temperatures consume additional energy which is drawn from their growth functions or the production of gametes (Schaefer and Ryan, 2006: zebrafish subject to a thermal regime of 28 ± 6 °C);
- in the larval stage, fish are more vulnerable to thermal stress, because they are less capable than adults of regulating membrane fluidity as well as of metabolic acclimation or behavioral thermoregulation (Brett, 1970; Rombough, 1997);
- on a daily scale, we must consider not only the maximum temperature tolerated but also its duration, and the temperature of nocturnal remission and its duration, which must be sufficient for the organism to repair its stress proteins. On a scale of several days, we must not underestimate the influence of cumulative exposure to temperatures close to the maximum tolerated temperatures;
- on a local scale (a few meters to a few hundred meters), there are temperature contrasts in streams and fish are able to seek out thermal refuges in tributaries, secondary channel, or cooler groundwater upwelling (Torgersen *et al.*, 2001). Salmonids use these contrasts very effectively (Torgersen *et al.*, 1999); the behavior of other families is less well documented; a radiotracking study conducted by Cooke *et al.* (2004) on small-mouth black bass (*Micropterus dolomieu*) showed that this species actively avoids the warmest

zones around industrial releases and that once having “experienced” them, they never return.

Temperature (°C)

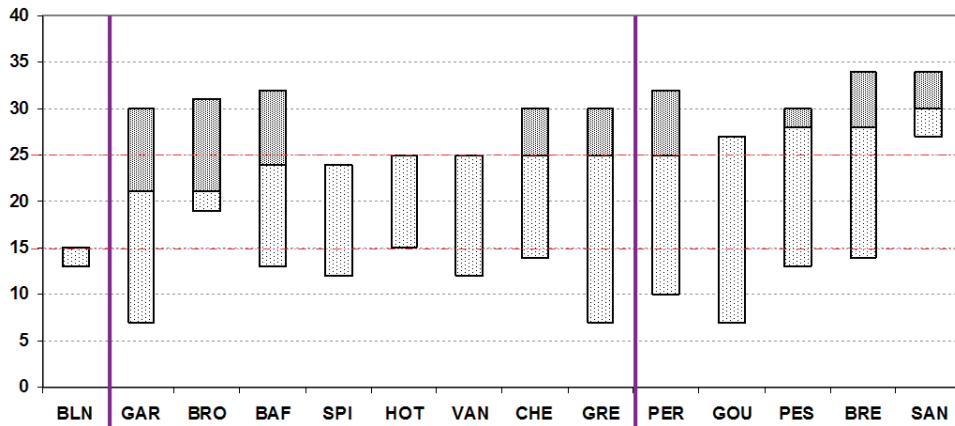


Figure 2

Optimum temperature range (light grey) and resistance temperature (dark grey) range for juvenile of each studied species. N species = 14.

Temperature (°C)

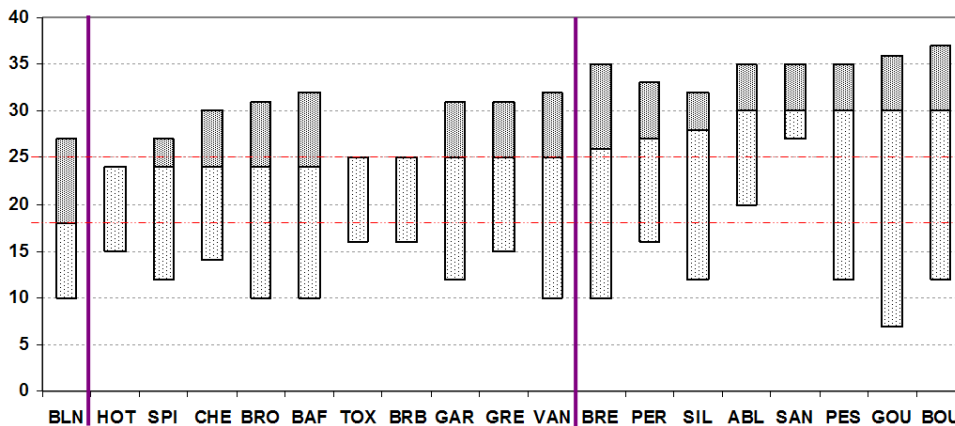


Figure 3

Optimum temperature range (light grey) and of the resistance temperature (dark grey) range for adult of each studied species. N species = 19.

