

River hydrological seasonality influences life history strategies of tropical riverine fishes

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Received: 12 April 2007 / Accepted: 13 February 2008 / Published online: 27 March 2008
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Abstract Under a particular set of selective forces, specific combinations of traits (strategies) will be favored in a given population, within the particular constraints of the considered species. For fishes, three demographic strategies have been suggested to result from adaptive responses to environmental predictability (i.e., seasonality): periodic, opportunistic and equilibrium [Winemiller KO, Rose KA (1992) Patterns of life-history diversification in North

American fishes: implications for population regulation. *Can J Fish Aquat Sci* 49:2196–2218]. These strategies optimize fitness within predictable, unpredictable and stable systems, respectively. We tested these predictions of life history trait distribution along a gradient of hydrologic seasonality in West African tropical rivers at the drainage basin scale. We used logistic regression of species presence–absence data to test whether dominant life history traits of species caused community compositional change in response to a gradient of seasonality in hydrologic regime across basins. After accounting for taxonomic relatedness, species body size and statistical redundancy inherent to related traits, we found a higher proportion of species producing a great number of small oocytes, reproducing within a short period of time and presenting a low degree of parental care (the periodic strategy) in highly seasonal drainage basins (e.g., rivers with a short and predictable favorable season). Conversely, in more stable drainage basins (e.g., rivers with a wet season of several months), we observed a greater proportion of species producing small numbers of large oocytes, reproducing within a long period of time and providing parental care to their offspring (the equilibrium strategy). Our results suggest that distributions of tropical freshwater fishes at the drainage basin scale can be partly explained by the match between life history strategies and seasonality gradients in hydrological conditions.

Communicated by Roland Brandl.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-008-1021-2) contains supplementary material, which is available to authorized users.

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Keywords Fish communities · Demographic strategies · Hydrological variability · West African rivers

Introduction

An organism's life history has been defined as “a set of co-adapted traits designed by natural selection, to solve

particular ecological problems” (Stearns 1992). Understanding the adaptive significance of life histories relative to other selective pressures linking organisms to each other and to their environments is a key component of our comprehension of evolutionary processes (Partridge and Harvey 1988). Starting with the r- and K-selection theory (MacArthur and Wilson 1967; Pianka 1970), many conceptual models were developed to describe general patterns in life histories and to explain trait divergences between species from an ecological and evolutionary perspective (e.g., Allan 1976; Grime 1977; Ricklefs 1977; Southwood 1977, 1988; Greenslade 1983; Kautsky 1988; Taylor et al. 1990). The common prediction of these models is that under a particular set of selective forces, specific combinations of traits (strategies) will be favored in a given population, constrained by the physiology and genotype of the species under consideration. Nevertheless, because of the great multiplicity of selective pressures and the diversity of organism responses, matching the particularities of every organism–environmental system (within a minimum number of selective pressures) remains a challenge.

Focusing on environmental and habitat characteristics, the “habitat templet” hypothesis (Southwood 1977, 1988) proposes that life history strategies summarize how evolution (i.e., optimization of fitness through evolutionary trade-off of traits to produce optimal life history) has shaped organisms in order to cope with the temporal and spatial variability of their environment (the templet). Townsend and Hildrew (1994) applied this hypothesis to running water systems in which spatial and temporal variability can be especially harsh. Together with the hierarchical “landscape filters” concept proposed by Tonn et al. (1990) and Poff (1997), which predicts that the distribution and abundance of species reflect specific biological traits that allow them to pass through multiple habitat filters, this constitutes a broad framework in which the distribution of species at different spatial scales can be predicted by their functional responses to selective habitat forces.

Habitat variability and predictability, defined in terms of resource level and availability for breeding and survival, are major selective forces that make up the templet (Grime 1977; Southwood 1977; Greenslade 1983). Early theoretical and empirical studies (Cody 1966; Boyce 1979; Baltz 1984; Koenig 1984) suggested that predictable environmental variation (e.g., seasonality in resource availability) should affect the evolution of life histories towards an optimization of fecundity. Based on mechanistic life history trade-offs between reproduction, growth and survival (Roff 1984), and on observed patterns of life history variation in fish, Winemiller (1989) and Winemiller and Rose (1992) proposed three reproductive strategies as endpoints of a triangular continuum resulting from adaptive

responses to environmental predictability and variability. These authors suggest that if optimal conditions for growth and survival of immature individuals are periodic, selection will favor (1) a synchronous reproduction strategy with the periodicity of these optimal conditions, and (2) a production of large numbers of small offspring requiring little or no parental care. They named it the “periodic” strategy. In turn, a suite of attributes associating low batch fecundity, high investment per offspring (e.g., parental care and large eggs) and aseasonal reproduction correspond to the “equilibrium” strategy, and is expected to be optimal in stable habitats. Finally, the “opportunistic” strategy, characterized by rapid colonization ability, associating small fish with early maturation, continuous reproduction and low fecundity, should be related to ephemeral habitat conditions.

As previously mentioned, the periodic strategy maximizes fitness when the environmental variation influencing survival during early life stages is periodic and predictable. Theoretical models (Boyce 1979; Winemiller and Rose 1993) have interpreted the egg size and egg number trade-off (Duarte and Alcaraz 1989; Elgar 1990; Fleming and Gross 1990) in terms of variability in resource availability. Periodic floodplain inundation is thought to enhance fish recruitment by providing suitable feeding and spawning environments for larvae (Welcomme 1979; Junk et al. 1989; Humphries et al. 1999; Winemiller 2005). Then, to ensure the persistence of populations in this habitat, the reproductive efforts of species must match suitable conditions of resource availability. For example, Winemiller and Rose (1993) have suggested that a fixed amount of reproductive effort should be partitioned into many small offspring in resource-rich habitats (i.e., periodic species breeding in floodplains under high water levels) or into a few large offspring in resource-poor habitats (i.e., equilibrium species able to breed despite high levels of competition for food).

