

## Life history strategies affect climate based spatial synchrony in population dynamics of West African freshwater fishes

Pablo Tedesco and Bernard Hugueny

Tedesco, P. and Hugueny, B. 2006. Life history strategies affect climate based spatial synchrony in population dynamics of West African freshwater fishes. – *Oikos* 115: 117–127.

Spatial synchrony in species abundance is a general phenomenon that has been found in populations representing virtually all major taxa. Dispersal among populations and synchronous stochastic effects (the so called “Moran effect”) are the mechanisms most likely to explain such synchrony patterns. Very few studies have related the degree of spatial synchrony to the biological characteristics of species. Here we present a case where specific predictions can be made to relate river fish species characteristics and synchrony determined exclusively by a Moran effect through the expected sensitivity of species to the regional component of environmental stochasticity. By analyzing 23-year time series of abundance estimates in two isolated localities we show that species associated with synchronized reproduction during the wet season, high fecundity, small egg size and high gonado-somatic index (the so called “periodic” strategy) have a higher degree of spatial synchrony in population dynamics than species associated with the opposite traits (the so called “equilibrium” strategy). This is supported by significant relationships ( $P$  values  $<0.01$ ) between species traits and the levels of synchrony after removing taxonomical relatedness. Spatial synchrony computed from summed annual total catches by groups of species, separated into strategy types also showed a significantly higher degree of synchrony for the periodic ( $r=0.83$ ) than the equilibrium ( $r=0.46$ ) group. Regional hydrological variability is likely to be partly responsible for the observed synchrony pattern and a regional discharge index showed better relationships with the periodic group, supporting the expected differential effect of regional environmental correlation on population dynamics.

*P. Tedesco and B. Hugueny, UR IRD 131, Laboratoire d'écologie des hydrosystèmes fluviaux, Univ. Claude Bernard Lyon 1, 43 Boulevard du 11 novembre 1918, FR-69622 Villeurbanne Cedex, France (pablo.tedesco@univ-lyon1.fr)*

Spatial synchrony in species abundance is a general phenomenon that has been found in populations representing virtually all major taxa (reviewed by Ranta et al. 1998, Koenig 1999, Leibhold et al. 2004). Studies showing synchrony patterns are closely related to the debate on the relative importance of intrinsic factors and extrinsic environmental variations in determining population size fluctuations. Indeed, the prevailing view is that the mechanisms most likely to explain the synchrony pattern are: (a) dispersal among populations and

(b) synchronous stochastic effects often referred to as the “Moran effect” (Moran 1953).

Several studies have reported differences in the degree of spatial synchrony among related species (Sutcliffe et al. 1996, Myers et al. 1997, Hawkins and Holyoak 1998, Koenig 1998, Myers 1998, Swanson 1998, Paradis et al. 1999, 2000, Swanson and Johnson 1999, Peltonen et al. 2002, Raimondo et al. 2004, Koenig and Leibhold 2005, Ruetz et al. 2005). Although synchrony in natural populations seems to be partly determined by species life

Accepted 28 March 2006  
Subject Editor: Esa Ranta

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ISSN 0030-1299

history traits (Paradis et al. 1999, 2000, Leibhold et al. 2004), very few works have actually related species characteristics to synchrony patterns. If dispersal occurs it can be expected a higher spatial synchrony for species that have good dispersal abilities. Analyses of breeding bird population time series (Koenig 1998, Paradis et al. 1999, 2000) indicated that species with greater dispersal capabilities are more highly synchronized, implying that dispersal is a major cause of the observed synchronous dynamics. Sutcliffe et al. (1996) found similar results among butterfly species. Other attempts (Koenig 1998, Paradis et al. 1999, 2000, Burrows et al. 2002) have failed to clearly explain patterns of synchrony among species by differences in their biological characteristics (e.g. reproductive biology and ecology, body size, survival rates, diet, etc.). Excluding the clear causal relationship between dispersal capabilities and synchrony due to dispersal, no specific predictions have been explicitly formulated to link synchrony patterns among species and their life histories. A theoretical framework for environmentally induced spatial synchrony, the Moran "theorem" (Moran 1953, Royama 1992), states that the correlation among population sizes is the same as that of environmental stochasticity. In addition to the absence of migration, the Moran theorem applies under the assumption of identical linear dynamics between populations (but see Hugueny 2006). This means that spatial synchrony does not depend on the deterministic skeleton of its dynamics (such as the strength of density dependence), leaving little hope to establish relationship between life-history and synchrony. Moreover, the few theoretical studies that relax the assumption of linearity offer few leads for identifying biological traits promoting spatial synchrony (Grenfell et al. 1998, Royama 2005). For the sake of simplicity environmental stochasticity may be decomposed into two components according to their spatial correlation: a local one, uncorrelated between localities; and a regional one, displaying spatial synchrony. Thus according to the Moran theorem, the strength of spatial synchrony in population dynamics will be driven only by the relative contribution of the regional component of environmental stochasticity. Here we present a case where specific predictions can be made to relate river fish species characteristics and synchrony determined by a Moran effect through the expected sensitivity of species to the regional component of environmental stochasticity (e.g. hydrology). As fish populations located in different drainage basins cannot be connected by dispersal, they are good models for studying strict environmentally induced spatial synchrony.

