

# SPATIAL SYNCHRONY OF A HIGHLY ENDEMIC FISH ASSEMBLAGE (SEGREDO RESERVOIR, IGUAÇU RIVER, PARANÁ STATE, BRAZIL)

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(With 3 figures)

## ABSTRACT

In this study, patterns of spatial synchrony in population fluctuations (cross-correlation) of an endemic fish assemblage of a Neotropical reservoir (Segredo Reservoir, Iguazu River, Paraná State, Brazil) were reported. First, the level of population synchrony for 20 species was estimated. Second, population synchrony was correlated, using the Mantel test, with geographical distances among sites ( $n = 11$ ) and also environmental synchrony (temperature). Nine species presented significant correlations between spatial synchrony and geographic distances (*Astyanax* sp. b, *Astyanax* sp. c, *Pimelodus* sp., *Hoplias malabaricus*, *Crenicichla iguassuensis*, *Hypostomus derbyi*, *Hypostomus myersi*, *Rhamdia branneri*, and *R. voulezi*). Considering the ecology of the species and the significant relationship between population and environmental synchronies, it seems that environmental stochasticity is the most plausible hypothesis in explaining the observed synchrony patterns.

*Key words:* spatial synchrony, fish assemblage, reservoirs.

## RESUMO

### Sincronia espacial de uma assembléia de peixes endêmica (reservatório de Segredo, rio Iguazu, Paraná, Brasil)

Neste estudo, os padrões de sincronia espacial de uma assembléia de peixes endêmica em um reservatório neotropical (reservatório de Segredo, rio Iguazu, Paraná, Brasil) foram descritos. Primeiro, foi estimado o nível de sincronia (correlação entre as densidades ao longo do tempo) para 20 espécies. Segundo, a matriz de sincronia populacional foi correlacionada, utilizando o teste de Mantel, com a distância geográfica entre os locais ( $n = 11$ ) e com a sincronia ambiental (temperatura da água). Nove espécies apresentaram correlações significativas entre sincronia espacial e distância geográfica (*Astyanax* sp. b, *Astyanax* sp. c, *Pimelodus* sp., *Hoplias malabaricus*, *Crenicichla iguassuensis*, *Hypostomus derbyi*, *Hypostomus myersi*, *Rhamdia branneri* e *R. voulezi*). Considerando a ecologia das espécies e a relação significativa entre a sincronia populacional e a sincronia ambiental, é possível inferir que estocasticidade ambiental é a hipótese mais plausível para explicar os padrões de sincronia detectados.

*Palavras-chave:* sincronia espacial, assembléia de peixes, reservatórios.

## INTRODUCTION

Temporal and spatial fluctuations in number of individuals are marked characteristics of all animal populations (Heino *et al.*, 1997; Lundberg *et al.*, 2000). Inspired by the seminal work of Elton & Nicholson (1942) and Moran (1953), the temporal dynamics in number of individuals from spatially distributed subpopulations are currently one of the main themes investigated by ecologists (Kendal *et al.*, 2000; Ylikarjula *et al.*, 2000; Grenouillet *et al.*, 2001).

The fact that conspecific populations fluctuate in synchrony over large spatial scales has turned a phenomenon known as spatial synchrony (see Koenig, 1999) into what is now considered a common ecological pattern. Several studies have convincingly demonstrated that local populations of different species present synchronized temporal dynamics (Koenig, 1998; Cattadori *et al.*, 1999; Shanker & Sukumar, 1999).

Spatial synchrony has several implications, among them that increasing spatial synchrony decreases the expected persistence of metapopulations (Hanski & Woiwod, 1993, and references therein). This is because if a harmful environmental event occurs over a large geographic area, all those that fluctuate synchronically suffer the same risk of being affected (Sutcliffe *et al.*, 1996). The validity of various metapopulation models and that of answers to many questions arising in population biology, including application issues (see Earn *et al.*, 1998, and Rohani *et al.*, 1999), depends on the degree of spatial synchrony (Hanski & Woiwod, 1993), as does conservation biology.

