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Relationships between life-history strategies of European freshwater fish species and their habitat preferences

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SUMMARY

1. Focusing on the current environmental characteristics, the 'habitat template' theory proposes that life-history strategies summarise how evolution has shaped species to cope with the temporal and spatial variability of their present environment. The hierarchical 'landscape filters' concept predicts that the distribution of species reflects their specific traits that allow them to pass through multiple habitat filters. Together, these theories showed the importance of identifying the functional relationships of species to selective habitat forces in order to predict the organisation and response of communities to the environment.
2. We test the relationships between life-history traits of European freshwater fish species' and their habitat preferences, to detect the strategies adopted by fish to cope with their current habitat. For this purpose, we use published data on species traits and habitat preferences (microhabitat hydraulics, temperature and oxygen level). We use multivariate analyses to classify fish species' strategies and test the relationships between strategies and habitat preferences.
3. We identified a continuum of life-history patterns between two extremes, with opportunistic and periodic species. Our study supports the idea that microhabitat hydraulics plays a more important role as a template for these species ecological strategies than temperature and oxygen level. Indeed, riffle habitats may select opportunistic species whereas weak relationships are found between species strategies and both their temperature and oxygen level preferences. In addition, the ratio between mortality and growth rate (dimensionless trait), reflecting a trade-off between growth and survival, varied among species according to the use of their hydraulic habitat, with species using deep habitats exhibiting the highest values.
4. These general relationships between hydraulics and traits may be of importance in community ecology to develop predictive models to understand how fish communities change with the hydraulic environment.

Keywords: European freshwater fish, life-history strategies, microhabitat hydraulics, oxygen level preferences, temperature preferences

Introduction

An organism's life-history has been defined as 'a set of coadapted traits designed by natural selection, to solve particular ecological problems' (Stearns, 1992). Through evolutionary time, selection will maximise fitness of organisms through optimum combinations of traits, leading to life-history strategies. Starting from the *r* and *K* selection theory (MacArthur & Wilson, 1967; Pianka, 1970), a large number of models have been developed to understand the adaptive significance of life-history traits from the selective pressures of the environment (Grime, 1977;

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Winemiller & Rose, 1992). The common prediction of these models is that under a particular set of selective forces, specific combinations of traits will be favoured in a given population, within the particular physiological and genotypic constraints of the considered species.

Now focusing on the ecological time and thus on the current environmental and habitat characteristics, the 'habitat template' theory proposes that life-history strategies summarise how evolution has shaped species to cope with the temporal and spatial variability of their present environment (Southwood, 1977, 1988; Poff & Ward, 1990). Townsend & Hildrew (1994) extended this theory to running water systems in which spatial and temporal variability can be especially harsh. Focusing on several spatial and temporal scales, the hierarchical 'landscape filters' concept proposed by Poff (1997) predicts that the distribution and abundance of species reflect their specific traits that allow them to pass through multiple habitat filters. Traits may thus drive species presence or absence in a site, depending of their ability to cope with their current environment. Together, these theories showed the importance of identifying the functional relationships of species to selective habitat forces in order to predict the response and organisation of communities to the environment.

Several studies focusing at the fish community level have identified relationships between community traits and their habitat (Mérigoux, Dolédec & Statzner, 2001; Lamouroux, Poff & Angermeier, 2002; Goldstein & Meador, 2004; Tedesco, 2006). For instance, Lamouroux *et al.* (2002) identified relationships between morphological and behavioural traits of fish communities and their physical environment that are valid in different continents. Communities found in streams with many pools (deep and slow-flowing habitats) had higher proportions of fecund, long-lived and large individuals than communities found in streams with many riffles (shallow and fast-flowing habitats). However, at the species level, the strength and generality of the links between traits and habitat remains little known. In the Rhône basin in France, Persat, Olivier & Pont (1994) found weak links between species traits and the temporal variability of their actual environment. Winemiller (1989) and Winemiller & Rose (1992) proposed three reproductive strategies of species as endpoints of a triangular continuum. They expected their classification to be associated with environmental predictability, but few tests of this expectation exist (Tedesco, 2006). The 'opportunistic' strategy associated small fish with early maturation, continuous reproduction and low fecundity; it is expected in ephemeral habitat conditions. The 'periodic' strategy associated large fish with late maturation, large fecundity and no parental care; it is expected under the periodicity of optimal conditions for growth and survival of immatures. Finally, the 'equilibrium' strategy associated fish with large fecundity and high investment per offspring (i.e. large eggs, parental care); it is expected in stable habitats. Comparable typologies of fish species' traits (Vila-Gispert & Moreno-Amich, 2002) have been related to coarse grain descriptions of the environment used by these species, such as their latitudinal position, their geographical range and the type of habitat (e.g. river, lake, sea) they used (Vila-Gispert, Moreno-Amich & Garcia-Berthou, 2002).

Freshwater fish species' use a large diversity of habitats, with a variety of selective pressures. In particular, hydrology, temperature and oxygen level impose important energetic constraints on individuals and influence the distribution of fish species' in streams. As reviews of species preferences for local hydraulic conditions (Lamouroux *et al.*, 1999), habitat temperature (Philippart & Vranken, 1983; Mann, 1996; Küttel, Peter & Wüest, 2002) and oxygen level (Philippart & Vranken, 1983) are now available, it is possible to specify the strength of the link between species traits and habitat preferences. Concerning microhabitat hydraulics, species that are small, short-lived and have a low reproductive effort may be suited for living in habitats with high velocities and shear stresses (e.g. as often found in riffles) because of the continuous high energetic constraints associated with these habitats (Lamouroux *et al.*, 2002). Species that grow faster, mature earlier, have a longer lifespan and a higher fecundity could be suited to warm habitats that may favour high metabolic rates (Beverton & Holt, 1959). Although most fish avoid hypoxic waters, some are known to survive in low-oxygen level habitats because they have morphological and physiological traits that permit them direct breathing of atmospheric oxygen (Jobling, 1994) or respiration at the aquatic surface and/or may exhibit an increase in anaerobic metabolism (Burton & Health, 1980). Low-oxygen environments may also select species producing small eggs because small embryos of small eggs need low oxygen concentrations to meet their metabolism demand (Krogh, 1959).

In this paper, we test the relationships between life-history traits of European freshwater fish species' and their habitat preferences, in order to detect the strategies adopted by fish to cope with their current habitat. For this purpose, we use published data on species traits and habitat preferences (microhabitat hydraulics, temperature and oxygen level), focusing on reviews in the estimation of traits and habitat preferences. We use multivariate analyses to classify fish species' strategies and test the relationships between strategies and habitat preferences.

Material and methods

Life-history data set

We used the trait database collected by Blanck & Lamouroux (2006) to define average life-history traits of 24 European freshwater fish species' (Table 1). This database summarises a large amount of quantitative data collected in original population studies and synopses throughout Europe, and involves information on a total of 1089 populations. Whenever trait data were reported separately for the sexes, the database reported the estimates for females. Blanck & Lamouroux (2006) checked that defining average trait values for species was relevant despite the variability of traits among populations. Traits involved were:

Table 1 Scientific name, common name and code of the 24 European freshwater fish species' included in our study. We noted the order (O), the family (F) and the infra family (IF) of each species. Species were grouped according to their hydraulic, temperature and oxygen level preferences. See Material and methods for the definition of each taxonomical grouping