The range of optimum temperatures and the range of resistance we have retained (Table III) are shown in Figure 2 for juveniles and Figure 3 for adults. Generally speaking, the juvenile stage is far less well documented than the adult stage. The data is similarly not exhaustive on the upper boundary of the range of resistance.

These figures allow us to distinguish three groups of species, according to their thermal requirements:

- The vairone shows behavior that is quite distinct from the other species, with growth at a low temperature (a maximum optimum of 15 °C for the juvenile and 18 °C for the adult). It is at the extreme end of the list of stenothermic coldwater fish; this is consistent with the position of these species in Verneaux’s theoretical zonation (1981);
- One group we might call mesothermic includes the French nase, spirin, chub, northern pike, barbel, sofie, white bream, roach, ruffe and dace, which grow at temperate

temperatures: a maximum optimum around 20–25 °C for juveniles and 25 °C for adults; maximum tolerated slightly above 30 °C;

Temperature (°C)

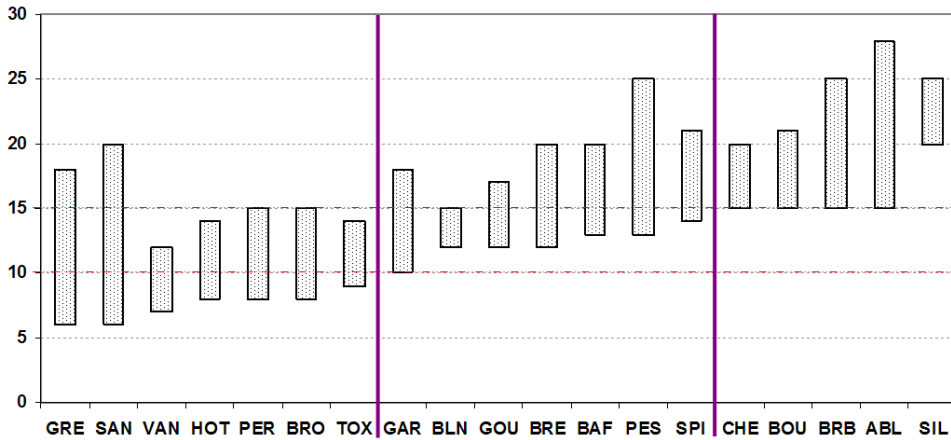


Figure 4

Optimal range of temperature for reproduction of each studied species.

- A third group far more tolerant of warm temperatures, consisting in the common bream, perch, catfish, bleak, pike-perch, pumpkinseed, gudgeon, and bitterling. The optimum temperature for adults can go up to 25–30 °C and the maxima tolerated may reach 37 °C (it is always over 32 °C for adults).

Figure 4 gives the temperature optima for reproduction in these species.

According to the optimum range for reproduction, the 19 species again break down into three groups:

- One group for which reproduction may take place below 10 °C: ruffe, pike-perch, dace, nase, perch, northern pike and sofie;
- An intermediate group that can reproduce between 10 °C and 15 °C: roach, vairone, gudgeon, common bream, barbel, pumpkinseed and spirlin;
- One group that reproduces at temperatures higher than 15 °C: chub, bitterling, white bream, bleak and catfish.

Depending on present and future thermal regimes, particularly in spring, which are reaching temperatures favorable to reproduction earlier and earlier (GIEC, 2007), some species will resist all the better because the amplitude of their thermal tolerance for reproduction is wide. These include the ruffe and pike-perch which have a broad thermal tolerance, unlike the dace, sofie and vairone. In addition, the species which show the greatest amplitude of tolerance for reproduction are often in the most tolerant group in the juvenile and adult stages and frequently, even, have a strategy of multiple spawning. These species will most likely develop better in hot years, as has been observed on the Rhône River at Bugey, France (Daufresne and Boët, 2007).