Within the tropics, a great range of seasonality is encountered in riverine systems (Lowe-McConnell 1987). These systems range from well-marked seasonally flooding regimes (e.g., tropical savanna regions) to regions where rain falls throughout the year (e.g., equatorial regions). However, the predictions relating reproductive strategies of fish to the temporal stability of their habitats are only supported by general observations, and have never been tested. Earlier field studies on tropical freshwater fish have found some evidence of particular combinations of reproductive traits (i.e., reproductive strategies). In her earliest study in British Guiana, Lowe-McConnell (1964) assigned large characid species (a family mainly associated with the periodic strategy; Winemiller 1989; Mériçoux et al. 2001) to what she called the “total-spawners in which all the eggs ripen and are shed at once” and have a “breeding season

very closely tied up to the hydrological cycle". She also associated cichlid species (a family associated with the equilibrium strategy; Winemiller 1989; Mériçoux et al. 2001) with a "partial-spawner" strategy related to some form of parental care, producing batches of fewer eggs at frequent intervals and being less affected by the hydrological cycle. Supporting the link between hydrology and life-history strategies, Ponton and Copp (1997) observed a major decrease in the abundance of characiforms (mainly periodic species) and an increase in perciforms (mainly equilibrium species) after a drastic change in the hydrological regime in the Sinnamary River (French Guiana) following dam construction which divided the river and radically decreased the downstream hydrological seasonality (see also Ponton and Vauchel 1998; Mériçoux and Ponton 1999). A comparison between the pre-dam and post-dam periods also showed changes in species abundance in terms of reproductive traits (Mérona et al. 2005). Furthermore, based on time series analyses from Côte d'Ivoire rivers (West Africa) over more than 20 years, Tedesco and Hugueny (2006) observed that climatic forcing (i.e., hydrological variability) induced a higher spatial synchrony in population fluctuations of periodic species compared to equilibrium ones. Although indirectly, all of these results closely link the reproductive strategies to current hydrological conditions.

Here we explicitly test Winemiller's predictions of life history traits on a seasonality gradient at an inter-drainage basin scale in West African tropical rivers by focusing on the periodic equilibrium dichotomy. We hypothesized that the distributions of freshwater fishes in this region are related to the match between their reproductive traits (e.g., fecundity, egg size, span of the reproductive period) and hydrologic seasonality (i.e., length of the annual flood period). Specifically, we expect greater proportions of periodic species in drainages marked by highly seasonal floods (short seasonal flood pulses followed by harsh conditions), and greater proportions of equilibrium species under more stable conditions (long annual periods of flooded conditions). Opportunistic species were not specifically considered because trait data for these species are currently almost nonexistent, and because no clear predictions can be drawn concerning the effect of seasonality on these species.

Material and methods

Species distributions

Species occurrence data were drawn from Paugy et al. (1994), who provide a current list of 462 freshwater fish species occurring among 39 West African drainage basins

(Table 1). Only riverine fish species were considered (secondary or migratory euryhaline fish were omitted). Drainage basins are defined here as watersheds including the main river and all its tributaries up to the ocean (Vörösmarty et al. 2000). However, because the Niger drainage basin spreads over several hydroclimatic zones, we only considered in this case the Bénoué River (the main eastern tributary of the Niger), which has a more precise seasonality pattern and for which a species list is available (McGregor Reid and Sydenham 1979). As a result, 438 species and 39 drainage basins (see "Electronic supplementary material," S1) ranging from north Senegal to east Nigeria were considered in this study (Fig. 1).

Seasonality indices

Because of the wide range of climates existing across Africa and the associated variability in the seasonal distribution of precipitations, hydrologic regimes of rivers in this continent vary widely. For West African rivers, a gradient of discharge seasonality is observed between Sahelian, tropical and equatorial regions (Lévêque and Paugy 1999) that differ mainly in the duration of their wet seasons. For example, the Senegal River exhibits a highly seasonal hydrologic regime characterized by a concentration of annual discharge in August–October, while the Pra River has a less seasonal regime with discharge more evenly distributed from May–December (Fig. 1). Monthly hydrological data were drawn from annual series of water discharge available from the IRD (Institut de Recherche pour le Développement) and the GRDC (Global Runoff Data Center). A total of 173 hydrologic stations (Fig. 1) proportionally distributed over drainage basins (Pearson's correlation between number of stations and drainage area, $r = 0.62$, $P < 0.05$, $n = 39$) were averaged to compute a seasonality index ($SP_1 = 1/\alpha$, where α is the mean number of months during a year with a water discharge greater than a third of the monthly annual maximum) in order to estimate the mean length of the wet season for each basin (Table 1). Since all our river systems have a wet and a dry season, this measure gives a good idea of the concentration of discharge within a short or a long period (Fig. 1a, b). A high seasonality index value is related to a short marked wet season, whereas a low value is related to a long wet season associated with a long period of high water levels. As we were unable to find hydrological data for three basins (rivers Du in Liberia, Mene in Cote d'Ivoire and Ogun in Nigeria), a mean of the indices obtained for adjacent rivers of similar area and flow regimes was used as a surrogate.

Although quite extensive, the hydrological data were neither consistent over time (i.e., number of available years among drainage basins) nor over space (i.e., number of

Table 1 List of the considered drainage basins with their areas, mean annual discharges (Lévêque and Paugy 1999) and runoffs (Fekete et al. 2002), as well as the values of seasonality indices

Basin code	Basin name	Basin area (km ²)	Mean annual discharge (m ³ /s)	Mean annual runoff (mm/year)	SP ₁	SP ₂
1	GEBA	8,000	N/A	759.94	0.35	0.70
2	MONO	22,000	104	74.41	0.32	0.54
3	GAMBIE	77,000	170	135.48	0.35	0.72
4	OGUN	22,370	N/A	236.78	0.33	0.49
5	OUEME	50,000	220	120.43	0.35	0.58
6	SENEGAL	4,41,000	687	31.15	0.41	0.71
7	TCHAD	7,00,000	1064	68.71	0.24	0.70
8	CROSS	75,000	569	1155.25	0.18	0.51
9	VOLTA	3,98,371	1260	89.32	0.36	0.64
10	BENOUE	3,40,000	3425	100.14	0.27	0.67
11	MENE	1,070	N/A	914.57	0.15	0.30
12	TABOU	800	27	914.57	0.15	0.30
13	DODO	850	10	911.90	0.18	0.27
14	NERO	985	16	911.90	0.15	0.27
15	SAN PEDRO	3,310	31	453.07	0.13	0.44
16	BIA	9,730	83	474.71	0.11	0.42
17	BOUBO	4,690	32	362.49	0.13	0.52
18	ME	3,920	32	257.13	0.13	0.53
19	PRA	22,710	238	252.51	0.16	0.32
20	NIPOUE	11,920	N/A	917.33	0.19	0.54
21	TANO	16,000	129	295.20	0.16	0.38
22	AGNEBI	8,520	50	257.13	0.18	0.53
23	CAVALLY	28,850	384	917.25	0.20	0.33
24	SASSANDRA	75,500	513	452.68	0.29	0.60
25	COMOE	78,000	206	100.72	0.33	0.50
26	BANDAMA	97,000	392	196.36	0.25	0.60
27	KONKOURE	16,470	353	1897.35	0.24	0.67
28	KOLENTE	7,540	135	1387.65	0.28	0.67
29	LITTLE SCARCIES	18,872	N/A	1513.67	0.30	0.65
30	ROKEL	10,600	181	1639.69	0.20	0.64
31	JONG	7,750	223	1913.93	0.21	0.60
32	SEWA	19,050	410	1534.03	0.19	0.56
33	MOA	18,760	534	1511.64	0.16	0.57
34	MANO	8,260	208	1835.30	0.15	0.54
35	LOFA	13,190	N/A	1754.24	0.21	0.54
36	SAN PAUL	18,180	N/A	1165.09	0.21	0.58
37	DU	2,625	N/A	917.33	0.22	0.54
38	SAINT JOHN	15,600	N/A	1198.33	0.23	0.32
39	CORUBAL	23,200	306	1827.75	0.29	0.67