Species	Common name	Code	O	F	IF	Hydraulic preference	Temperature preference	Oxygen level preference
Abramis brama (L., 1758)	Common bream	Abbr	1	1	2	4	4	2
Alburnoides bipunctatus (Bloch, 1782)	Spirlin	Albi	1	1	2	1	2	1
Alburnus alburnus (L., 1758)	Bleak	Alal	1	1	3	4	3	2
Barbatula barbatula (L., 1758)	Stone loach	Baba	1	6	1	1	3	2
Barbus barbus (L., 1758)	Barbel	Bubu	1	1	2	1	2	1
Blicca bjoerkna (L., 1758)	Silver bream	Blbj	1	1	2	2	3	2
Carassius carassius (L., 1758)	Crucian carp	Caca	1	1	1	2	4	3
Chondrostoma nasus (L., 1758)	Nase carp	Chna	1	1	3	4	2	1
Cottus gobio (L., 1758)	Bullhead	Cogo	4	4	1	1	1	1
Cyprinus carpio (L., 1758)	Common carp	Cyca	1	1	1	2	4	3
Esox lucius (L., 1758)	Pike	Eslu	5	5	1	2	2	2
Gobio gobio (L., 1758)	Gudgeon	Gogo	1	1	1	1	3	2
Gymnocephalus cernuus (L., 1758)	Ruffe	Gyce	2	2	1	2	3	2
Lepomis gibbosus (L., 1758)	Pumpkinseed	Legi	2	7	1	2	4	2
Leuciscus cephalus (L., 1758)	Chub	Lece	1	1	3	4	3	1
Leuciscus leuciscus (L., 1758)	Dace	Lele	1	1	3	4	2	1
Phoxinus phoxinus (L., 1758)	Minnow	Phph	1	1	1	1	2	1
Rhodeus sericeus (Pallas, 1776)	Bitterling	Rose	1	1	1	3	3	1
Rutilus rutilus (L., 1758)	Roach	Ruru	1	1	3	2	3	2
Salmo trutta (L., 1758)	Brown trout	Satr	3	3	2	1	1	1
Sander lucioperca (L., 1758)	Pikeperch	Salu	2	2	2	2	3	2
Scardinius erythrophthalmus (L., 1758)	Rudd	Scer	1	1	2	3	4	2
Thymallus thymallus (L., 1758)	Grayling	Thth	3	3	1	4	1	1
Tinca tinca (L.,1758)	Tench	Titi	1	1	1	3	4	3

Note: Hydraulic preferences: 1, species preferring fast-flowing and shallow microhabitats within a given reach; 2, species preferring slow-flowing and deep microhabitats; 3, species preferring slow and shallow microhabitats; 4, species preferring deep and fast-flowing microhabitats. Temperature preferences: 1, stenotherm species preferring cold waters; 2, stenotherm species preferring cool waters; 3, eurytherm species preferring cool waters; 4, eurytherm species preferring warm waters. Oxygen level preferences: 1, species requiring a high-oxygen level; 2, species requiring a lower oxygen level and able to live in habitats where the oxygen concentration down periodically into 1.5–3.0 mg L^{-1}; 3, species requiring a low-oxygen level and able to live and to maintain populations in habitats where the oxygen level is continuously <2.0 mg L^{-1}.

1. *Longevity*: Maximum age reported in the population (year). Ages were determined from scale analysis for 21 species and from otoliths for *Barbatula barbatula*, *Cottus gobio* and *Phoxinus phoxinus*.

2. *Maximal length*: Mean total length at maximum age reported in the population (mm).

3. *K*: Growth rate estimated by fitting a Von Bertalanffy model on length-at-age data (year^{-1}). The model used is $L_t = L_\infty\{1 - \exp[-K(t - t_0)]\}$ where L_t is the length (mm) at age t (year). The parameters of the model are L_∞ (asymptotic length estimate, mm), K and t_0 (age at which length is theoretically zero, year). This model was fitted to the back-calculated lengths either using the Ford–Walford method (Ford, 1933; Walford, 1946) or nonlinear least squares fits. K was estimated using females only or individuals of indeterminate sex, and using various ranges of age classes. Because we could not detect a systematic bias on K because of these methodological issues, we involved all K values in our analyses.

4. L_∞: Asymptotic length according to the Von Bertalanffy growth model (mm).

5. α: Age at maturation estimated as the mean age at 50% maturity (year). Gonads of females were examined to assess whether or not they were fully developed. In some studies, this variable was estimated using a sub-sample of the population.

6. L_α: Length at maturation of females estimated as the total length at 50% maturity (mm).

7. *Fecundity*: Mean number of eggs per mature female. Gonads from mature females were preserved and the number of eggs estimated. Fecundity was estimated on all mature females or only on mature females with a specific age. In some studies, this variable was estimated using a sub-sample of the population.

8. *Egg size*: Mean diameter of mature oocytes (mm). In some studies, this variable was estimated using a sub-sample of the population, when gonads of mature females had been collected.

9. Length of breeding season (months).

In the few cases (7/216) where no reliable data were found for a given trait, we completed that cell in the species life-history trait matrix by general information found in Buslé & Quignard (2001). The trait matrix finally obtained is shown in Table 2.

Allometric and dimensionless traits

The choice of traits is a critical issue in studies such as ours, and other traits or combinations of traits could be good candidates for explaining relationships with the environment. For instance, according to the constraints imposed by body size on the evolution of some life-history traits (e.g. longevity, fecundity, Wootton, 1992), the use of allometric traits may help in separating the relative importance of each life-history trait. Similarly, the use of dimensionless traits has been successful for identifying trait combinations that are comparable within biological groups and may account for compromises between traits (Beverton, 1963; Charnov, 1993; Roff, 2001). However, some dimensionless traits seem to differ according to the habitat used by the different species, for instance between marine and freshwater species (Heibo & Vollestad, 2006). It is possible that these optimum compromises between traits vary with the energetic constraints experienced by species in their particular habitats. Thus, we included such combinations of traits (allometric and dimensionless traits) in our analyses to test their relationships with the environment.

We used allometric combinations of traits defined as: trait/(maximal length)$^\beta$ where β is the slope of the linear regression (log scale) between a given trait and maximal length, for traits significantly related to maximal length.

Concerning dimensionless traits, we used three dimensionless combinations of traits (Table 2) described by Beverton & Holt (1959); Charnov (1993); Jensen (1996) and He & Stewart (2001) as life-history 'invariants':

1. The trait $Z{*}\alpha$, where Z is adult mortality, reflects a trade-off between mortality and age at maturation. Because, Z was not available for many species in Blanck & Lamouroux (2006), we used (6/longevity) as an estimator of adult mortality (Beverton, 1963; Charnov, 1993). Beverton (1963) showed that for large samples of fish (more than 5000) longevity is highly correlated with mortality, so that $Z = 6/\text{longevity}$.

2. The trait Z/K expresses that mortality is growth-dependant, suggesting a trade-off between survival and growth. Z was estimated here from longevity as for $Z{*}\alpha$.

Table 2 Mean (SE when multiple populations were reviewed) of life-history traits and estimation of three dimensionless traits for 24 European freshwater fish species' (data from Blanck & Lamouroux, 2006). See Material and methods for the definition of traits.