In a recent study, Tedesco et al. (2004) have illustrated a high degree of synchrony in the population dynamics of four freshwater fish species between different drainage basins that cannot be connected by dispersal, demonstrating the action of a climatic synchronizing factor (the

Moran effect). Hydrological variability is known to affect riverine fish population dynamics (Welcomme 1985) and hence is a good candidate for a Moran effect in freshwater fish (Tedesco et al. 2004, Ruetz et al. 2005). Flood affects many species of fish through improved breeding, growth and survival as flood level and duration increase. Nevertheless, it is unlikely that all species are equally affected by climate or hydrology. Tropical riverine fish assemblages, evolving under the same environmental forcing, are very suitable for revealing relationships between species characteristics and synchrony patterns because they exhibit a wide diversity of morphological, physiological and ecological attributes (Lowe-McConnell 1987). Based on patterns of life history variation in tropical freshwater fish, Winemiller (1989) proposed three reproductive strategies as endpoints of a triangular continuum resulting from adaptive responses to environmental variation in terms of its predictability (i.e. seasonality). A suite of attributes associating low batch fecundity, high investment per offspring (e.g. parental care, large eggs) and aseasonal reproduction correspond to the "equilibrium" strategy. The "opportunistic" strategy characterized by rapid colonization abilities, associates small fishes with early maturation, continuous reproduction and low fecundity. Finally, the "periodic" strategy present traits associated with synchronized reproduction during the wet season, high fecundity, small eggs and absence of parental care.

Here we compare the degree of synchrony induced by a Moran effect (Tedesco et al. 2004) among several tropical freshwater fish species belonging to the periodic and equilibrium strategies, from two different drainage basins of Ivory Coast. We expect periodic species to have a higher degree of synchrony than equilibrium species mainly for two reasons: (1) reproduction of periodic species is highly related to hydrological variability (i.e. the synchronizing factor), contrasting with the aseasonal reproduction timing of equilibrium species, and (2) reproduction of equilibrium species strongly depends on local habitat conditions (e.g. availability of specific solid substrate for building nests and for territorial defense) that can greatly differ between sites and species, contrasting with the "open water" spawning of periodic species (Tweddle et al. 1998, Lévêque and Paugy 1999). We test the degree of synchrony among species by using differences in their reproductive characteristics (e.g. fecundity, egg size and time-span of reproductive period). Furthermore, we also studied synchrony at the reproductive guild level by separating species into two groups, periodic and equilibrium and by considering time series of total abundance per guild (aggregated "communities", sensu Micheli et al. 1999). We expect the total abundance of periodic species to be more synchronous than the total abundance of equilibrium species because within this guild intra-specific as well as inter-specific synchronies should be high. Inter-specific

synchrony can occur when each species in a community respond similarly to long-term changes in abiotic factors (Micheli et al. 1999). Since the reproduction of periodic species depends on the same factor (hydrology), the degree of inter-specific synchrony of this group should be high. For equilibrium species, local habitat conditions favorable for reproduction can vary between sites and species, presumably resulting in lower inter-specific synchrony.

## Material and methods

### Time series data

A monitoring programme for West African rivers, the Onchocerciasis Control Programme (OCP) sponsored by the World Health Organization (Lévêque et al. 1988), provided the species time series data (catch per unit effort (CPUE): number of fish caught in 100 m<sup>2</sup> of gill-net per night) as in Tedesco et al. (2004). From the several surveyed localities, we selected two sites on the basis of the length of the time series (23 years), their location within the same biogeographical unit, the Eburneo-Ghanean region (Hugueny and Lévêque 1994) and because they were situated in two distinct drainage basins in Ivory Coast (Fig. 1): the Comoé basin, with 52 species sampled (locality 1, Ganse, monitored 98 times over 23 years) and the Bandama basin, with 59 species sampled (locality 2, Niakaramandougou, monitored 112 times over 24 years). The choice for two sites instead of four as in our previous paper (Tedesco et al. 2004) was made in order to have the longest time series for a maximum number of species occurring in distinct

drainages. Both sites belong to the same hydro-climatic zone, the “Nordgolf” (Mahé 1993). Sites, sampling conditions, experimental fishing and pre-treatment of the time series are described in Tedesco et al. (2004).