Basin code refers to Fig. 1 and to species occurrence data reported in the “[Electronic supplementary material](#),” S1

localities per drainage basin). For that reason, monthly runoff data based on a combination of observed river discharge and simulated water balances over the past decades and over the surface area of each drainage basin were obtained through GIS mapping from 0.5° × 0.5° grid cell data (in mm/month) available from Fekete et al. (2002). To evaluate the robustness of our seasonality index SP₁, a second index (SP₂) was derived from circular statistics of

monthly mean runoff values according to Markham (1970). SP₂ is a measure of the concentration of a variable (runoff in our case) over the course of the year. An index of SP₂ = 0 means that every month has the same amount of runoff, and an index of SP₂ = 1 means that all the annual runoff is concentrated within one month of the year (Table 1). Therefore, our approaches are complementary since SP₁ gives a somewhat incomplete but real view, while SP₂ gives

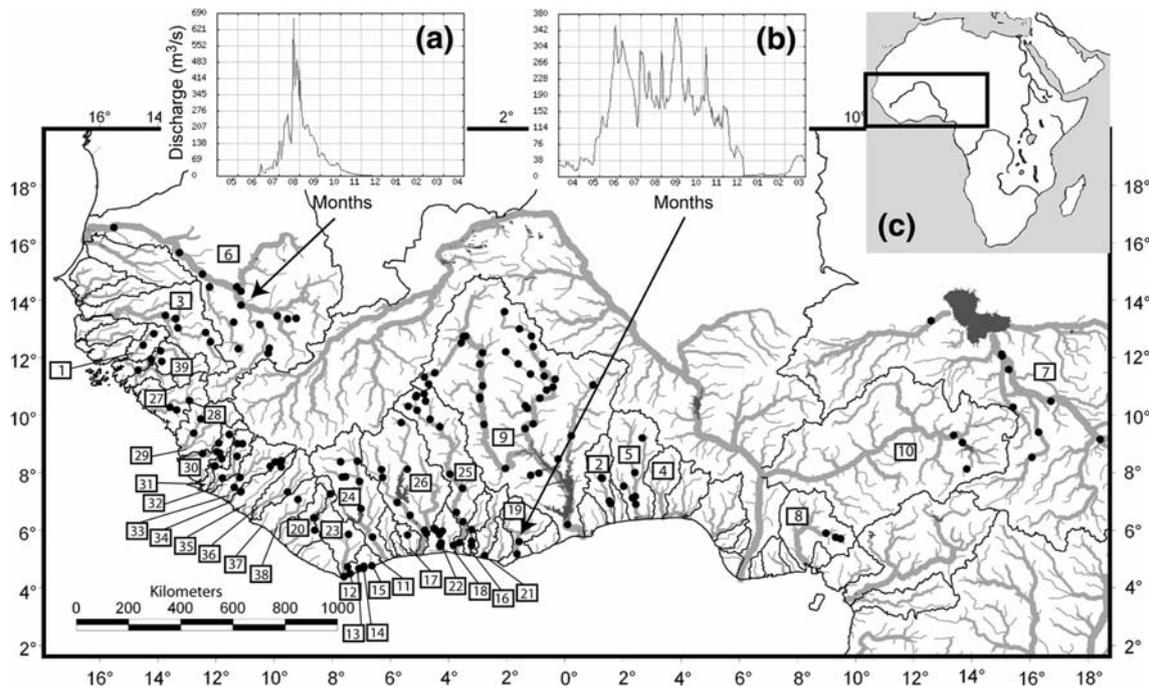


Fig. 1a–c Map of West Africa showing the drainage basins analysed in this study (see Table 1). Hydrological stations providing discharge data are represented by *black dots* and stream order is proportional to river width. *Numbers* refer to basin codes reported in Table 1. Two distinct patterns of seasonality are represented by hydrologic regimes

from the Senegal River (a) and the Pra River (b) (hydrological regime graphs are available at <http://aochycos.ird.ne/>). In subpanels (a) and (b), the numbers on the x-axis tick labels represent months (e.g., month 01 = January). A map tracing West Africa on the larger continent is also presented (c)

a complete but simulated view of discharge patterns. A third seasonality index proposed by Walsh and Lawler (1981) has been tested but was not considered further as it provided similar results to SP₁ and SP₂.

Life history traits

All data on species life history were obtained from West African water bodies. To test the predictions of Winemiller (1989), we used data for five reproductive traits (111 references available on request, completed with information from Fishbase: <http://www.fishbase.org>): (1) absolute batch fecundity (mean egg number per batch; available for 113 species), (2) relative batch fecundity (mean egg number per batch per kg; available for 112 species), (3) mean diameter of mature oocytes (in mm; available for 113 species), (4) time-span of reproductive period within a year (in months; available for 133 species), and (5) parental care (binary variable: presence = 1, absence = 0; available for 103 species; presence was considered for guarders and breathers guilds; Lévêque and Paugy 1999, p. 139). Variables (1) and (2) are supposed to be positively associated with the equilibrium-periodic gradient, while the remaining variables are supposed to be negatively associated. We accounted for the potentially confounding effect of body size when testing our predictions. This trait was quantified

for every species using the maximum adult standard length given by Lévêque et al. (1990, 1992). When several values of a quantitative trait were available for a single species, a mean value was computed. All continuous traits were log-transformed to achieve normality.

Strategy index

We performed a principal component analysis (PCA) using the above reproductive traits, to position species along the equilibrium-periodic gradient. Data from closely related species (i.e., the same genus) were used to complete unknown values of reproductive time-span (16%) and parental care (42%), leading to a matrix of 96 species (representing nearly 50% of the species richness of each drainage basin; “Electronic supplementary material,” S2). Since reproductive modes have evolved from an ancestral behavior through particular genera and families (e.g., Cichlidae, Osteoglossidae; Lévêque and Paugy 1999), and because our quantification of parental care is rather coarse, the high proportion of replaced missing values should not influence our results. From the resulting correlations between species traits and axes, we identified the axis that best separated species according to the equilibrium-periodic gradient. Species score along this axis was considered a synthetic index of its strategy.