Species	Longevity (year)	Maximal length (mm)	K (year^{-1})	L_∞ (mm)	α (year)	L_α (mm)	Fecundity (number of eggs)	Egg size (mm)	Length of breeding season (months)	$Z^*\alpha$	Z/K	L_α/L_∞
Abbr	10.8 (0.6)	367 (17)	0.14 (0.01)	667 (28)	5.9 (0.4)	244 (10)	147204 (32657)	1.33 (0.06)	2.33 (0.33)	3.28	3.97	0.37
Albi	5.9 (0.7)	113 (12)	0.33	182	2.3 (0.3)	87	4991 (2766)	0.38	2.00	2.34	3.08	0.48
Alal	6.9 (0.4)	138 (9)	0.18 (0.03)	168 (17)	2.6 (0.4)	80 (9)	25244 (17723)	1.60 (0.00)	3.50 (0.29)	2.26	4.83	0.48
Baba	6.3 (0.6)	137 (8)	0.61 (0.27)	123 (9)	2.6 (0.2)	75	5768 (1242)	0.87 (0.08)	2.22 (0.36)	2.48	1.56	0.61
Bubu	9.8 (0.7)	352 (30)	0.48 (0.17)	720 (86)	3.3 (0.3)	175 (19)	5777 (2140)	2.17 (0.83)	2.17 (0.83)	2.02	1.28	0.24
Blbj	9.7 (1.3)	241 (22)	0.18 (0.09)	296 (62)	5.0 (3.0)	100	40200 (15998)	1.47 (0.53)	2.67 (0.33)	3.09	3.44	0.34
Caca	5.5 (0.4)	226 (48)	0.23 (0.13)	263 (35)	2.0	89	26850 (7850)	1.25	2.75 (0.48)	2.18	4.74	0.34
Chna	9.1 (0.5)	297 (11)	0.13 (0.01)	477 (31)	6.2 (0.7)	340	63607	2.30	2.00 (0.58)	4.09	5.07	0.71
Cogo	6.1 (0.7)	62 (16)	0.45 (0.05)	69 (4)	1.0	46	117 (31)	2.00	3.67 (0.67)	0.98	2.19	0.67
Cyca	10.7 (1.0)	610 (43)	0.23 (0.04)	730 (82)	3.2 (0.3)	366 (66)	365834 (104112)	1.42 (0.16)	3.56 (0.38)	1.79	2.44	0.50
Eslu	10.4 (0.6)	819 (44)	0.22 (0.02)	954 (41)	2.7 (0.2)	379 (24)	49526 (7965)	2.55 (0.08)	1.55 (0.33)	1.56	2.62	0.40
Gogo	4.6 (0.3)	124 (5)	0.24 (0.02)	177 (6)	2.1 (0.3)	96 (23)	6009 (2235)	1.11 (0.28)	2.40 (0.40)	2.74	5.43	0.54
Gyce	5.6 (0.3)	121 (4)	0.34 (0.04)	217 (33)	2.1 (0.3)	68 (29)	34572 (17179)	1.18 (0.06)	2.17 (0.53)	2.25	3.15	0.31
Legi	6.8 (0.2)	130 (8)	0.26 (0.02)	149 (9)	3.0 (0.6)	61	7485	1.02 (0.11)	2.75 (0.25)	2.65	3.39	0.41
Lece	10.8 (0.7)	407 (29)	0.15 (0.02)	494 (28)	4.2 (0.5)	172 (27)	26696 (5562)	1.55 (0.22)	1.88 (0.25)	2.33	3.70	0.35
Lele	8.8 (0.6)	227 (6)	0.27 (0.02)	250 (7)	3.6 (0.5)	170	8325 (1500)	2.05 (0.15)	2.33 (0.42)	2.45	2.53	0.68
Phph	7.0 (1.2)	76 (3)	0.55	91	3.3 (0.6)	51 (2)	1501 (891)	1.36 (0.02)	3.08 (0.37)	2.83	1.56	0.56
Rose	7.0	90 (1)	0.32	96	2.1 (0.5)	51 (7)	207 (39)	1.70	3.33 (0.33)	1.80	2.68	0.53
Ruru	10.5 (0.5)	239 (10)	0.16 (0.01)	347 (15)	3.4 (±0.2)	181 (20)	23909 (1337)	1.13 (0.06)	1.30 (0.21)	1.94	3.57	0.52
Satr	8.2 (0.8)	405 (32)	0.28 (0.02)	600 (21)	3.5 (0.2)	204 (14)	477 (138)	4.28 (0.33)	2.50 (0.74)	2.56	2.61	0.34
Salu	7.2 (1.0)	648 (143)	0.19 (0.03)	824 (61)	3.9 (0.3)	367 (16)	260000	0.95 (0.08)	2.42 (0.66)	3.25	4.39	0.45
Scer	11.8 (0.9)	259 (15)	0.25 (0.06)	251 (38)	3.0 (0.2)	97 (3)	71190 (28433)	1.54 (0.02)	1.83 (0.16)	1.53	2.03	0.39
Thth	5.9 (0.4)	401 (26)	0.27 (0.09)	522 (25)	3.0	300	2432 (739)	2.75	2.83 (0.31)	3.05	3.77	0.57
Titi	7.7 (0.6)	359 (24)	0.35 (±0.13)	421 (58)	3.9 (0.6)	280	194645 (44532)	1.03 (0.06)	2.15 (0.33)	3.04	2.23	0.67

3. The trait L_α/L_∞ expresses the relative length at maturation. This dimensionless trait suggests that there is an inherent relationship between length at maturation and the maximum attainable length.

Before using our estimates of dimensionless traits, we tested whether these traits are indeed invariant between species. For this purpose, we tested the slope of the linear regression between the two traits involved on a log–log scale. If the dimensionless trait is invariant among species, we should obtain a slope not significantly different from one (*t*-tests). We also expected the variance of the dimensionless traits to be small, and analysed this by estimating their coefficient of variation (CV).

Ecological groups based on species habitat preferences

Species were grouped according to their hydraulic, thermal and oxygen level habitat preferences (Table 1). Preferences for many other habitat characteristics (e.g. disturbance regime, productivity, temperature and oxygen temporal variability) could be related to species life-history traits, but were not considered here because quantitative models describing species' preferences for these characteristics are not available yet.

The 'hydraulic' ecological groups were defined according to species preferences for the hydraulic conditions of the microhabitat, according to the classification proposed by Lamouroux & Cattanéo (2006). This classification is based on repeated electrofishing surveys performed in different rivers of southern France (Lamouroux *et al.*, 1999) that demonstrated the possibility of deriving regional preference models for species despite some variations in hydraulic preferences across rivers and sampling dates. Though limited in geographical range (e.g. compared with that of the traits review of Blanck & Lamouroux, 2006), this classification provides a quantitative and comparative study of species habitat preferences conducted in multiple river basins. Lamouroux & Cattanéo (2006) identified four guilds of species according to their local hydraulic preferences observed at the microhabitat scale (Table 1). Guild 1 grouped species preferring fast-flowing and shallow microhabitats within a given reach, i.e. riffle microhabitats. Guild 2 grouped species preferring slow-flowing and deep microhabitats, i.e. pool microhabitats. Guild 3 grouped three species preferring slow and shallow microhabitats, i.e. bank microhabitats. Guild 4 grouped species preferring deep and fast-flowing microhabitats, i.e. midstream microhabitats. Species that were not involved in Lamouroux & Cattanéo (2006), i.e. seven of 24 species, were assigned to the four guilds from knowledge on their hydraulic preferences found in other sources (Mallet *et al.*, 2000; Bruslé & Quignard, 2001).

The 'temperature' ecological groups were defined according to the classifications of species temperature preferences proposed both by Philippart & Vranken (1983) and Küttel *et al.* (2002), which review temperature tolerances for European freshwater fish species'. These classifications are based, for each species, on the estimation of the optimum temperature for fish growth according either to field observations or laboratory studies. By contrast with North American studies (Matthews & Maness, 1979; Smale & Rabeni, 1995; Beitinger, Bennett & McCauley, 2000), no European reviews, in our knowledge, focus on the estimation of temperature tolerance from quantitative laboratory studies for European species. Philippart & Vranken (1983) and Küttel *et al.* (2002) identified four guilds of species according to their temperature preferences (Table 1). Guild 1 grouped stenothermic species preferring cold waters (optimal growth temperature between 7 and 17 °C). Guild 2 grouped stenothermic species preferring cool waters (optimal growth temperature between 14 and 23 °C). Guild 3 grouped eurythermic species preferring cool waters (optimal growth temperature between 14 and 23 °C). Guild 4 grouped eurythermic species preferring warm waters (optimal growth temperature between 20 and 28 °C).