### Life history strategies

Information on species traits summarized in Appendix A1 was drawn from the literature (37 references available on request). Mainly because of their body size, small species from the opportunistic strategy (belonging to Cyprinidae, Cyprinodontidae and Clupeidae families; Winemiller 1989, Lévêque and Paugy 1999, Méricoux et al. 2001) were rarely caught by gillnets and thus were removed from our analysis (n=9). Species without available life history information even at higher taxonomic levels (n=7) could not be considered. The 52 remaining species were assigned to a periodic or equilibrium group (Appendix A1) based on data for six biological traits: egg size, relative fecundity, gonadosomatic index (GSI), time-span of reproductive period, and presence of multiple spawning and parental care. Maximum body size (standard length) and size at maturity were also considered but without any specific prediction because periodic and equilibrium species do not present great differences in size.

Since fecundity and juvenile survival are the most discriminating factors for periodic and equilibrium species (Winemiller 1989, 2005), we mainly used the fecundity/egg size tradeoff ( $r = -0.87$  between these traits) and the presence of parental care to distribute species to strategy groups. Species combining a large fecundity ( $>60000$  eggs kg<sup>-1</sup>) and small eggs ( $<1.4$  mm diameter) without providing parental care were assigned to the periodic strategy. Species with a smaller fecundity ( $<40000$  eggs kg<sup>-1</sup>) and larger eggs ( $>1.4$  mm diameter) were assigned to the equilibrium strategy. This was supplemented with information inferred from higher taxonomic levels for groups clearly assigned to a specific strategy (i.e. the family Cichlidae which belongs to the equilibrium strategy (Winemiller 1989, Lévêque and Paugy 1999, Méricoux et al. 2001) and genus *Synodontis* and *Labeo* to the periodic strategy (Lévêque and Paugy 1999). Some species with ambiguous biological features like species belonging to the Clariidae family or the *Marcusenius* genus were not assigned to any strategy (“intermediate” species in Appendix A1).

### Removing taxonomical relatedness

As phylogenetic relationships between West African freshwater fish species were not available, the taxonomical relatedness of species was removed from values of synchrony and life history traits by an autoregressive comparison approach (Cheverud et al. 1985). Similarity

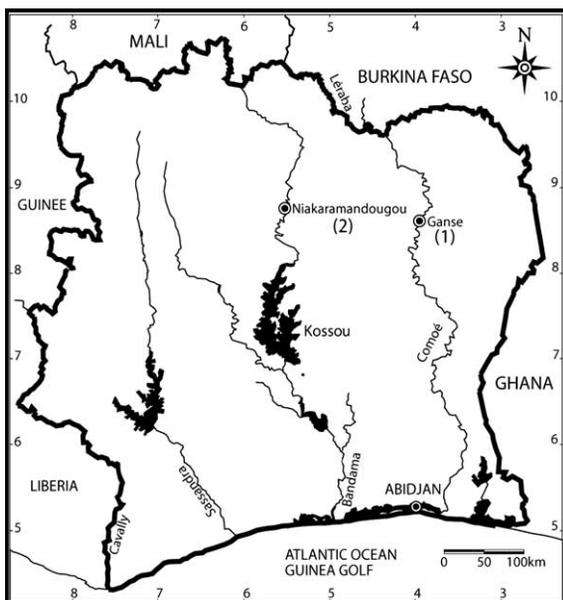


Fig. 1. Ivory Coast map showing the location of sampling sites.

between species descended as the reciprocal of taxonomical distance. That is, 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 synchrony and life history values into a combination of (1) a shared taxonomic component and (2) the residual vector: the specific independent component (Cheverud et al. 1985, Gittleman and Luh 1992).

### Comparing synchrony among species

The degree of spatial synchrony within species among both sites was evaluated using correlations with zero time lag (Ranta et al. 1998, Koenig 1999, Leibhold et al. 2004) for annual means of log-transformed time series of catch per unit effort (CPUE) as performed in Tedesco et al. (2004). This was achieved only for species that were abundant enough (at least 5 individuals fished on average per year and site) in both sites ( $n = 27$ ; Appendix A1). After removing taxonomical relatedness, we then evaluated the relationships between synchrony and reproductive species traits by applying Pearson's correlation tests to verify the expected relationships. Since periodic species (i.e. high fecundity, high GSI, small eggs, short reproductive period) are expected to show a higher degree of synchrony, we expected synchrony to be (a) positively correlated with fecundity and GSI, (b) negatively correlated with egg size and time-span of reproductive period and (c) unrelated with maturity size and body size.

### Comparing synchrony among strategies

Two groups of species were defined on the basis of their life history traits so that they correspond to the periodic and equilibrium reproductive strategies (see above). Unconverted time series were summed across species to obtain total annual catch for both strategies at both sites. These four time series were log-transformed as in Tedesco et al. (2004). Spatial synchrony within strategies among both sites was evaluated using cross correlations, resulting in two correlation coefficients. Because it is likely that time series contain temporal autocorrelation, violating the assumption of serial independence required for most standard inference tests, the difference between these coefficients was evaluated by a permutation test: 1000 simulated layouts were generated by randomly permuting species between the two groups. Correlation coefficients were calculated from these random groups as performed for the observed groups. The 1000 resultant differences of correlation values provided the expected distribution under the null hypothesis of no difference between periodic and equilibrium degree of synchrony,

against which the statistical significance of the observed difference was assessed.