Dependence on the degree of synchrony between local populations and the distance that separates them is a second factor that should be quantified. Recurrently, the degree of synchrony between pairs of population levels off with increasing distance between them (Ranta *et al.*, 1995). This dependence may help in distinguishing processes that produce spatial synchrony (Hanski & Woiwod, 1993; Ranta *et al.*, 1999). Among the main causal processes possibly producing synchronized population dynamics are migration, regional

stochasticity, and the presence of nomadic predators. Basically, identifying one of these processes as the most important is the final objective of this research (Cattadori *et al.*, 1999).

Despite the importance of the theme, studies on spatial synchrony in fish are rare (Myers *et al.*, 1997; Lande *et al.*, 1999; Grenouillet *et al.*, 2001). To the best of our knowledge, they are inexistent for Neotropical freshwater fishes. Lack of familiarity with spatial synchrony patterns for Neotropical fish in general, and species of economic interest in particular, results from a paucity of historical data. However, due to legal requirements, data gathered by monitoring programs in Brazilian dammed rivers already provide enough information for beginning spatial synchrony studies on the dynamics of Neotropical fish populations.

The general objective of the present study was to quantify the spatial synchrony (at a specific level) of a fish assemblage in a recently created Neotropical reservoir. The following questions were addressed: (1) On short time scales and in an unstable environment, can the degree of synchrony be considered high, and (2) is there a relationship between synchrony (estimated for different species) and distance between the populations compared? In light of the results obtained, possible causal mechanisms behind spatial synchrony were discussed.

## METHODS

### *Study area*

With an 82.5 km<sup>2</sup> expanse and a drainage area of approximately 34,100 km<sup>2</sup>, the Segredo Reservoir (10 years old) was constructed in the Iguaçu River (Paraná State, Southern Brazil, 25°45' and 25°58'S and 51°30' and 52°05'W; Fig. 1). The Segredo Reservoir is the second one in a cascade of five reservoirs constructed in the main channel of the Iguaçu River, and the area it drains lies entirely within a subtropical-humid region with annual precipitation of 1,980 mm and no a dry season. Temperature values vary seasonally, averaging between 12 and 16°C in winter and 20 and 23°C in summer.

The Iguaçu River is of special interest for conservation biology because approximately 80%

of the fish species are endemic (Agostinho *et al.*, 1997), a probable consequence of geographic isolation produced by Iguaçú Falls, a 72-meter-high barrier, and at least two other falls.