The 'oxygen level' ecological groups were defined according to species oxygen level preferences according to the classification proposed by Philippart & Vranken (1983). This classification is based on a review of the dissolved oxygen level in which species are able to survive. Philippart & Vranken (1983) identified three guilds of species according to their oxygen level preferences (Table 1). Guild 1 grouped species that tolerate a high-oxygen level and are able to live in habitats where the oxygen concentration decreases periodically to 2.5–3.0 mg L^{-1}. We also grouped in this guild *C. gobio* and *Thymallus thymallus* that are able to live in well oxygenated waters only, critical dissolved oxygen concentration being for these species between 5 and 7 mg L^{-1}. Guild 2 grouped species that tolerate a lower oxygen level and are able to live in habitats where the oxygen concentration decreases periodically to 1.5–3.0 mg L^{-1}. Guild 3 grouped species that tolerate a low-oxygen level and are able to live and to maintain populations in habitats where the oxygen level is continuously <2.0 mg L^{-1}.

Data analysis

We $\log_{10}$-transformed all life-history traits, dimensionless and allometric traits in all analyses to approximate normality. The evolutionary history of species may affect species traits and influence the relationships observed between actual habitat features and species traits. Therefore, in order to detect the functional responses of species to their current environment, regardless of their phylogenetic history, we removed taxonomical relatedness of species on traits and combinations of traits in all analyses.

For describing taxonomic links, each species was coded according to its order, family and infra family (Table 1). We used the infra family level instead of the genus level, because all species in our study belong to different genera, except *Leuciscus cephalus* and *Leuciscus leuciscus*. Orders ranged from 1 to 5 with 1 = Cypriniformes, 2 = Perciformes, 3 = Salmoniformes, 4 = Scorpaeniformes and 5 = Esociformes. Family ranged from 1 to 7 with 1 = Cyprinidae, 2 = Percidae, 3 = Salmonidae, 4 = Cottidae, 5 = Esocidae, 6 = Balitoridae and 7 = Centrarchidae. The infra family level was defined according to each family phylogenetic tree obtained from literature sources (Zardoya & Doadrio, 1999; Osinov & Lebedev, 2000; Sloss, Billington & Burr, 2004). Groups were defined as a function of the number of nodes separating each species from the root of the family phylogenetic tree. Species with a higher infra family level have diverged more recently than species with a lower infra family level.

The taxonomic relatedness of species was removed on traits, dimensionless traits and allometric traits (all traits Log_{10}-transformed) through a phylogenetic eigenvector regression (P.V.R.) method (Diniz-Filho, Ramos De Saint Ana & Mauricio Bini, 1998). This method uses a principal coordinate analysis on a species taxonomic similarity matrix. Similarity between species declined as a reciprocal of taxonomic distance. In this matrix, the similarity between a pairs of species of the same infra family is assigned a value of 1.0, the similarity between species of the same family is 0.5, the similarity between species of the same order is 0.33 and the similarity between species from different orders is 0.25. In this analysis, traits are regressed on the eigenvectors of the principal coordinate analysis in such a way that the projected values express phylogenetic trends in traits, and residuals (that will be used in our analyses) reflect species trait patterns independent of taxonomy. Using standardised Moran's I coefficients on the residual vectors of each trait, we checked that this method effectively removed phylogenetic correlation in data, for each trait (Diniz-Filho *et al*., 1998).

We identified life-history strategies of species, using a principal component analysis (PCA) on life-history data from our 24 species. We excluded L_α and L_∞ from this analysis, because these traits are highly correlated with maximal length. We projected allometric and dimensionless traits on this PCA as supplementary variables to evaluate their position on our traits typology.

To investigate redundancy among our ecological groups, we tested correlations between groups, using Fisher's exact tests. We also defined multivariate ecological groups using a multiple correspondence analysis (MCA) of species habitat preferences for our three variables. Then, we tested if the coordinates of species on the axes of the PCA on traits varied among our multivariate ecological groups, using an analysis of variance (ANOVA). In order to compare the importance of the different habitat variables (microhabitat hydraulics, temperature and oxygen level) on the selection of species traits, we tested if the coordinates of species on PCA axes varied among our hydraulic, temperature and oxygen ecological groups, using ANOVA. The variance in trait explained by the different ecological groups was also calculated for each habitat variable to identify the traits (raw, allometric and dimensionless) that vary the most between ecological groups.

Results

Allometric and dimensionless traits

Fecundity, longevity, α and K exhibited significant linear regressions with maximal length ($P < 0.01$ in all cases) [$\log_{10}$ fecundity = 1.93 $\log_{10}$ maximal length + 1.50 ($r^2 = 0.34$); $\log_{10}$ longevity = 0.23

$\log_{10}$ maximal length + 0.58 ($r^2 = 0.35$); $\log_{10} \alpha = 0.32$ $\log_{10}$ maximal length + 0.04 ($r^2 = 0.34$) and $\log_{10} K = -0.30$ $\log_{10}$ maximal length − 0.17 ($r^2 = 0.25$)]. We therefore defined for these traits, size-corrected traits (noted SC trait).

Concerning dimensionless traits, the regression slopes between pairs of traits were significantly different from one for $Z^*\alpha$ (Fig. 1a) and for Z/K (Fig. 1b), suggesting that these traits were not invariant between species. By contrast, the slope was not significantly different from 1 for L_α/L_∞, suggesting that this trait could reflect a scaling relationship among species (Fig. 1c). The CV for each dimensionless trait was relatively high (0.27 for L_α/L_∞, 0.28 for $Z^*\alpha$ and 0.34 for Z/K).

Life-history strategies

The first two axes of the PCA on traits explained 51% and 16% of the total variation, respectively, in the data set. We could identify two groups of species on the factorial map of the PCA along axis 1 (Fig. 2a,b). One group of species was characterised by large individuals with late maturation, high fecundity, high longevity, short length of breeding season and slow growth (*Chondrostoma nasus*, *Abramis brama*, *Blicca bjoerkna*, *Rutilus rutilus*, *Tinca tinca*, *Esox lucius*, *Scardinius erythrophthalamus*, *L. cephalus*, *Salmo trutta*, *Cyprinus carpio* and *Sander lucioperca*). This group corresponded well to the periodic life-history style described by Winemiller (1989) and Winemiller & Rose (1992). A second group was characterised by small individuals with early maturation, low fecundity, increased longevity, long length of breeding season and fast growth (*C. gobio*, *B. barbatula*, *Alburnus alburnus*, *Alburnoides bipunctatus*, *Gobio gobio*, *T. thymallus*, *Carassius carassius*, *Gymnocephalus cernuus*, *Lepomis gibbosus*, *Rhodeus sericeus* and *P. phoxinus*). This group corresponded well to the opportunistic life-history style described by Winemiller (1989) and Winemiller & Rose (1992). *Lepomis gibbosus* and *Barbus barbus* appeared to be intermediate species in the opportunistic–periodic gradient. Winemiller (1989) and Winemiller & Rose (1992) described another group of species called equilibrium species characterised by small or medium size species with a low fecundity, late maturation, prolonged length of breeding season and producing large eggs. Although this strategy does not appear clearly in our traits typology, egg size, SC longevity and SC fecundity were associated with axis 2 (Fig. 2b). Low scores on axis 2 corresponded to species producing large eggs with a low fecundity, long longevity and prolonged length of breeding season (corresponding to equilibrium species) independently of the species opportunistic–periodic gradient. However, no individual species in our study seems clearly associated with the equilibrium strategy.