All typologies are at least partially arbitrary and our own is no exception. We have tried to report on data relating to the 19 species studied, identifying three thresholds for the metrics of maximum thermal optimum for the adult, 18 °C, 25 °C and 30 °C; because we did not include salmonids and other species in the apical zone in streams, it is not surprising to find only the vairone in the first group of coldwater stenothermic fish, for which Raat (1988) places the upper boundary at 19 °C and the optimum at 15 °C, while Hokanson (1977) sets it at 20 °C. We quite clearly distinguish a group of mesothermic fish, within which most rheophilic cyprinids are found, and a group more tolerant to warmer temperatures that includes

essentially more lenitophilic cyprinids. We suggest some nuances in relation to Raat (1988), whose boundary values for these same groups were closer, respectively (19–21 °C, optimum for growth 19 °C, and >21 °C, optimum for growth, 27 °C) or Hokanson (1977) (<28 °C and >28 °C). With respect to certain species, we differ from Daufresne and Boët (2007) in classifying the white bream (mesothermic group in our synthesis, rather than warmwater group), pumpkinseed and perch (warmwater as opposed to coldwater group in this synthesis).

The thermal tolerance groupings we find already provide indicative values which may be valuable in situating the probabilities of modifications in the fish communities within given thermal ranges. It nonetheless remains indispensable to look both at thermal regime (temperature intensity, duration, frequency and seasonality and rate of changes) and the different life stages of the species.

We recommend, on the one hand, giving priority to species-specific data for any analysis of past trends and, on the other, being careful to analyze coupled regimes, *i.e.* biology (different life stages) and temperature. This will be all the more important for any attempt to make trend forecasts corresponding to scenarios of global change, in which it will be necessary to allow not only for seasonal temperature changes but also for a modified hydrological regime (Graham and Harrod, 2009).

CONCLUSION AND PROSPECTS

Temperature is one of the key variables in the dynamics of a hydrosystem: it is subject to local changes downstream of urbanized or industrial sites or rural areas in which wooded riparian corridors capable of acting as a thermal buffer have been significantly reduced. More global changes of a climatic origin have also been recorded in recent decades and may continue into the future according to various scenarios of climate change. Ecologists are therefore naturally forced to investigate the sensitivity of the environment to these changes and the tolerance of aquatic species. With this synthesis, we provide elements of knowledge which until now have been disparate and sometimes, in the case of early literature, difficult to access. In diagnoses or prognoses of sensitivity to thermal changes, it is important that we be able to share information based on a common set of knowledge. This synthesis enables identifying the species capable of withstanding a rise in temperature better than others. Above and beyond these results, it is still important to remember that other factors impact the ability of species to withstand rising temperatures.

This synthesis also points up the knowledge that is lacking for certain life stages or certain species (in particular, the vairone, sofie, bitterling and white bream); this may help direct further investigations in the future, whether of an ecological nature, through field studies coupling temperatures and the presence of fish, or more physiological in the laboratory, on boundary thermal tolerances.

These results could also be extremely valuable to improve our understanding of the present geographical distribution of fish and our ability to interpret changes in the communities over time on sites with sufficiently documented time series data.

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Web sites

Fishbase data:

<http://www.fishbase.org/>

Minnesota University, USA (Ruffe data):

<http://fwcb.cfans.umn.edu/research/ruffe/ginfo/ginfo.htm>

Natura 2000 on the web site of Ministry of Ecology, France:

Vairone/Blageon:

<http://www.ecologie.gouv.fr/IMG/natura2000/habitats/pdf/tome7/1131.pdf>

French Nase/Toxostome: <http://www.ecologie.gouv.fr/IMG/natura2000/habitats/pdf/tome7/1126.pdf>

Bitterling/Bouvière:

<http://www.ecologie.gouv.fr/IMG/natura2000/habitats/pdf/tome7/1134.pdf>

APPENDIX

Table. Data and bibliographic references detailed for the 19 species.