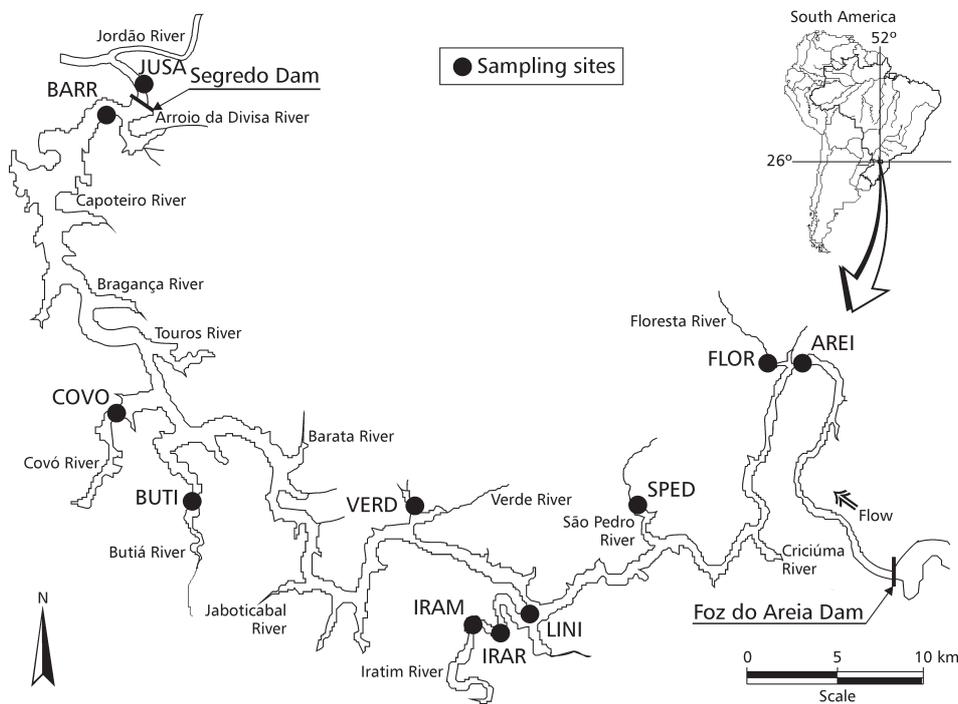
**Sampling**

This study included three sampling sites within the reservoir, seven others in tributaries, and another located downstream from the dam (Fig. 1). Samples were taken monthly, from March 1993 to February 1995, using gill nets (sizes varying from 3 to 14 cm knot-to-knot) set for 24 hours. Catch per unit of effort (CPUE in number of individuals per 1,000 m<sup>2</sup> caught by each gill net per 24 hours) was used as an abundance index. Monthly temperature values were recorded at all sites (°C, using a thermistor).

**Data analysis**

Spatial synchrony was estimated following methods described by Pyper & Peterman (1998). Autocorrelation was initially removed from each time series by fitting the first-order autoregressive

model  $X_t = pX_{t-1} + e_t$ , where  $X_t = \log(\text{CPUE}_t + 1)$ ,  $\text{CPUE}_t$  is the abundance index for month  $t$ ,  $p$  is the autoregressive coefficient, and  $e$  is the prewhitened series (white noise in the terminology used in temporal series; see Box & Jenkins, 1976). In this study, the first-differencing technique was also used to remove autocorrelation. The series of first differences is given by  $sX_t = X_t - X_{t-1}$ , where  $sX$  denotes the new first-differenced time series. (This is another very simple approach that is generally effective in removing autocorrelation (Pyper & Peterman, 1998).) Prewhitened ( $e$ ) and first-differenced ( $sX$ ) time series were then used to estimate the degree of spatial synchrony in the dynamics of conspecific populations. Transformed rather than original time series were used in calculating spatial synchrony in order to avoid spurious correlations due to autocorrelation generated by local dynamics and not by processes related to migration or regional stochasticity (see Hanski & Woiwod, 1993). In addition, these methods are effective to control Type I error rates in tests of correlations (Pyper & Peterman, 1998).



**Fig. 1** — Location of the eleven sampling sites in the Segredo Reservoir.

For each species, Pearson product-moment correlation coefficients (cross-correlations with lag zero) were calculated for all pairs of sampling sites ( $i$  and  $j$ ) using transformed time series (Hanski & Woiwod, 1993; Sutcliffe *et al.*, 1996; Bjørnstad *et al.*, 1999). Thus, for each species there are  $k = 55$  correlation coefficients ( $r_{ij}$ ), which is because data from  $n = 11$  sampling sites yield  $k = [(n \times n - 1) / 2]$  pairwise correlations (for  $i \neq j$ ) (Koenig, 1999). Two species-specific measures of spatial synchrony were used. The arithmetic mean of the 55 ( $r_{ij}$ ) values was used as a first species-specific measure of spatial synchrony. A bootstrap confidence interval for these means was estimated by sampling with replacement among the sampling sites (deleting cross-correlations arising from comparing a site with itself). The percentile bootstrap (with 5,000 bootstrap iterations) was used to construct the bootstrap confidence intervals (Bjørnstad *et al.*, 1999). Following the methods used by Hanski & Woiwod (1993), the intercept of the linear regression of  $r_{ij}$  against the geographic distances between sampling sites ( $d_{ij}$ ) was used as a second species-specific measure of spatial synchrony. This is a preferable measure when there is a significant relationship between  $r_{ij}$  and  $d_{ij}$  (Hanski & Woiwod, 1993; Ranta *et al.*, 1995).