When projecting SC trait as supplementary variables on the PCA, we noted a weak relationship between these traits and our typology (Fig. 2b,c). Size-corrected fecundity and SC longevity were associated with axis 2 (Fig. 2c) whereas raw traits were mostly positioned along axis 1 (Fig. 2b). When projecting dimensionless traits as supplementary variables on the PCA, we noted also a weak relationship between these combinations of traits and traits typology (Fig. 2b,d). $Z^*\alpha$ and Z/K seemed positioned along

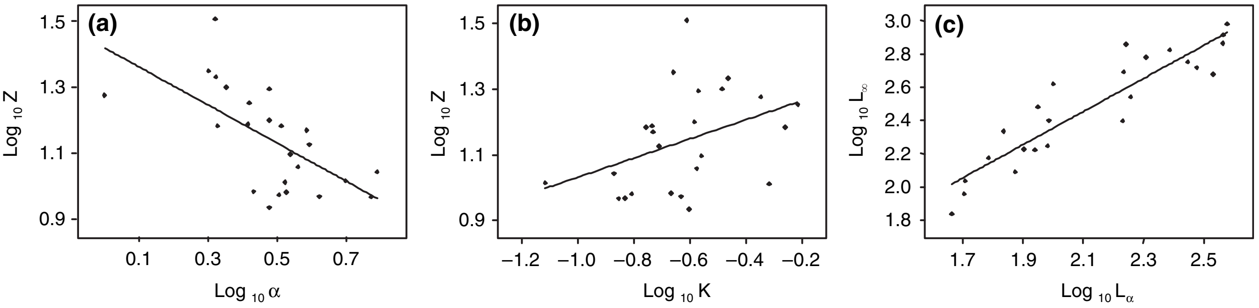

Fig. 1 Relationships between various life-history trait (log $_{10}$-transformed) for the 24 freshwater fish species' of Table 1. (a) Adult mortality (Z) versus age at maturation (α) ($\log_{10} \alpha = -0.70 \log_{10} Z + 1.28$; $r^2 = 0.41$; $P < 0.001$; mean of $Z^*\alpha = 2.43$; CV of $Z^*\alpha = 0.28$). (b) Z versus the Von Bertalanffy growth rate (K) ($\log_{10} K = 0.48 \log_{10} Z - 1.13$; $r^2 = 0.16$; $P = 0.05$; mean of $Z/K = 3.17$; CV of $Z/K = 0.34$). (c) Length at maturation (L_α) versus asymptotic length (L_∞) ($\log_{10} L_\alpha = 0.88 \log_{10} L_\infty - 0.02$; $r^2 = 0.86$; $P < 0.001$; mean of $L_\alpha/L_\infty = 0.49$; CV of $L_\alpha/L_\infty = 0.27$). Only in case C was the slope not significantly different from 1.

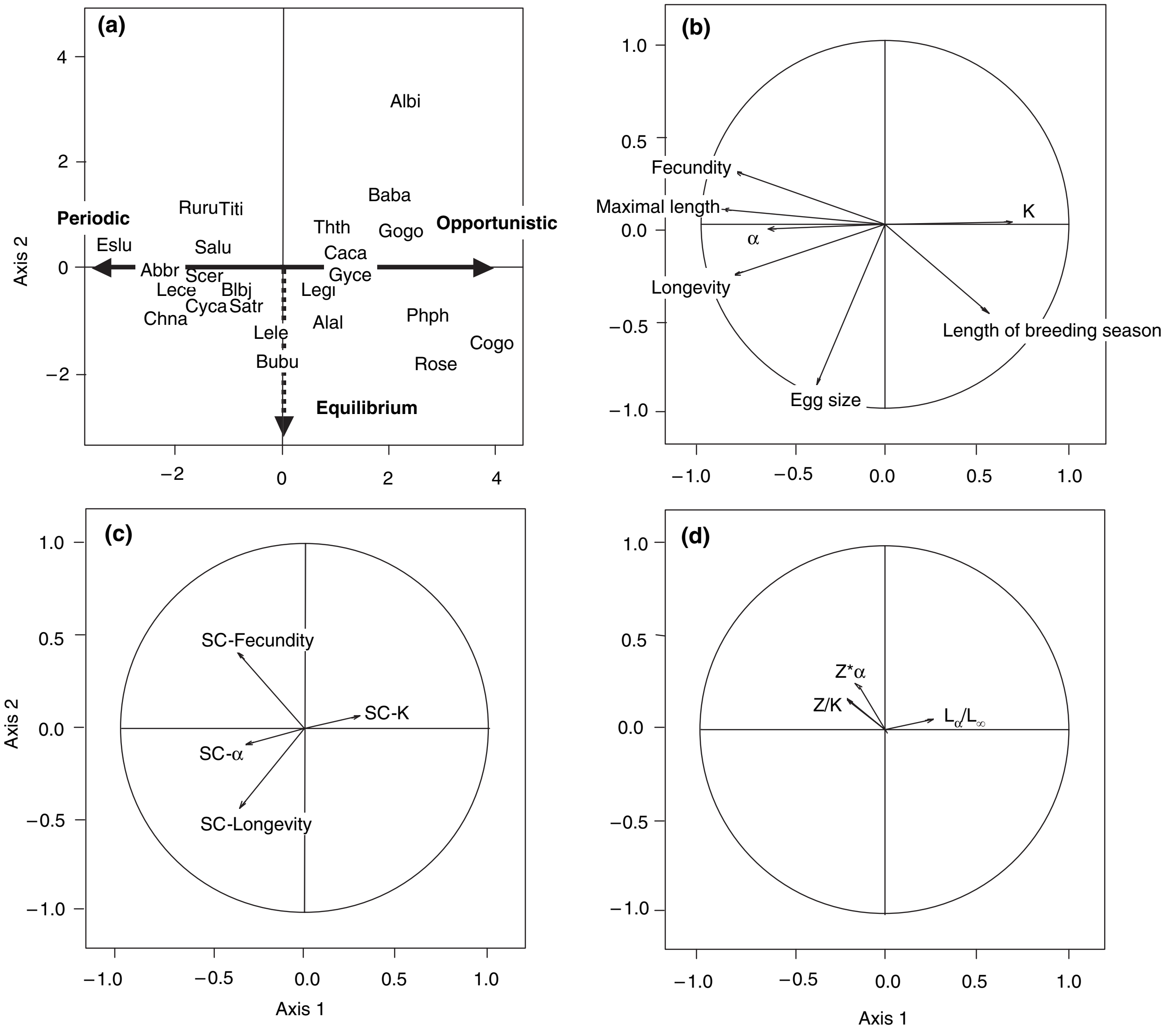

Fig. 2 Principal component analysis results of seven life-history trait of 24 European freshwater fish species': (a) species scores, (b) traits scores, (c) size-corrected trait (SC-trait) added as supplementary variables and (d) dimensionless traits added as supplementary variables. SC traits are defined as: trait/(maximal length)$^{\beta}$ where β is the slope of the linear regression (log scale) between trait and maximal length. Taxonomic relatedness of species was removed both on life-history traits and on combinations of traits (dimensionless and allometric traits), all $\log_{10}$-transformed. See Material and methods for the definition of the traits. Species codes are given in Table 1.

axis 2 (Fig. 2d), whereas raw traits were mostly positioned along axis 1 (Fig. 2b).