To assess the relationship between regional climatic hydrology and the fish population dynamics of the periodic and equilibrium strategies, we used the data of Mahé (1993) as in Tedesco et al. (2004). The correlation between annual discharges at the mouths of the Comoé and Bandama rivers is 0.84 (0.88 on a log-scale) over the period 1974–1986 (Mahé 1993) which is consistent with the probable role of hydrology as a synchronizing factor. The regional discharge index computed by Mahé provides a measure of the inter-annual hydrological variability based on the flood intensity of each year's wet season in the considered region, the "Nordgolf". The permutation layouts were used as above to test for a stronger relationship between hydrology and dynamics of the periodic group. Correlations were calculated between randomized groups and hydrology providing the expected distribution under the null hypothesis of no differential effect of hydrology on the dynamics of both strategies.

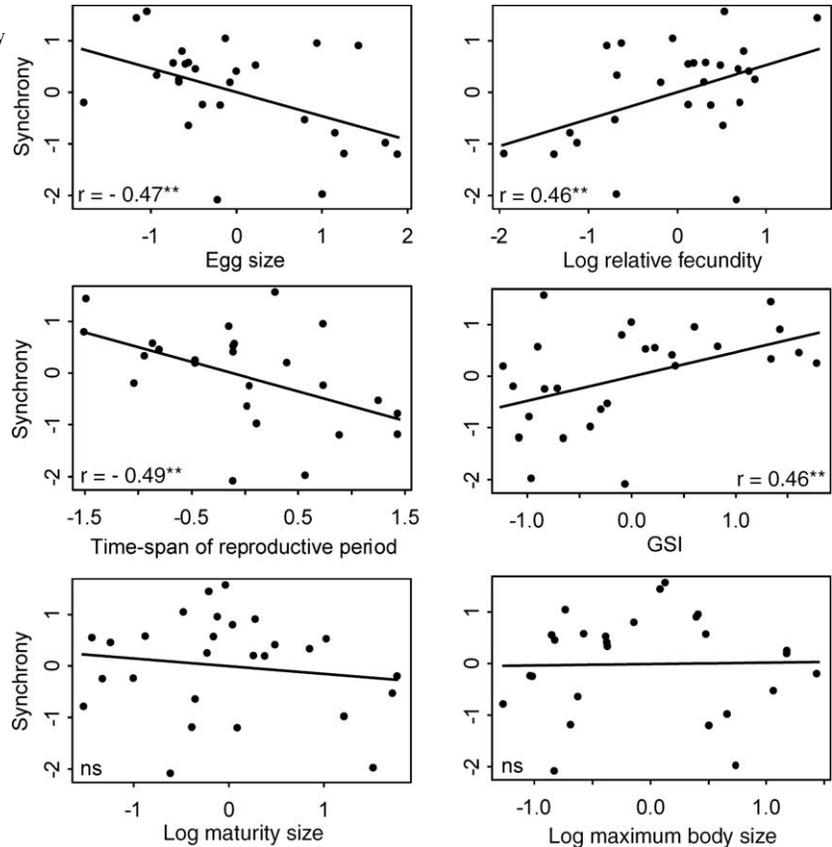
## Results

Life history traits related to the reproductive strategies of freshwater fishes had a significant effect on the degree of spatial synchrony in population dynamics. This result is supported by both tests: by directly comparing synchrony among species or by separating species in strategy groups. Along with the expected sensitivity to the regional component of environmental stochasticity, our specific predictions relating synchrony to species characteristics were that periodic species should have a higher degree of synchrony than equilibrium species.

### Synchrony levels among species

According to the expected relationships and after controlling for taxonomical relatedness, spatial synchrony was significantly and negatively related to egg size and time-span of reproductive period; and positively related to relative fecundity and GSI (Fig. 2). Species having periodic characteristics (i.e. high fecundity, high GSI, small eggs, short reproductive periods) presented a higher degree of synchrony than species having equilibrium characteristics (i.e. low fecundity, low GSI, large eggs, long reproductive period). Species from both strategies should not greatly differ in their size at maturity, and no relationship was found between synchrony and size at maturity. Furthermore, no significant relationship was observed between synchrony and maximum body size (Fig. 2). These relationships were not greatly affected by removing taxonomical relatedness since correlation values between traits or synchrony

Fig. 2. Relationships between the degree of synchrony and life history traits for the considered species (Appendix A1) after removing taxonomical relatedness. Pearson's correlation coefficient and the corresponding P values for a one-sided test are given: \* $P < 0.05$ ; \*\* $P < 0.01$ ; ns = not significant.



before and after controlling for taxonomy were highly significant ( $P < 0.001$ ).