Name	Life stage	Thermal conditions		Thermal tolerance			Experimental temperatures						Lethal T°		Oxygen		Location		Reference	T	In			
		Degree days	Temp.	Min	Opt.	Max	CTmin	ILLT	IULTns	IULT24	IULT1000	IULT100	CTmax	TA	Min	Max	CL24	TA				River	Country	
<i>Leuciscus cephalus</i> Chub	Embryo	110,7	12,3	16	24									30				England		Elliott (1981)	O	Küttel et al. (2002)		
		60	15	12,3	27,5									9,5	29					Alabaster and Lloyd (1982)	C			
		78,5	15,7	12,3																	Mamcarz et al. (2005)	C		
		60	17,5																		Bruslé and Quignard (2001)	C		
		68,4	18																		Kupren et al. (2008)	O		
		76	19																		Teletchea et al. (2008)	O		
		51,7	20																		Cowx and Welcomme (1998)	C		
		73,6	23																		Kupren et al. (2008)	O		
		50	25																		Philippart et al. (1989)	C		
		41,25	27,5																		Kupren et al. (2008)	O		
						17,5																Teletchea et al. (2008)	O	
				14		14																Penaz and Sterba (1969)	O	
				19		19																Shin Harzevili et al. (2003)	O	
						22,5																http://www.fishbase.org	C	
						25																Wolnicki and Myszowski (1999)	O	
		150	25	25																Philippart et al. (1989)	C			
		525	25	25																Kwiatkowski et al. (2008)	C			
	Juvenile			7	24															Zarski et al. (2008)	O			
	Adult			7	24															Gnot et al. (1996)	O			
				8	25															Elliott (1981)	O	Küttel et al. (2002)		
				14	20															Cowx and Welcomme (1998)	C			
														37,9						Horoszewicz (1973)	O	Alabaster and Lloyd (1982)		
														30,8						Horoszewicz (1973)	O	Alabaster and Lloyd (1982)		
	Repro			14	20															Philippart et al. (1989)	C			
				15																Kucharczyk et al. (2008)	O			
				16,5																Poncin (1986)	O			
				18,3																Teletchea et al. (2008)	O			
																				Kryzhanovskii (1949)	C	Alabaster and Lloyd (1982)		

Name	Life stage	Thermal conditions		Thermal tolerance			Experimental temperatures							Lethal T°		Oxygen		Location		Reference	T	In	
		Degree days	Temp.	Min	Opt.	Max	CTmin	ILLT	IULTns	IULT24	IULT1000	IULT100	CTmax	TA	Min	Max	CL24	TA	River				Country
<i>Blicca blicerkna</i> Silver bream	Embryo	75	15																	Cox and Welcomme (1998)	C		
		80	20																		Cox and Welcomme (1998)	C	
	Adult			15		19,6													Wloclawek lake	Poland	Brylinska and Zbikowska (1997)	O	
	Repro			9,6		25													Volga	Russia	Roenko (1965)	O	
				15		29													Meuse	Belgium	Poncin (1996)	O	
				16		25													Firth of Szczecin	Poland	Mann (1996)	C	
				17															Wloclawek lake	Poland	Peczalska (1979)	O	
				18															Wloclawek lake	Poland	Brylinska and Zbikowska (1997)	O	