Ecological correlates of life-history strategies

Oxygen level ecological groups exhibited significant correlations with both hydraulic (Fisher's exact test, $P = 0.02$) and temperature ecological groups (Fisher's exact test, $P = 0.001$), whereas temperature and hydraulic ecological groups were not correlated (Fisher's exact test, $P = 0.40$). We identified two multivariate ecological groups of species on the first axis of the MCA of habitat preferences (Fig. 3a,b). This axis explained 29% of the variance in habitat preferences. One group of species (those with positive scores on axis 1) prefers fast flowing, oxygenated and cold waters (*C. gobio*, *S. trutta*, *T. thymallus*, *P. phoxinus*, *B. barbus*, *L. leuciscus*, *C. nasus*, *L. cephalus*, *R. sericeus* and *A. bipunctatus*). The other species prefer slow flowing, cool or warm habitats with intermediate

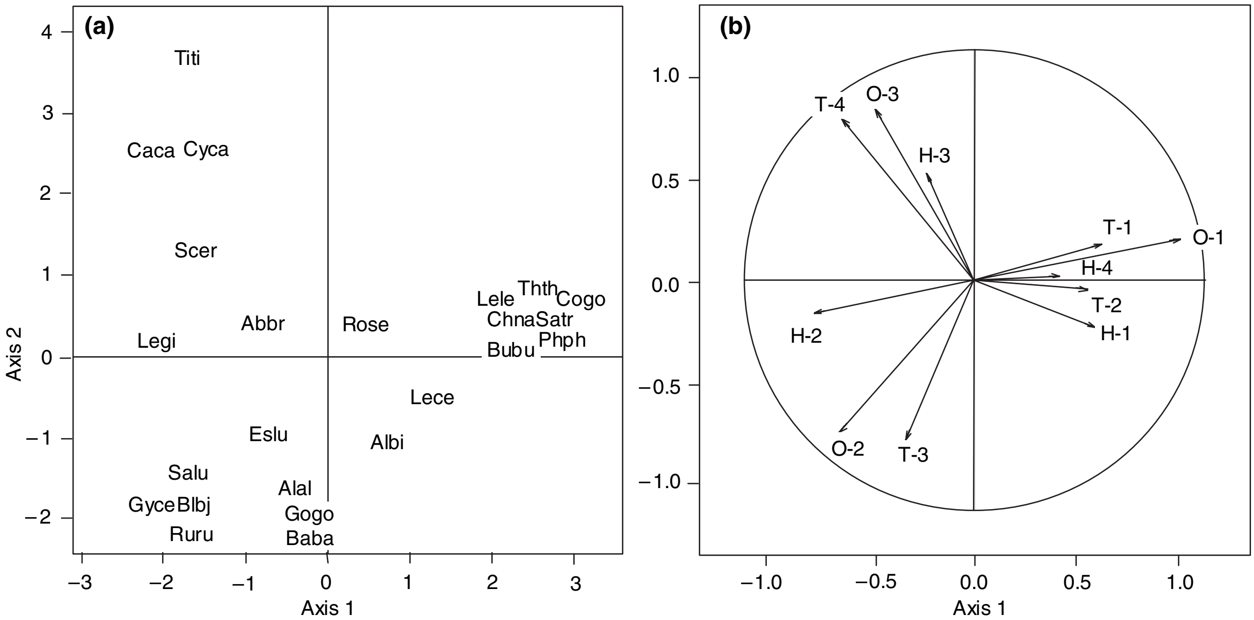

Fig. 3 Multiple correspondence analysis results of 24 European freshwater fish species' habitat preferences for hydraulics (groups H-1 to H-4), temperature (groups T-1 to T-4) and oxygen level (groups O-1 to O-3): (a) species scores and (b) habitat preferences scores. Species and habitat codes are given in Table 1.

or low-oxygen level conditions. Our multivariate ecological groups were not significantly discriminated along axes 1 and 2 ($P = 0.12$ and 0.18, respectively, Fig. 4a) of the factorial map of the PCA on traits. However, species preferring fast flowing, oxygenated and cold waters (group 1 in Fig. 4a) tended to be more associated with the opportunistic and equilibrium endpoints.

Our hydraulic ecological groups were well discriminated along axis 1 ($P = 0.03$, $r^2 = 0.35$): riffle-dwelling species (group 1) were generally associated with the opportunistic strategy whereas species preferring deep microhabitats (groups 2 and 4) were generally associated with the periodic strategy (Fig. 4b). Traits most responsible for this pattern appeared to be longevity, maximal length, growth and fecundity (Table 3). Correspondingly, riffle-dwelling species (group 1) grew approximately twice as fast as species preferring deep habitats (groups 2 and 4) and were 26-fold and 12-fold less fecund than species preferring pools (group 2) and midstream habitats (group 4), respectively (Table 3). Size-corrected trait correlations with hydraulic ecological groups indicated that SC fecundity, SC age at maturation and SC growth remained associated with hydraulic preferences ($r^2 = 0.16$, 0.40 and 0.16, respectively, Table 3), whereas SC longevity did not ($r^2 = 0.03$, Table 3). Dimensionless traits correlations with hydraulic ecological groups reflect that Z/K is associated with hydraulic preferences ($r^2 = 0.30$, Table 3): species preferring shallow microhabitats (groups 1 and 3) exhibited a lower Z/K than the others (Table 3).

Our temperature ecological groups were not significantly discriminated along axes 1 and 2 ($P = 0.47$ 0.94, respectively, Fig. 4c). However, species preferring cold habitats (group 1) were 142-fold less fecund than species preferring warm habitats (group 4) (Table 3). Correspondingly, SC fecundity was the only SC trait showing some correlation with temperature preferences ($r^2 = 0.20$, Table 3). Dimensionless traits were not associated with species temperature preferences ($r^2 \leq 0.11$ in all cases, Table 3).

Our oxygen level ecological groups were not significantly discriminated along axes 1 and 2 ($P = 0.37$ and 0.42, respectively, Fig. 4d). However, species preferring low-oxygen habitats (group 3) were 47-fold more fecund than species preferring high-oxygen habitats (group 1) (Table 3). Correspondingly, SC fecundity was the only SC trait associated with oxygen preferences ($r^2 = 0.38$, Table 3). Dimensionless traits were not associated with species oxygen level preferences ($r^2 \leq 0.04$ in all cases, Table 3).