### Synchrony levels among strategies

Spatial synchrony computed from summed annual total catches by groups of species belonging to both strategies resulted in  $r = 0.46$  and  $r = 0.83$  for the equilibrium and periodic groups, respectively (Fig. 3). The difference between these two correlations was significant (permutation test:  $P = 0.02$ ), the periodic group of species showing a higher degree of synchrony than the equilibrium group. The gill net sampling procedure is such that only fish large enough to be caught by the smaller mesh size contribute to the total catch. In our case, this would correspond to fish at least one-year old. Thus, if a high discharge during the wet season is positively linked to young survival, then CPUE and discharge should be positively correlated with one year time lag or more. According to Table 1, correlations between time series of population fluctuations for periodic and equilibrium strategy groups and the regional discharge index at time lags of one, two and three years, showed better relationships for the periodic group, though not always sig-

nificant. This is consistent with the assumption that periodic species recruitment undergo hydrological variability more strongly than equilibrium species, and that this climate-based factor is at least partly responsible for the observed synchrony patterns.

### Discussion

The main general conclusion of our study is that population dynamics from different related species are not equally affected by synchronous stochastic effects (i.e. a Moran effect). As predicted, species having a periodic life history strategy, and therefore more linked to the synchronizing climatic factor (i.e. hydrology), did show a higher degree of spatial synchrony.

The observed differences in the degree of synchrony among species reflect a differential incidence of the present synchronizing mechanism (a Moran effect through spatially correlated hydrological variability) on different life history strategies. Although the life history construction proposed by Winemiller (1989) has not yet been explicitly tested, empirical data suggested the same triangular continuum for West African fish species (Lévêque and Paugy 1999). Our results support

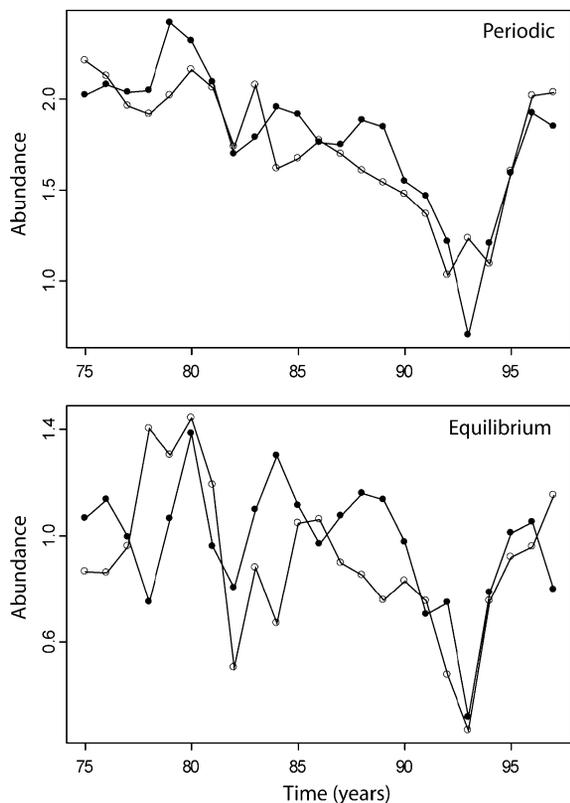


Fig. 3. Time series of annual total catches (log-transformed CPUE as in Tedesco et al. (2004)) by groups of species belonging to periodic and equilibrium strategies for site 1 (●) and site 2 (○).

Winemiller's hypothesis by comparing the strength of the relationship between strategies and climatic forcing. The periodic strategy maximizes fitness when environmental variation influencing survival during early life stages is periodic and predictable. In work on change in community structure before and after the construction of a dam in French Guiana, which modified the hydrological seasonality of the river, Ponton and Copp (1997) observed a major decrease in the abundance of Characiformes species (mainly periodic) at the expense of Perciformes species (mainly equilibrium). In seasonal tropical freshwaters, reproductive timing of periodic species is restricted to a short period of a few months

Table 1. Correlation coefficients between summed annual total catches by strategy for the period 1975–1986 and the regional climatic hydrology index provided by Mahé (1993) at different time lags. Corresponding P values of the differences between correlation values are given (ns = not significant).

Strategy	t-1	t-2	t-3
Periodic	0.51	0.42	-0.02
Equilibrium	0.37	-0.15	-0.43
P value	ns	<0.001	ns

of high waters (Fig. 4). The reproductive success of these species depends to great extent on the favorable conditions created by flooding and the temporary availability of floodplain habitats and resources (Winemiller 1989, Lévêque and Paugy 1999) resulting in a high degree of spatial synchrony. Hydrological data drawn from Mahé (1993) is merely a rough indicator and further studies are needed to properly assess the role of hydrology, for example by evaluating the extent of the yearly inundated floodplain area.