Removing taxonomical relatedness

Statistical analyses conducted on species traits should account for the non-independence of species resulting from their phylogenetic relationships (Harvey and Pagel 1991). As a complete phylogenetic relationship between West African freshwater fish species was not currently available, we used taxonomic relatedness as a surrogate. The taxonomic component was removed from life history traits and strategy index values (described by the PCA axis) by using an autoregressive comparison approach (Cheverud et al. 1985). All species within the same genus were assigned a value of 1.0, all species within the same family a value of 0.5, all species within the same order a value of 0.33 and all species from different orders a value of 0.25. The resulting distance matrix was used to partition life history strategy index values into a combination of (1) the shared taxonomic component, and (2) the residual vector: the specific independent component (Cheverud et al. 1985; Gittleman and Luh 1992).

Data analysis

Our hypothesis was that the probability of occurrence of periodic species should increase and that of equilibrium species should decrease with increasing seasonality. We also considered the potential confounding effect of body size. Because the probability of presence increases faster with drainage basin area for large species than for small ones (Tedesco and Hugueny, unpublished results) and because our seasonality index is positively related to the drainage area ($r = 0.62$ for SP₁ and $r = 0.61$ for SP₂, both $n = 39$, both $P < 0.0001$), an interaction between body size and seasonality is expected. As body size is usually related to most other life history traits (Blueweiss et al. 1978; Peters 1983; Duarte and Alcaraz 1989), spurious interactions between strategy and seasonality could result.

To test our hypothesis, a logistic regression procedure (Sokal and Rohlf 1995) was applied to the presence/absence data of freshwater fish species among the West African drainage basins to compute the probability of occurrence (P_{ij}) of a species (j) in a drainage (i) as a function of the seasonality index (x_i), the species trait or strategy index (y_j) and the interaction term between these variables ($x_i y_j$), while taking into account the effect of body size (s_j) and its interaction with seasonality ($x_i s_j$)

$$\log\left(\frac{P_{ij}}{1 - P_{ij}}\right) = a + bx_i + c's_j + cy_j + d'x_i s_j + dx_i y_j \quad (1)$$

where the parameters b , c , c' , d' and d are the regression coefficients, and a is the intercept. If the probability of occurrence of periodic species increases and that of equilibrium species decreases with increasing seasonality, we

should observe a significant interaction between the seasonality index and the species traits or the species strategy index. More precisely, if trait y increases along the equilibrium-periodic gradient, the coefficient, d , for the interaction between x_i and y_j should be significant and positive. It is worth noting that all of the species are considered jointly in the model to get an overall assessment of the relationship between strategy and seasonality.

The significance of the interaction between strategy and seasonality has been assessed by a likelihood ratio test based on the difference, D , between the deviances of two nested models: model (1) and model (1) with $d = 0$. Under the null hypothesis that the model including the interaction term does not significantly increase the fit of the data compared to the one without interaction, D follows a χ^2 distribution with one degree of freedom (number of parameters of the more complex model minus the number of parameters of the less complex model). If the null hypothesis is rejected, we can conclude that species are not distributed at random with regard to their strategy.

We tested our working hypothesis by considering the sign of the interaction between our strategy index and seasonality. Similar analyses were also performed separately with individual life history traits in order to use all of the information available. However, because these traits are part of a strategy and hence are likely to covary, these analyses are not independent and will be considered here only for informative purposes. All continuous traits were log-transformed to correct any heteroscedasticity and interaction terms were tested after removing taxonomical relatedness from species traits and strategy index values.

To obtain a visual representation of the relationship between the strategy index or a life history trait (taxonomically uncorrected) and seasonality, average values were computed over species occurring within each basin and plotted as a function of seasonality index values. Statistical analyses were performed using the S-plus (Mathsoft, Inc.) and ADE-4 (Thioulouse et al. 1997) software packages.

Results

Patterns of species traits and seasonality

Relationships observed among the species traits (Fig. 2) reflected the physiological constraints and life history trade-offs that make up the divergent reproductive strategies previously defined by Winemiller (1989). The first principal component of the PCA on the 96-species matrix (see “Electronic supplementary material,” S2) accounted for 54.3% of the total variance and was most influenced by

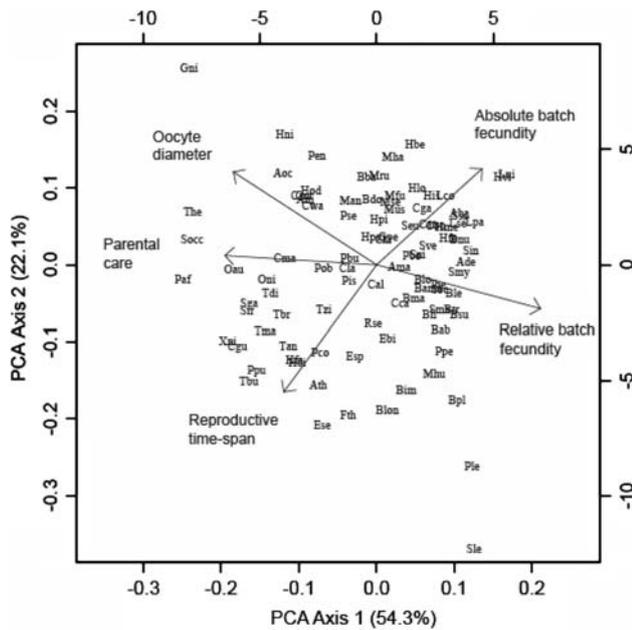


Fig. 2 Results of the principal component analysis (PCA) performed on five life history traits of 96 species (see “Electronic supplementary material,” S2 for species codes and traits values). The associations between these life history variables show the periodic and equilibrium strategies (since opportunistic species were almost absent from our dataset; see “Methods”)

relative batch fecundity, oocyte diameter and the presence of parental care (loadings 0.899, -0.787 and -0.833 , respectively), revealing the dichotomy between periodic and equilibrium species (Fig. 2). This axis was positively related to periodic traits (i.e., high fecundity, small oocytes, narrow reproductive period and no parental care) and was used as a “species strategy” index to test species distribution patterns along seasonality gradients. Examples of species with heavy loadings along axis 1 (i.e., periodic strategists) included species from several families (e.g., Centropomidae, Characidae, Schilbeidae, Cyprinidae and Mochokidae). Extreme examples of these are *Schilbe intermedius* (mean relative batch fecundity of 3,46,900 eggs/kg, mean oocyte diameter of 0.86 mm, no parental care), *Hydrocinus vittatus* (mean relative batch fecundity of 2,01,000 eggs/kg, mean oocyte diameter of 0.72 mm, no parental care) or *Labeo parvus* (mean relative batch fecundity of 4,11,590 eggs/kg; mean oocyte diameter of 1 mm, no parental care). At the opposite endpoint of the gradient (i.e., equilibrium strategists), examples of species with small loadings along axis 1 include *Papyrocranus afer* (Notopteridae; mean relative batch fecundity of 531 eggs/kg; mean oocyte diameter of 3.6 mm), *Tylochromis jentinki* (Cichlidae; mean relative batch fecundity of 1,100 eggs/kg; mean oocyte diameter of 5 mm) or *Gymnarchus niloticus* (Gymnarchidae; mean relative batch fecundity of 296 eggs/kg; mean oocyte diameter of