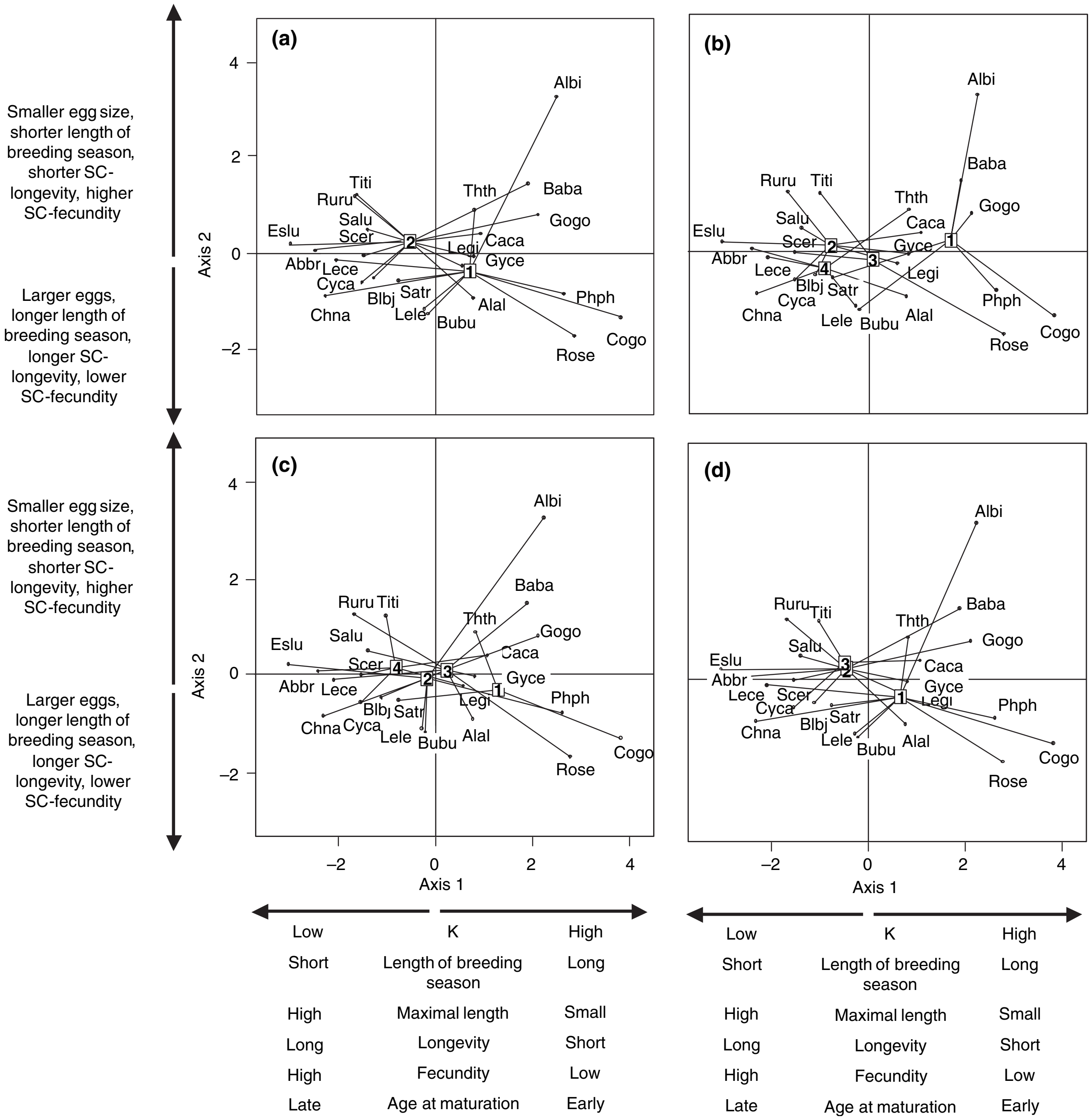

Fig. 4 Position of species groups on the species factorial map of Fig. 2 (physical component analysis on species traits). Groups are defined according to (a) their multivariate habitat preferences analysed in Fig. 3, (b) their hydraulic preferences, (c) their temperature preferences and (d) their oxygen level preferences. See Table 1 for species and group labels.

Discussion

Life-history strategies

We identified a continuum of life-history patterns between two extremes that were similar to the opportunistic and periodic strategies observed by Winemiller (1989), Winemiller & Rose (1992) and Vila-Gispert & Moreno-Amich (2002) for Neotropical, North American and European freshwater fish respectively. Small species with early maturation, increased longevity, low fecundity, fast growth and prolonged length of breeding season corresponded well to the opportunistic strategy (Fig. 2a). Large species with late maturation, long longevity, high

Table 3 Mean life-history, dimensionless and allometric traits (geometric mean) across species for each group of species sharing comparable habitat preference (for hydraulics, temperature and oxygen level). Allometric traits [size-corrected trait (SC trait)] are defined as: trait/(maximal length)$^{\beta}$ where β is the slope of the linear regression (log scale) between trait and maximal length. We noted in parentheses and in italics the proportion of variance of each trait ($\log_{10}$-transformed and taxonomic relatedness of species removed) explained by the habitat (r^2). See Material and methods for the definition of the traits and habitat codes.

Habitat variable	Raw traits							Dimensionless traits			Allometric traits			
Ecological groups	Longevity (year)	Maximal length (mm)	K (year^{-1})	α (year)	Fecundity (number of eggs)	Egg size (mm)	Length of breeding season (months)	$Z^*\alpha$	Z/K	L_α/L_∞	SC fecundity	SC longevity	SC α	SC K
Hydraulics	(0.18)	(0.27)	(0.58)	(0.06)	(0.33)	(0.13)	(0.02)	(0.18)	(0.30)	(0.07)	(0.16)	(0.03)	(0.16)	(0.40)
1	6.65	143.94	0.40	2.40	1883	1.37	2.52	2.11	2.20	0.50	11.87	3.60	1.02	0.89
2	8.01	301.97	0.22	3.03	48665	1.31	2.29	2.30	3.29	0.40	75.72	3.66	1.02	0.61
3	8.60	203.12	0.30	2.92	14201	1.39	2.36	2.03	2.30	0.51	46.51	4.30	1.12	0.75
4	8.53	286.85	0.18	4.04	22441	1.87	2.43	2.84	3.88	0.51	38.15	3.94	1.38	0.50
Temperature	(0.06)	(0.10)	(0.06)	(0.17)	(0.18)	(0.02)	(0.10)	(0.02)	(0.12)	(0.02)	(0.20)	(0.02)	(0.02)	(0.10)
1	6.65	215.96	0.32	2.18	514	2.87	2.96	1.97	2.78	0.60	1.50	3.28	0.82	0.81
2	8.33	234.50	0.48	3.37	10213	1.54	2.14	2.44	2.43	2.43	25.47	4.03	1.23	0.76
3	7.34	194.00	0.24	2.96	15136	1.25	2.34	2.42	3.45	0.45	54.10	3.71	1.14	0.58
4	8.56	293.08	0.23	3.32	72890	1.25	2.51	2.32	2.98	0.43	120.40	3.94	1.13	0.65
Oxygen level	(0.02)	(0.13)	(0.08)	(0.03)	(0.33)	(0.02)	(0.10)	(0.00)	(0.07)	(0.03)	(0.38)	(0.14)	(0.14)	(0.10)
1	7.68	193.93	0.30	2.95	2651	1.79	2.52	2.31	2.65	0.51	9.48	3.88	1.14	0.72
2	7.89	232.45	0.23	3.13	31411	1.28	2.21	2.38	3.30	0.43	79.63	3.83	1.14	0.59
3	7.68	371.55	0.26	2.93	124115	1.22	2.76	2.28	2.95	0.48	132.20	3.35	0.92	0.78

fecundity, slow growth and short length of breeding season corresponded well to the periodic strategy (Fig. 2a). In accordance with Winemiller's results, we also found intermediate species at the boundaries of these two strategies, such as *L. gibbosus* and *B. barbatula*. For the 10 species in common with the study of Vila-Gispert & Moreno-Amich (2002), eight were classified similarly. By contrast with our results, *P. phoxinus* was classified as a periodic species by Vila-Gispert & Moreno-Amich (2002), although it appeared at the limit of the opportunistic strategy. *Salmo trutta* was the only species classified as an equilibrium species in Vila-Gispert & Moreno-Amich's results. Thus, in our study and in the Vila-Gispert & Moreno-Amich (2002) study, no or few species belonged to the equilibrium strategy described by Winemiller (1989) and Winemiller & Rose (1992). This confirms that European freshwater fish present a more restricted range of styles within life-history space than Neotropical and North American fish. This may arise because it may constitute a less diversified group of species (Matthews, 1998). In addition, by removing the taxonomic relatedness of species on all traits in our study, we have reduced the observation of some life-history strategies that are restricted to some phylogenetic clades, such as the range of strategies between the equilibrium and periodic extremes that are restricted to Salmoniforme species in North American fish (Winemiller & Rose, 1992), and such as the classification of *S. trutta* (Salmoniform species) as an equilibrium species (Vila-Gispert & Moreno-Amich, 2002).

Hydraulics: a template for species traits

Among our different ecological groups, hydraulic groups were those most associated with species strategies. In particular, our multivariate ecological groups separating species preferring fast flowing, oxygenated and cold waters (i.e. species generally found in headwaters in European streams) from others were not significantly discriminated along the PCA axes on traits, though headwaters species tended to be intermediate in the opportunistic-equilibrium gradient. It is therefore likely that this non-significant trend is mostly because of the relationships between hydraulics and traits. Traits that contribute to the important relationship found between hydraulic groups and species strategies were longevity, maximal length, growth, fecundity, SC growth and SC fecundity. Part of these results was in agreement with the observations made at the community level (Lamouroux *et al*., 2002) as communities in riffle habitats have higher proportions of small and short-lived fish with low fecundity.