Name	Life stage	Thermal conditions		Thermal tolerance			Experimental temperatures					Lethal T°		Oxygen		Location		Reference	T	In				
		Degree days	Temp.	Min	Opt.	Max	Ctmin	ILLT	IULTns	IULT24	IULT1000	IULT100	Ctmax	TA	Min	Max	River				Country			
<i>Perca fluviatilis</i> Eurasian Perch	Embryo			5		20												L Hokanson and Kleiner (1974)	O					
				7		16												L Gillet (1989)	O					
				8	13	18												L Saat and versaluu (1996)	O					
	Larva				12		20												L Wang and Eckmann (1994)	O	O Küttel et al. (2002)			
					12		18		6	22									L Elliott (1981)	O	O Küttel et al. (2002)			
					13	21	16		6	16									L Hokanson (1977)	O	O Küttel et al. (2002)			
		165				12		18		6	20									L Swift (1965)	O	O Karas (1996)		
						13		16		8	26									L Alabaster and Lloyd (1982)	O	O Küttel et al. (2002)		
						12,5		19		6	16									L Alabaster and Lloyd (1982)	O	O Karas (1996)		
			160	14			5	11	19												L Elliott (1981)	O	O Küttel et al. (2002)	
							12	13,1	18													L Karas (1987)	O	O Karas (1996)
							25	15,5	25													L Karas (1996)	O	O Küttel et al. (2002)
	Juvenile				25		30												L EIFAC (1969)	O	O Küttel et al. (2002)			
					14		25		36										L Karas (1996)	O	O Küttel et al. (2002)			
					8		30		34										L Karas (1996)	O	O Küttel et al. (2002)			
Adult				10	25	31												L Karas (1990)	O	O Karas (1996)				
				12		27,3												L Alabaster and Downing (1966)	O	O Karas (1996)				
				14		25													L Horoszewicz (1973)	O	O Karas (1996)			
				18		25													L Weatherley (1963)	O	O Karas (1996)			
				20		25													L Willmensen (not published)	O	O Karas (1996)			
						25		33											L Willmensen (not published)	O	O Karas (1996)			
				10		31												L Keith and Allardi (2001)	O	O Karas (1996)				
				12		27,3													L Thorpe (1977b)	O	O Karas (1996)			
				14		25													L Craig (1978)	O	O Karas (1996)			
				18		25													L Horoszewicz (1973)	O	O Karas (1996)			
				20		25													L Müller (1987)	O	O Karas (1996)			
						30													L Horoszewicz (1973)	O	O Karas (1996)			
						30													L Müller (1987)	O	O Karas (1996)			
						30													L Horoszewicz (1973)	O	O Karas (1996)			
						30													L Horoszewicz (1973)	O	O Karas (1996)			
						30													L Horoszewicz (1973)	O	O Karas (1996)			
						30													L Horoszewicz (1973)	O	O Karas (1996)			
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				30														L Horoszewicz (1973)	O	O Karas (1996)				
				30														L Horoszewicz (1973)	O	O Karas (1996)				
				30														L Horoszewicz (1973)	O	O Karas (1996)				
				30														L Horoszewicz (1973)	O	O Karas (1996)				
				30																				

Name	Life stage	Thermal conditions		Thermal tolerance			Experimental temperatures						Lethal T°		Oxygen		Location		Reference	T	In				
		Degree days	Temp.	Min	Opt.	Max	CTmin	ILLT	IULTns	IULT24	IULT1000	IULT100	CTmax	TA	Min	Max	TA	River				Country			
<i>Lepomis gibbosus</i> Pumpkinseed	Embryo	70	22.5																						
	Larva			20.4																					
	Juvenile			23.5																					
				13	31,5	28																			
	Adult			11,9	24,2	40																			
				27,7	28																				
				30	30																				
				30	30																				
					32,8																				
					35																				
				35,6																					
					2																				
					4																				
					9																				
					12																				
	Repro			22,5	20																				
					21																				
					25																				
<i>Silurus glanis</i> Wels	Embryo	55	22																						
		62,5	22,5																						
		50	24																						
		62,5	25																						
	Larva																								
	Adult																								
					7	24,5																			
					8																				
					10																				
					12																				
				14																					
				25	27	28																			
					30																				
					32																				
					33																				
	Repro			17																					
				18																					
				18																					
				20																					
				20																					
				20																					
				22																					
				22,5																					
				23																					