In contrast, equilibrium species are associated with a long breeding season (Fig. 4) and a high parental investment in individual offspring. Rather than being influenced by seasonal flood conditions, the reproductive success of these species is more strongly affected by local density dependent and independent factors (e.g. intra-specific resource competition, inter-specific trophic interactions and availability of spawning substratum) that can greatly differ between sites and species, resulting in reduced spatial synchrony. For example, in order to protect their territory, attract potential mates and finally spawn, equilibrium species need some kind of solid substrate that allows them to build different kinds of nests: *Oreochromis aureus*, *Tilapia* species, *Sarotherodon multifasciatus*, *Pelvicachromis pulcher* and *Protopterus annectens* build burrows on different substrates (Whyte 1975, Trewavas 1983, Martin and Taborsky 1997, Tweddle et al. 1998, Lévêque and Paugy 1999); *Auchenoglanis occidentalis* accumulates bivalve shells and gravels to build their nests (Ochi et al. 2001); *Gymnarchus niloticus* makes floating nest by uprooting and gathering aquatic weeds (Oladosu 1997, Lévêque and Paugy 1999); *Hepsetus odoe* produces foam-bubble nests among emergent reeds and sedges (Merron et al. 1990); and *Hemichromis fasciatus* and *Chrysichthys* species look for stone cavities or pieces of wood to spawn in (Whyte 1975, Oteme et al. 1996).

A potential bias in our results could come from sampling noise, as sampling noise decreases the observed spatial synchrony with regard to the actual one (Tedesco et al. 2004). Data for less abundant species in catches could be less accurate because their low catch rates may be due to inefficient and noisy sampling. As equilibrium species were generally less abundant in catches than periodic ones this may have introduced a bias concordant with the observed synchrony pattern. However, we did not detect a significant relationship between synchrony and log-transformed CPUE ( $r = 0.34$ ,  $P > 0.05$ ), and nearly identical sampling error values were found by Tedesco et al. (2004) for species from different strategies. Furthermore, considering guilds, we can expect that the influence of sampling noise would be minimized when species were aggregated into groups.

Paradis et al. (1999) and Koenig (1998) reported a positive link between one of the main synchronizing factors (dispersal) with its related species characteristic

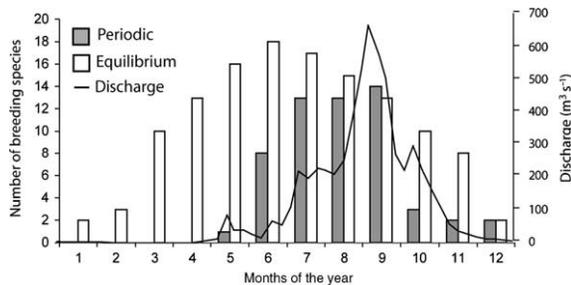


Fig. 4. Number of breeding species by month from January to December separated for periodic and equilibrium species from Appendix A1. The line shows an example year 1991 of the seasonal shape of the discharge at site 2.

(dispersal ability) in geographically connected populations, but most studies have failed to detect clear synchrony-species traits trends, other than for dispersal (Koenig 1998, Paradis et al. 1999, 2000, Burrows et al. 2002). This could be explained by the confounding effect that dispersal can produce on population dynamics evolving under environmental correlation. The relative contributions of dispersal and environmental correlation in the synchrony pattern are likely to be species dependent. Moreover, according to the Moran theorem (Moran 1953, Royama 1992), spatial synchrony in population dynamics should be independent of demographic characteristics of the species. This offers little hope for finding a general pattern between demographic features and environmentally induced spatial synchrony. However some demographic features may be associated to a life-history strategy that renders the species dependent on some regionally correlated factor. But it is likely that these relationships will be system or taxon specific (see Koenig and Leibold 2005 for an example of a very specific system). For instance in tropical freshwater fishes it is not fecundity per se which increases spatial synchrony. The pattern emerges because the periodic species, those that depend highly on seasonal flood to reproduce, tend to be fecund. Thus there is no guarantee that the relationship between fecundity and synchrony will still hold for other taxa than fishes, or for fishes in other climatic conditions.

For most species, we still lack a predictive understanding of the causes of synchronous or asynchronous population fluctuations, although this is crucial for evaluating species persistence since synchrony is related to some extent with extinction risk (Heino et al. 1997, Palmqvist and Lundberg 1998). Thus a general model allowing for the prediction of the level of synchrony based on biological features would be useful. Unfortunately this goal is beyond our present state of knowledge. However one of the main synchronizing agent has been identified here, and providing a sufficient knowledge of life history of the focal taxa, our study suggest that patterns can be found between synchrony and biological features. But conclusions drawn from such studies should be generalized with great caution.