7.5 mm), all providing parental care to their offspring. Axis 2 (22.1% of the total variance) was most influenced by reproductive time-span (loading -0.703). Examples of equilibrium strategists with low loadings along axis 2 include Cichlidae species such as *Anomalochromis thomasi* or *Tilapia busumana* which can breed almost all year round.

Species strategy index values show that periodic strategists (high strategy index values) constitute a greater proportion of the community in highly seasonal basins, and that equilibrium strategists (low strategy index values) make up a greater proportion in more stable ones (Fig. 3a). Mean values of each reproductive trait per drainage as a function of the seasonality indices (SP_1 or SP_2) also depict this shift in community composition along the seasonality gradient (Figs. 3b–f). In highly seasonal basins (i.e., rivers with a short and predictable favorable season), species tend to produce a great number of small oocytes, to reproduce during a short period of time and to display a low degree of parental care (i.e., periodic species). Conversely, in less seasonal basins (i.e., rivers with several months of wet season), we noticed a greater proportion of species producing small numbers of large oocytes, reproducing within a long time period and providing parental care to their offspring (i.e., equilibrium species).

Testing the patterns

After accounting for taxonomical relatedness and body size, the logistic regression including an interaction between the seasonality indices (SP_1 or SP_2) and the strategy index performed significantly better than the one without this interaction (significant deviance D ; Table 2). As expected, the sign of the interaction coefficient was positive (Table 2), meaning that periodic strategists have a higher probability of occurrence in seasonal basins than equilibrium strategists, which is in agreement with Winemiller’s hypothesis. When considering each trait separately, the logistic regressions showed consistent results, e.g., species reproducing within a long time period (i.e., equilibrium strategists) had a lower probability of occurring in highly seasonal basins. For each trait, observed signs of the interaction term matched our expectations (Table 2), confirming the validity of the equilibrium-periodic gradient as a whole for explaining species distribution as a function of seasonality. The interaction terms relating individual traits to seasonality were all statistically significant except for absolute batch fecundity [although Fig. 3b suggests the contrary, the interaction term of absolute fecundity with seasonality is not significant, likely because of its high correlation with body size ($r = 0.68$, $P < 0.001$, $n = 113$)].

Fig. 3a–f Average values of the strategy index and of each individual trait per drainage as a function of river basin seasonality indices (SP₁ and SP₂). All but strategy index and parental care are log-transformed variables (see “Methods”). Lowess regression curves ($f = 0.87$) show the general trend in each case. Seasonality approaches SP₁ and SP₂ produce similar results, revealing the robustness of the variability in hydrologic data availability

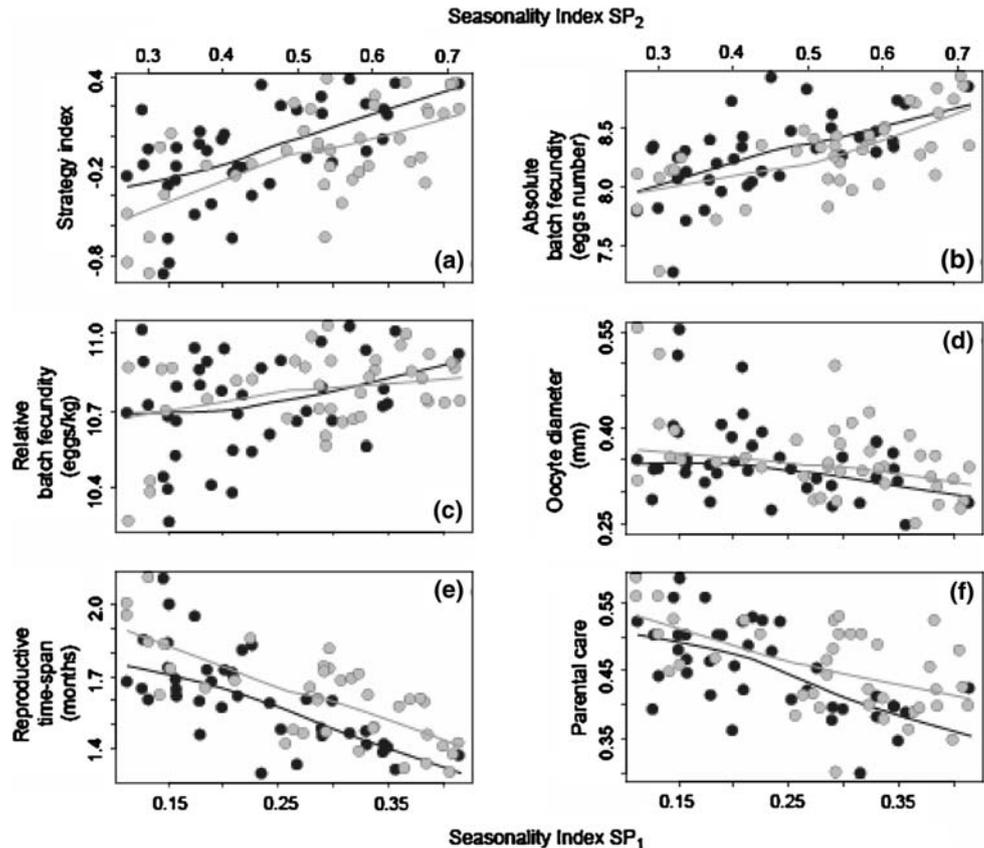


Table 2 Results of the logistic regressions linking presence/absence data of freshwater fish species to both seasonality indices (SP₁ and SP₂), and controlling for the effect of body size and taxonomic relatedness