Compared with results observed at the community level (Lamouroux *et al*., 2002), we found that lower longevity in riffles can be partially because of a positive correlation of longevity with body size and that lower fecundity in riffles can be due to an interaction between hydraulic constraints and high-oxygen conditions. Our study reveals the importance of taking into account the growth rate in traits–hydraulics relationships, though this trait shows a high intraspecific variability (Blanck & Lamouroux, 2006), because growth rate appears in our analysis as highly selected in riffles. In addition, we found that several riffle-dwelling species of different families (i.e. *A. alburnus*, *C. gobio*, *B. barbatula*, *G. gobio*, *P. phoxinus*) are clearly associated with the opportunistic strategy, which suggests that many species contribute to community-level response to the habitat template.

Our study and others made at the community level, suggest that hydraulics at the microhabitat scale is a critical filter that selects species with appropriate life-history traits to deal with energetic constraints in riffles. For instance, riffles are identified as potential size refuge for smaller fish against predation (Schlosser & Ebel, 1989). Strong energetic constraints in riffle habitats may also select species characterised by rapid colonisation abilities (indicated by fast growth). In addition, good oxygen conditions in riffles and higher temporal stability of riffles (Leopold, Wolman & Miller, 1964) may select lithophilic species whose low fecundity is compensated by a high survival rate of eggs.

Temperature and oxygen level: weak relationships with species traits

We found no significant association between life-history patterns of species and both temperature and oxygen level ecological groups. The only notable associations observed between individual traits and these ecological groups concerned fecundity; species preferring warm habitats and low-oxygen conditions appear to be more fecund than species preferring cold habitats and requiring high-oxygen level. The relationships observed between fecundity and both temperature and oxygen preferences seem independent of the constraint imposed by body size on fecundity. We expect that fish with a high fecundity may be selected in warm habitats that may favour high metabolic rates (Lobon Cerviá *et al.*, 1996). As discussed above, lower fecundity in high-oxygen conditions can be due to an interaction between good oxygen conditions and hydraulic constraints. By contrast with Krogh (1959) who suggests that low-oxygen conditions may select species producing small eggs, we found no correlation between egg size and oxygen level ecological groups in our study.

Several studies identified temperature and oxygen level as important effects on the distribution of fish in streams at respectively the stream and the microhabitat scale (Matthews, 1998). For instance, temperature variation is an ecological factor that varies with the distance from the source along the longitudinal gradient that explains a part of the spatial variation in fish species' richness (Boët, Allardi & Leroy, 1991). The observation of weak relationships between species traits and both their temperature and oxygen level preferences in our study could be explained by several reasons. First, important traits associated with temperature and oxygen level (i.e. physiological or morphological traits) may be lacking in our analyses. For instance, it is well known that some species have morphological and physiological traits to permit either direct breathing of atmospheric oxygen (Jobling, 1994) or respiration at the aquatic surface, and are thus able to live in low-oxygen conditions. Secondly, oxygen preferences may be more related to the behaviour of species at particular life stages (e.g. spawning habits; Balon, 1975) than to their life-history traits considered here: phytophilic species (e.g. *C. carassius*, *C. carpio*, *T. tinca*) are generally adapted to survive in very low-oxygen concentration environments, whereas lipophilic species (e.g. *C. nasus*, *L. cephalus*, *P. phoxinus*) are adapted to well-oxygenated waters (Balon, 1975). Thirdly, the presence of species in their actual temperature and oxygen level habitat could be explained by other mechanisms than their traits-habitat relationships. For instance, exclusive competition between species associated with the same life-history strategy can explain the use of different ecological niches by these species. The environmental past of species sharing the same life-history strategy may also prevent them from using the same habitat (i.e. no ability to colonise some habitats because of genetic constraints). Finally, temperature varies mostly at a larger spatial scale than the microhabitat (e.g. along longitudinal gradient) and thus, association between temperature preferences and traits may be confounded by association between traits and other environmental variables varying at large scales (e.g. nutriment availability, hydrological variability, stream size) (Santoul *et al.*, 2005).

The use of dimensionless traits in traits–habitat preferences relationships

Of the three dimensionless traits estimated in our study that were described by Beverton (1963); Charnov (1993) and Roff (2001) as constants, two were not 'invariant' between species in our study: $Z^*\alpha$ and Z/K.

$Z^*\alpha$ is assumed to reflect a trade-off between adult mortality and age at maturation. One reason for this trade-off is that, according to classic life-history theory (Gadgil & Bossert, 1970), individuals maturing early should also have high-reproductive output. This leads to an increased cost of reproduction, and thus an increased mortality and a reduced longevity. Our results showed that Z and α do not scale inversely. We found a mean value of $Z^*\alpha$ in our study of 2.43 exceeding the typical range of this trait reported by Charnov (1993) for fish (1.75–2.2). In addition, $Z^*\alpha$ was not linked to habitat preferences. This trait does not appear as an attractive variable for reflecting general patterns relating freshwater fish traits and their habitat preferences.

Z/K is assumed to reflect a trade off between adult survival and growth. Our results showed that Z and K do not scale linearly. We found an average value of Z/K of 3.17 in agreement with parameters values found in freshwater fish (Beverton, 1987; Vollestad, L'Abée-Lund & Saegrov, 1993; Vollestad & L'Abée-Lund, 1994; Heibo & Vollestad, 2006). We also found that Z/K was lower for species preferring shallow microhabitats. Interestingly, in literature Z/K seemed to vary with habitat use. For instance, marine species of teleosts and elasmobranches usually have a ratio between adult mortality and the growth rate between 1 and 2 (Beverton & Holt, 1959; Pauly, 1980), whereas freshwater fish species' have parameter values varying between 2 and 3.55 (Vollestad *et al.*, 1993; Vollestad & L'Abée-Lund, 1994; Heibo & Vollestad, 2006). We could speculate that species living in deep microhabitats exhibit a high-intraspecific competition, which lead to a reduced growth rate and a higher mortality (increasing Z/K). Z/K may thus reveal interesting patterns between species life-history strategies and their habitat preferences.

Finally, L_α/L_∞ expresses the relative length at maturity, indicating that there is an inherent relationship between length at maturity and maximal attainable length. Our results showed that L_α and L_∞ scaled linearly. We found an average value of L_α/L_∞ of 0.49 in agreement with parameters values found in freshwater fish (Beverton & Holt, 1959; Charnov, 1993; Vollestad *et al.*, 1993; Vollestad & L'Abée-Lund, 1994; Heibo & Vollestad, 2006). We noted that L_α/L_∞ was not linked to habitat preferences and thus does not appear useful to reveal relationships between species strategies and their habitat preferences.

Conclusions and implications

Whereas studies focusing on traits–habitat relationships often define axes of the habitat template as a function of habitat heterogeneity (Townsend & Hildrew, 1994), our study is, to our knowledge, the first to test the relationships between life-history patterns of European freshwater fish species' and their local habitat preferences. Although it does not consider species preferences for habitat variability (that are generally little known) but only preferences for some average habitat characteristics, it supports the idea that microhabitat hydraulics plays a more important role as a template for these species ecological strategies than temperature and oxygen level. Indeed, riffle habitats may select opportunistic species, whereas weak relationships are found between species strategies and both temperature and oxygen level ecological groups.

Though limited by its geographical range and the number of species involved, our study reveals general associations between fish species' and their local hydraulic habitat that validate the observations made at the community level concerning the opposition of strategies between communities of fish using riffle and pool habitats (Lamouroux *et al.*, 2002). These general relationships between hydraulics and traits may be of importance in community ecology to develop predictive models to understand how fish community change with the hydraulic environment. Such models may be of importance to quantify for instance the ecological consequences of discharge management (Lamouroux *et al.*, 2006) and to identify priorities for the management of stream networks.

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