**Acknowledgements** – The financial support which made this work possible came from a PhD fellowship of the IRD (Institut de Recherche pour le Développement) within the Research Unit 131. The World Health Organisation (WHO) Onchocerciasis Control Programme (OCP) has given the main part of the financial support for the aquatic monitoring. We are very grateful to T. Oberdorff, J. Trexler for their helpful comments on the manuscript, and to D. Paugy, Y. Fermon and the technical staff from the OCP for realizing the 23-year data sets. We thank Crane Rogers for improving the English of the text.

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Appendix A1 can be found at: [www.oikos.ekol.lu.se](http://www.oikos.ekol.lu.se)

Appendix A1. Available biological traits for 52 species.

Order Family Species	Authority	St1	St2	Maximal body size (mm)	Egg size (mm)	Relative fecundity (eggs/kg)	Maturity size (mm)	GSI	Time-span of reproductive period (months)	Multiple or fractionated spawn	Parental care	Strategy
Polypteriformes												
Polypteridae												
<i>Polypterus endlicheri</i> *	Heckel, 1849	1	1	630	2.5	15000	320	9.2	5		Yes	equilibrium
Osteoglossiformes												
Notopteridae												
<i>Papyrocranus afer</i>	Günther, 1868		1	590	3.6	531	431	2			Yes	equilibrium
Mormyridae												
<i>Marcusenius furcidens</i> *	Pellegrin, 1920	1	1	286	1.8	39250	228	14.4	3	Yes <sup>1</sup>	No <sup>1</sup>	intermediate
<i>Marcusenius senegalensis</i> *	Steindachner, 1870	1	1	321	1.3	14670	190	18.7	2	Yes	No	intermediate
<i>Marcusenius ussheri</i> *	Günther, 1867	1	1	305	1.7	51800	130	15.3	3	Yes <sup>1</sup>	No <sup>1</sup>	intermediate
<i>Mormyrops anguilloides</i> *	Linnaeus, 1758	1	1	1365	2.1	15550	397	11	6	Yes	No	equilibrium
<i>Mormyrus hasselquistii</i>	Valenciennes, 1846	1	1	480	1.85	24300	190	12	3	Yes	No <sup>1</sup>	equilibrium
<i>Mormyrus rume</i> *	Valenciennes, 1846	1	1	870	2.2	15820	340	8	5	Yes	No	equilibrium
<i>Petrocephalus bane</i>	Lacépède, 1803	1		183	1.3	46000	110		3	Yes	No <sup>1</sup>	intermediate
<i>Petrocephalus bovei</i> *	Valenciennes, 1846	1	1	100	1.4	61000	67	11.7	4	Yes	No	periodic
Characiformes												
Hepsetidae												
<i>Hepsetus odoe</i> *	Bloch, 1794	1	1	580	2.5	15150	60	8.4	6	Yes	Yes	equilibrium
Characidae												
<i>Alestes baremoze</i> *	Joannis, 1835	1	1	325	1.1	224100	175	11.5	2	No	No	periodic
<i>Brycinus imberi</i> *	Peters, 1852	1	1	167	1	211000	65	14.6		No	No	periodic
<i>Brycinus longipinnis</i>	Günther, 1864		1	101	0.95	166000	46	13.5		No	No	periodic
<i>Brycinus macrolepidotus</i> *	Valenciennes, 1849	1	1	530	1.2	182400	180	13.8		No	No	periodic
<i>Brycinus nurse</i> *	Rüppell, 1832	1	1	218	1.05	339000	80	19.5	3	No	No	periodic
<i>Hydrocynus forskalii</i> *	Cuvier, 1819	1	1	780	1.05	127300	150	8.2	4	No	No	periodic
<i>Hydrocynus vittatus</i>	Castelnau, 1861		1	550	0.65	201000	300		3	No <sup>1</sup>	No <sup>1</sup>	periodic
Cypriniformes												
Cyprinidae												
<i>Labeo coubie</i> *	Rüppell, 1832	1	1	750	1.25	122000	200	8.6	3	No	No	periodic
<i>Labeo parvus</i> *	Boulenger, 1902	1	1	350	1	292000	100	19	3	No	No	periodic