	Number of species	Expected sign	SP ₁		SP ₂			
			Sign	<i>D</i>	<i>P</i> value	Sign	<i>D</i>	<i>P</i> value
Species strategy								
Strategy index (first axis of the PCA)	96	+	+	15.5026	<0.0001	+	12.8283	<0.0001
Species traits								
Absolute batch fecundity	113	+	+	0.168	0.6815	+	1.467	0.2258
Relative batch fecundity	112	+	+	9.809	0.0079	+	6.979	0.0082
Oocyte diameter	113	-	-	11.424	0.0007	-	11.306	0.0007
Time-span of reproductive period	133	-	-	64.704	<0.0001	-	56.181	<0.0001
Parental care	103	-	-	20.116	<0.0001	-	5.681	0.0171

Signs, deviance *D* and *P* values of the interaction terms between strategy index or species traits and seasonality indices are presented with the number of species considered in each case

Discussion

The periodic-equilibrium dichotomy

The observed trends in species traits and species strategy index indicated a clear response of species distributions to hydrologic seasonality of drainage basins. Along the seasonality gradient, periodic species (exhibiting high fecundity, small oocytes, narrow reproductive period and absence of parental care) were associated with drainages characterized by a short annual favorable period for species

reproduction (e.g., two or three months of wet season). In contrast, equilibrium species were linked to drainages with more than six months of wet season. Both seasonality indices produced similar results. These findings were supported by the results of logistic regressions accounting for taxonomical relatedness, species body size and redundancy in species traits (by using a “species strategy” index).

The life history strategies hypothesis proposed by Winemiller (1989) considered observed patterns in species composition as adaptive suites of species characteristics responding to particular environmental variability

conditions (in terms of predictability and frequency). Previous studies on marine and freshwater fish (e.g., Kawasaki 1980; Baltz 1984; Vila-Gispert et al. 2002; Vila-Gispert and Moreno-Amich 2002; King and McFarlane 2003) support Winemiller's hypothesis, but the present results go a step further by formally relating species adaptive strategies to environmental gradients. Given this framework, we hypothesized that seasonal environments should harbor more periodic fish species than more stable habitats. Our data confirmed this hypothesis and complemented the study of Bruton and Merron (1990) which compared the percentage of bearers and guarders (forms of parental care) in the fish faunas of various African rivers, wetlands and lakes, and reported a higher proportion of those equilibrium species in highly stable ancient lakes (e.g., the Great Lakes). However, their study mainly contrasted rivers with lakes, and these two kinds of ecosystems may differ in many respects, not just in terms of their hydrological stability. Moreover, as the African Great Lakes are dominated by cichlids, a taxonomic bias cannot be ruled out. Our study circumvents some of these potential problems by comparing faunas from similar ecosystems (rivers) and by controlling for taxonomic relatedness. Our results focused on the seasonal endpoint (rivers) of the gradient studied by Bruton and Merron (1990) and confirmed that the pattern observed across systems (rivers and lakes) is also observed within systems (at least for rivers).

Intra-specific trait variability

Intra-specific variability in the life histories of fish determined by environmental conditions has been suggested in numerous cases (e.g., Fleming and Gross 1990; Tamate and Maekawa 2000; Heibo et al. 2005; Blanck and Lamouroux 2007). As we assigned the same trait value to each species regardless of the basin, our results could be an oversimplification of reality. However, our observed patterns of life history variation should not have been strongly affected by intra-specific variability for two reasons. First, variability in reproductive traits such as fecundity or egg size is, to a large extent, weaker within than between species (Blanck and Lamouroux 2007). For instance, the absolute fecundity of *Sarotherodon galilaeus* (an equilibrium strategist) ranges from 407 eggs (min.–max.: 130–685) in Benin lakes (Adite and Van Thielen 1995) to 2,458 eggs (min.–max.: 834–4,634) in the Niger River (Nwadiaro 1987), whereas for *Schilbe mystus* (a periodic strategist) it ranges from 20,290 eggs (min.–max.: 13,905–26,675) in Lake Kainji (Olatunde 1978) to 55,565 eggs (min.–max.: 35,460–75,670) in the Ogun drainage basin (Adebisi 1987). Second, based on the above examples, the existing intra-specific variability seems to be related to variability of environmental conditions, i.e., variations in intra-specific

responses to environmental predictability (rivers vs. lakes) appear to follow the same trends as suggested by our results for inter-specific variations. This is a likely result if reproductive traits reflect adaptations to the hydrological regime in the way suggested by Winemiller (1989) and Winemiller and Rose (1992). These arguments lead us to state that if data were available for each trait and each species, and in sufficient detail to account for intra-specific variability between drainage basins, the observed relationships between life history traits and seasonality would have been stronger. As the available data on traits for widely distributed species increase, further tests should elucidate this issue.

Variability in species data

Except for body size, data were not available for each species–trait combination, and so this could be a potential source of bias. It is worth noting that given the way data were analyzed (see “Methods”), it is not necessarily important to have a complete coverage of species distribution per basin but rather to have an inter-specific variability per trait that is representative of that displayed across the whole fauna. If, for instance, only species with a high fecundity were analyzed, a link between seasonality and fecundity, even if present, would be unlikely to be demonstrated. Nevertheless, analyzing a subset of the regional pool may have had two consequences. First, this might have reduced the power of the analyses if too few species were considered and/or the resulting gradient in life history traits was too narrow. Second, if the species analyzed were not a random sample of the regional pool, potential bias might have been introduced. For instance, the mean length of species with available trait data was larger than that for species for which trait data was missing (i.e., 354 vs. 124 mm, respectively). We believe that this potential bias weakly affected our results for two reasons. First, body size was not related to the periodic-equilibrium gradient (Pearson's correlation between strategy index and body size, $r = -0.03$, $n = 96$, $P > 0.05$). Second, body size was accounted for in the analyses. It is likely that species with missing trait values are in some way rare species (average occurrence of 4 and 13 basins, respectively, for species without information and species with known values for all the considered traits), though this phenomenon could not significantly bias our results since the periodic-equilibrium gradient is not related to species occurrence (Pearson's correlation between strategy index and occurrence, $r = -0.036$, $n = 96$, $P = 0.727$). Data-deficient species may have been a non-random sample with regard to taxonomy (e.g., only 36% of perciformes without any informed trait vs. 75% for cypriniformes). However, as taxonomic relatedness has been accounted for in the

analyses, the problem of taxonomic bias should have been marginal.

Spatially related factors

Given the numerous causes that can affect the probability of presence of a species in a basin, our conclusions could have been weakened to some extent by other factors possibly related to seasonality, e.g., drainage area (but see “[Methods](#)”), climatic history (see below), productivity or latitudinal cline. Our dataset was restricted within a very narrow latitudinal range (less than 10°), implying little or no effect of cline gradient and productivity (also related to latitude) on species occurrence (Tedesco et al. 2005). Furthermore, as both seasonal and less seasonal drainages occur in northern and southern parts of our study area (Lévêque and Paugy 1999), latitudinal gradient could not have produced the observed patterns of demographic strategies or any unwanted spatial correlation in the analyses.

Historical issues

Within the hierarchical “landscape filters” framework (Tonn et al. 1990; Poff 1997), the hydrological seasonality of rivers acts as a selective filter for species reproductive strategy at an inter-drainage basin scale. The absence of easy migration between drainages over large temporal scales for freshwater fish (because of land or ocean barriers) implies that differential extinction and/or speciation rates within a basin with regard to life-history strategies are probably the underlying mechanism of the observed pattern. Unfortunately, given the low number of reliable phylogenies, it is difficult to infer how speciation has worked for West African fishes in general. However, there is indirect evidence suggesting that within-basin differentiation (speciation minus extinction) processes played an important role in structuring present fish communities within West African rivers. For instance, the West African rivers that currently display relatively more stable hydrological conditions are those located in historically stable regions (i.e., Pleistocene refuges; Dupont et al. 2000). These rivers tend also to have higher species richness (when river size has been accounted for), and higher historical hydrological stability that could have allowed the speciation and/or the persistence of a higher proportion of equilibrium species (Tedesco et al. 2005).

Concluding remarks

Our results add to a growing amount of literature associating functional organization of aquatic assemblages with hydrologic variability. It has been previously demonstrated

for fish that patterns of discharge variability can directly influence community structure. Fish community functional structure–hydrology relationships have been observed at the regional (Poff and Allan 1995; Cattaneo 2005b), local (Cattaneo 2005a) and microhabitat scales (Lamouroux et al. 2002; Blanck et al. 2007), which stress the importance of hydrologic conditions in shaping community characteristics.

Our results suggest that large-scale species distribution of West African freshwater fish can be partly explained by a functional relationship between their life history strategies (i.e., a combination of traits placing species within the triangular continuum of strategies proposed by Winemiller (1989)] and the degree of seasonality in hydrological conditions of rivers. Highly seasonal conditions were related to the small/numerous offspring tactic (periodic strategy) conferring all the reproductive effort to a short but favorable period (flood), whereas less seasonally marked rivers were related to the large/few offspring tactic (equilibrium strategy). Consequently, river hydrological variability acts as a “landscape filter” for species life-history traits (Winemiller 1989; Winemiller and Rose 1992; Poff 1997). As differential extinction and/or extinction rates with regard to life-history strategy are the mechanisms most likely to explain how the hydrological filter acts between rivers, the present-day distribution of species probably also reflects the hydrological histories of the rivers.

Acknowledgments The authors thank the IRD (Institut de Recherche pour le Développement) and the ANR-06-BDIV-010 project for financial support. Thomas Lüellwitz from the GRDC (Global Runoff Data Center) and Patrick Raous from the IRD kindly provided the hydrological data. We are very grateful to Kirk Winemiller, Thierry Boulinier, Emili García-Berthou and two anonymous reviewers for their thoughtful comments that greatly improved the manuscript.

References

- Adebisi AA (1987) The relationships between the fecundities, gonado-somatic indices and egg sizes of some fishes of Ogun River, Nigeria. *Arch Hydrobiol* 3:151–156
- Adite A, Van Thielen R (1995) Ecology and fish catches in natural lakes of Benin, West Africa. *Environ Biol Fishes* 43:381–391
- Allan JD (1976) Life history patterns in zooplankton. *Am Nat* 110:165–180
- Baltz DM (1984) Life history variation among female surfperches (Perciformes: Embiotocidae). *Environ Biol Fishes* 10:159–171
- Blanck A, Lamouroux N (2007) Large-scale intraspecific variation in life-history traits of European freshwater fish. *J Biogeogr* 34:862–875
- Blanck A, Tedesco PA, Lamouroux N (2007) Relationships between life history strategies of European freshwater fish species and their habitat preferences. *Freshw Biol* 52:843–859
- Blueweiss L, Fox H, Kudzma V, NaKashima D, Peters R, Sams S (1978) Relationships between body size and some life history parameters. *Oecologia* 37:257–272