Order Family Species	Authority	St1	St2	Maximal body size (mm)	Egg size (mm)	Relative fecundity (eggs/kg)	Maturity size (mm)	GSI	Time-span of reproductive period (months)	Multiple or fractionated spawn	Parental care	Strategy
<i>Labeo roseopunctatus</i>	Paugy, Guégan & Agnèse, 1989	1		203								periodic
<i>Labeo senegalensis</i> *	Valenciennes, 1842	1	1	550	1	181500	175	14.3	4	No	No	periodic
<i>Raiamas senegalensis</i>	Steindachner, 1870	1	1	205	1.35	47700	100	8.3	7	No		intermediate
Siluriformes												
Clariidae												
<i>Clarias anguillaris</i>	Linnaeus, 1758	1	1	605	1.3	62000	235	9.6	5	Yes	No	intermediate
<i>Clarias gariepinus</i>	Burchell, 1822		1	1500	1.8	43700	330	17	5	No	No	intermediate
<i>Heterobranchus bidorsalis</i>	Geoffroy Saint-Hilaire, 1809	1		688	1.5'	22260	285	15.5	4	No <sup>1</sup>	Yes <sup>1</sup>	intermediate
<i>Heterobranchus isopterus</i>	Bleeker, 1863	1	1	430	1.5	122000	255	13.8		No	Yes <sup>1</sup>	intermediate
<i>Heterobranchus longifilis</i>	Valenciennes, 1840	1	1	505	1.6	65000		15	8	No <sup>1</sup>	Yes	intermediate
Schilbeidae												
<i>Schilbe intermedius</i> *	Rüppell, 1832	1	1	500	0.8	505000	125	17	2	No	No	periodic
<i>Schilbe mandibularis</i> *	Günther, 1867	1	1	300	0.85	217000	154	9.6	4	No	No	periodic
<i>Schilbe mystus</i>	Linnaeus, 1758	1	1	350	0.85	253700	100	8	4	No	No	periodic
Bagridae												
<i>Auchenoglanis occidentalis</i>	Valenciennes, 1840	1	1	480	2.6	4150	123	4	4		Yes	equilibrium
<i>Chrysichthys auratus</i>	Geoffroy Saint-Hilaire, 1808		1	270	2.2	11980	140	13.2	7	Yes	Yes <sup>1</sup>	equilibrium
<i>Chrysichthys maurus</i> *	Valenciennes, 1839	1	1	415	2.3	19400	120	16.7	6	No	Yes	equilibrium
<i>Chrysichthys nigrodigitatus</i> *	Lacépède, 1803	1	1	485	2.5	17000	195	19.5	5	No	Yes	equilibrium
Mochokidae												
<i>Synodontis bastiani</i> *	Daget, 1948	1	1	202	1.2 <sup>1</sup>	107000 <sup>1</sup>	80 <sup>1</sup>	15.4 <sup>1</sup>	3	No <sup>1</sup>	No <sup>1</sup>	periodic
<i>Synodontis comoensis</i>	Daget & Lévêque, 1981	1		174						No <sup>1</sup>	No <sup>1</sup>	periodic
<i>Synodontis ocellifer</i>	Boulenger, 1900		1	360	0.9	126300	151	26.3	5	No	No	periodic
<i>Synodontis schall</i> *	Bloch & Schneider, 1801	1	1	370	1.2	125000	150	11.5	4	No	No	periodic
Malapteruridae												
<i>Malapterurus electricus</i>	Gmelin, 1789	1	1	1220		11900	160		3		Yes	equilibrium

## Appendix A1 (Continued)

Order Family Species	Authority	St1	St2	Maximal body size (mm)	Egg size (mm)	Relative fecundity (eggs/kg)	Maturity size (mm)	GSI	Time-span of reproductive period (months)	Multiple or fractionated spawn	Parental care	Strategy
Perciformes												
Cichlidae												
<i>Chromidotilapia guntheri</i> *	Sauvage, 1882	1	1	145	2.25	8100	60	3.4	9	Yes	Yes	equilibrium
<i>Hemichromis bimaculatus</i>	Gill, 1842	1	1	92	1.2	11700	45	7.1	9	Yes	Yes	equilibrium
<i>Hemichromis fasciatus</i> *	Peters, 1852	1	1	204	1.5	30000	90	4.5	8	Yes	Yes	equilibrium
<i>Oreochromis aureus</i>	Steindachner, 1864	1		370	2.5	1800	190		9	Yes	Yes	equilibrium
<i>Oreochromis niloticus</i>	Linnaeus, 1758		1	395	2.55	3720	160	2.6	9	Yes	Yes	equilibrium
<i>Sarotherodon galileus</i> *	Linnaeus, 1758	1	1	340	2.3	3900	145	3	9	Yes	Yes	equilibrium
<i>Tilapia dageti</i>	Thys van den Audenaerde, 1971		1	310				4.8	7	Yes	Yes	equilibrium
<i>Tilapia zillii</i> *	Gervais, 1848	1	1	210	1.6	38600	70	4	7	Yes	Yes	equilibrium
Centropomidae												
<i>Lates niloticus</i> *	Linnaeus, 1762	1	1	1800	0.7	86000	520	4.5	4	No	No	periodic
Anabantidae												
<i>Ctenopoma kingsleyae</i>	Günther, 1896	1	1	135	1.05	103000	115	8.7			Yes	periodic
Channidae												
<i>Parachanna obscura</i>	Günther, 1861		1	341	1.3	19640	245	3.9	5		Yes <sup>1</sup>	intermediate
Synbranchiformes												
Mastacembelidae												
<i>Aethiomastacembelus nigromarginatus</i>	Boulenger, 1898	1	1	330	2.35	19800	150	12.5	3	No		equilibrium

\*Species considered for testing synchrony vs life history traits

<sup>1</sup>data from closely related species