- Boyce MS (1979) Seasonality and patterns of natural selection for life histories. *Am Nat* 114:569–583
- Bruton MN, Merron GS (1990) The proportion of different ecological sections of reproductive guilds of fishes in some African waters. *Environ Biol Fishes* 28:179–187
- Cattaneo F (2005a) Does hydrology constrain the structure of fish assemblages in French streams? Local scale analysis. *Arch Hydrobiol* 164:345–365
- Cattaneo F (2005b) Does hydrology constrain the structure of fish assemblages in French streams? Regional scale analysis. *Arch Hydrobiol* 164:367–385
- Cheverud JM, Dow MM, Leutenegger W (1985) The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution* 39:1335–1351
- Cody ML (1966) A general theory of clutch size. *Evolution* 20:174–184
- Duarte CM, Alcaraz M (1989) To produce many small or few large eggs: a size-independent reproductive tactic of fish. *Oecologia* 80:401–404
- Dupont LM, Jahns S, Marret F, Ning S (2000) Vegetation change in equatorial West Africa: time-slices for the last 150 ka. *Palaeogeogr Palaeoclimatol Palaeoecol* 155:95–122
- Elgar MA (1990) Evolutionary compromise between a few large and many small eggs: comparative evidence in teleost fish. *Oikos* 59:283–287
- Fekete BM, Vörösmarty CJ, Grabs W (2002) High-resolution fields of global runoff combining observed river discharge and simulated water balances. *Global Biogeochem Cycles* 16(3):1042. DOI: [10.1029/1999GB001254](https://doi.org/10.1029/1999GB001254)
- Fleming IA, Gross MR (1990) Latitudinal clines: a trade-off between number and size in pacific salmon. *Ecology* 71:1–11
- Gittleman JL, Luh HK (1992) On comparing comparative methods. *Annu Rev Ecol Syst* 23:383–404
- Greenslade PJM (1983) Adversity selection and the habitat templet. *Am Nat* 122:352–365
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169–1194
- Harvey PH, Pagel M (1991) *The comparative method in evolutionary biology*. Oxford University Press, Oxford
- Heibo E, Magnhagen C, Vollestad LA (2005) Latitudinal variation in life-history traits in Eurasian perch. *Ecology* 86:3377–3386
- Humphries P, King AJ, Koehn JD (1999) Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray–Darling River system, Australia. *Environ Biol Fishes* 56:129–151
- Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. In: Dodge DP (ed) *Proceedings of the International Large River Symposium*. *Can Spec Publ Fish Aquat Sci* 106:110–127
- Kautsky L (1988) Life strategies of aquatic soft bottom macrophytes. *Oikos* 53:126–135
- Kawasaki T (1980) Fundamental relations among the selections of life history in the marine teleosts. *Bull Jpn Soc Sci Fish* 46:289–293
- King JR, McFarlane GA (2003) Marine life history strategies: applications to fishery management. *Fish Manag Ecol* 10:249–264
- Koenig WD (1984) Geographic variation in clutch size in the northern flicker (*Colaptes auratus*): support for Ashmole's hypothesis. *Auk* 101:698–706
- Lamouroux N, LeRoy Poff N, Angermeier PL (2002) Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology* 83(7):1792–1807
- Lévêque C, Paugy D (1999) *Les poissons des eaux continentales africaines*. IRD Editions, Paris
- Lévêque C, Paugy D, Teugels GG (1990) *Faune des poissons d'eaux douces et saumâtres d'Afrique de l'Ouest*, vol I. ORSTOM/MRAC, Paris
- Lévêque C, Paugy D, Teugels GG (1992) *Faune des poissons d'eaux douces et saumâtres d'Afrique de l'Ouest*, vol II. ORSTOM/MRAC, Paris
- Lowe McConnell RH (1964) *The fishes of the Rupununi savanna district of British Guiana, South America, Part 1*. *Zool J Linn Soc* 45:103–144
- Lowe McConnell RH (1987) *Ecological studies in tropical fish communities*. Cambridge University Press, London
- MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ
- Markham CG (1970) Seasonality of precipitation in the United States. *Ann Assoc Am Geogr* 60:593–597
- McGregor Reid G, Sydenham H (1979) A checklist of Lower Benue river fishes and an ichthyogeographical review of the Benue River (West Africa). *J Nat Hist* 13:41–67
- Mérigoux S, Dolédec S, Statzner B (2001) Species traits in relation to habitat variability and state: neotropical juvenile fish in floodplain creeks. *Freshw Biol* 46:1251–1267
- Mérigoux S, Ponton D (1999) Spatio-temporal distribution of young fish in tributaries of natural and flow-regulated sections of a neotropical river in French Guiana. *Freshw Biol* 42:177–198
- Merona B (2005) Alteration of fish diversity downstream from Petit-Saut dam in French Guiana. Implication of ecological strategies of fish species. *Hydrobiologia* 551:33–47
- Nwadiaro CS (1987) Fecundity of cichlid fishes of the Sombriero River in the lower Niger delta, Nigeria. *Rev Zool Afr* 101:433–437
- Olatunde AA (1978) Sex, reproductive cycle and variations in the fecundity of the family Schilbeidae (Osteichthyes: Siluriformes) in Lake Kainji, Nigeria. *Hydrobiologia* 57:125–142
- Partridge L, Harvey PH (1988) The ecological context of life history evolution. *Science* 241:1449–1454
- Paugy D, Traoré K, Diouf PS (1994) *Faune ichtyologique des eaux douces d'Afrique de l'Ouest*. *Ann Mus R Afr Centr Zool* 275:35–66
- Peters RH (1983) *The ecological implications of body size*. Cambridge University Press, London
- Pianka ER (1970) On “r” and “K” selection. *Am Nat* 104:592–597
- Poff NL (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J North Am Benthol Soc* 16:391–409
- Poff NL, Allan JD (1995) Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76:606–627
- Ponton D, Copp GH (1997) Early dry season community structure and habitat use of young fish in tributaries of the River Sinnamary (French Guiana, South America) before and after hydrodam operation. *Environ Biol Fishes* 50:235–256
- Ponton D, Vauchel P (1998) Immediate downstream effects of the Petit-Saut dam on young neotropical fish in a large tributary of the Sinnamary river (French Guiana, South America). *Regul River* 14:227–243
- Ricklefs RE (1977) On the evolution of reproductive strategies in birds: reproductive effort. *Am Nat* 111:453–478
- Roff DA (1984) The evolution of life history parameters in Teleosts. *Can J Fish Aquat Sci* 41:989–1000
- Sokal RR, Rohlf FJ (1995) *Biometry*. WH Freeman and Co., New York
- Southwood TRE (1977) Habitat, the templet for ecological strategies? *J Anim Ecol* 46:337–365
- Southwood TRE (1988) Tactics, strategies and templates. *Oikos* 52:3–18
- Stearns S (1992) *The evolution of life histories*. Oxford University Press, New York

- Tamate T, Maekawa K (2000) Interpopulation variation in reproductive traits of female masu salmon, *Oncorhynchus masou*. *Oikos* 90:209–218
- Taylor DR, Aarssen LW, Loehle C (1990) On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos* 58:239–250
- Tedesco PA, Hugueny B (2006) Life history strategies affect climate based spatial synchrony in population dynamics of West African freshwater fishes. *Oikos* 115:117–127
- Tedesco PA, Oberdorff T, Lasso CA, Zapata M, Hugueny B (2005) Evidence of history in explaining diversity patterns in tropical riverine fish. *J Biogeogr* 32:1899–1907
- Thioulouse J, Chessel D, Dolédec S, Olivier JM (1997) ADE-4: a multivariate analysis and graphical display software. *Stat Comput* 7:75–83
- Tonn WM, Magnuson JJ, Rask M, Toivonen J (1990) Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. *Am Nat* 136:345–375
- Townsend CR, Hildrew AG (1994) Species traits in relation to habitat templet for river systems. *Freshw Biol* 31:265–275
- Vila-Gispert A, Moreno-Amich R (2002) Life history patterns of 25 species from European freshwater fish communities. *Environ Biol Fishes* 65:387–400
- Vila-Gispert A, Moreno-Amich R, Garcia-Berthou E (2002) Gradients of life history variation: an intercontinental comparison of fishes. *Rev Fish Biol Fish* 12:417–427
- Vörösmarty CJ, Fekete BM, Meybeck M, Lammers RB (2000) The global system of rivers: its role in organizing continental land mass and defining land-to-ocean linkages. *Global Biogeochem Cycles* 14:599–621
- Walsh PD, Lawler DN (1981) Rainfall seasonality: description, spatial patterns and change through time. *Weather* 36:201–208
- Welcomme RL (1979) Fisheries ecology of floodplain rivers. Longman, London
- Winemiller KO (1989) Patterns of variation in life history among South America fishes in seasonal environments. *Oecologia* 81:228–241
- Winemiller KO (2005) Floodplain river food webs: generalizations and implications for fisheries management. In: Welcomme RL, Petr T (eds) Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries, vol 2. Mekong River Commission, Phnom Penh, pp 285–310
- Winemiller KO, Rose KA (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Can J Fish Aquat Sci* 49:2196–2218
- Winemiller KO, Rose KA (1993) Why do most fish produce so many tiny offspring? *Am Nat* 142:585–603