The matrix of spatial synchrony for each species was transformed into a matrix of distance (chord) using the formula  $c_{ij} = \sqrt{(2 - 2r_{ij})}$ , where  $c_{ij}$  is the chord distance between sites  $i$  and  $j$ . In this case, values of  $c_{ij}$  equal to zero indicate that the temporal dynamics of local populations are perfectly correlated. Thereafter, the Mantel test was used to test the significance of the correlation between values of  $c_{ij}$  and  $d_{ij}$  (Euclidian distance between sampling points  $i$  and  $j$ ) (Shanker & Sukumar, 1999). Both matrices were previously normalized so that the Mantel statistic ( $m$ ) behaved as a product-moment correlation varying between  $-1$  and  $+1$  (Mantel, 1967; Fortin & Gurevitch, 1993). Due to the transformation of  $r_{ij}$  in  $c_{ij}$ , a positive value of  $m$  indicates that the degree of population synchrony decreases with increasing distance among the populations compared. In order to evaluate the significance of  $m$ , a randomization test was conducted. After each permutation the  $m$  statistic was calculated and the resulting values provided an empirical distribution (under the null hypothesis

of no relationship between matrices) that was then used for the significance test. For each species, 20,000 random permutations of the data were used to ensure relative stability in the estimated level of significance (Jackson & Somers, 1989).

The same procedures described above were used to analyze geographical synchrony in air temperature. Thus, the chord distance between sampling sites was derived from Pearson's correlation coefficient (cross-correlations with lag zero) between prewhitened time series. The resulting matrix thus reflects the similarity level in the pattern of air temperature variation among sampling sites. Following the application of the procedures previously referred to, Mantel tests were used to evaluate the relative influence of spatially correlated environmental stochasticity on the spatial synchrony level in the dynamics of fish populations.

In this study, the model proposed by Hanski & Woiwod (1993) was used to evaluate the relative roles played by correlated environmental fluctuations (the Moran effect) and migration on the level of population synchrony. According to Hanski & Woiwod (1993), a positive relationship between maximum growth rate (see below) and the degree of spatial synchrony is consistent with the migration hypothesis. This prediction may be tested by assuming that species with high maximum population growth rates present a greater degree of intrinsically generated variability than species with low maximum population growth rates. Therefore, application of this model requires for each species measures of population synchrony, population variability, and growth rate. Following Hanski & Woiwod (1993), a species-specific measure of spatial synchrony was provided by the  $y$ -intercept of the linear regression of  $r_{ij}$  against the geographic distances between sampling sites ( $d_{ij}$ ). For a given species, the arithmetic mean of the standard deviation values estimated for each sampling site (i.e., standard deviation of  $X_t$ ) was used as a species-specific measure of population variability. There are no data to estimate intrinsic growth rate for every species. As an alternative, the maximum value of  $\log(\text{CPUE}_{t+1}/\text{CPUE}_t)$  was calculated for each time series with no zero. A species-specific measure of maximum growth rate was calculated by averaging these values across conspecific populations. Linear multiple regression

analysis was used to test the model proposed by Hanski & Woiwod (1993). Thus, the degree of species-specific spatial synchrony was regressed against maximum growth rate and population variability.

## RESULTS

Captured individuals belonged to 7 orders, 13 families, 21 genera, and 40 species. The 20 most abundant species were analyzed in this study (see Table 1). The high number of species designed with epithets is explained by endemism. However, these clearly constitute different morphotypes, which justified their treatment as distinct taxa in this paper.

Species-specific spatial synchronies, as indicated by the  $y$ -intercept of the linear regression of  $r_{ij}$  against  $d_{ij}$ , estimated by either prewhitening or first-differencing the original time series strongly correlated with each other ( $r = 0.95$ ;  $n = 20$  species). Thus, only the results obtained with the last method are presented.

Considering the different species, the mean spatial synchrony (cross-correlation) between the 11 sites varied from  $-0.01$  to  $0.31$ . For mean spatial synchrony, the confidence intervals that are positive indicate species with significantly regionalized dynamics (Table 2). *C. iguassuensis*, *Astyanax* sp. c, *H. myersi*, *P. gymnodontus*, and *H. derbyi* stand out among them. Judging by the confidence intervals, the species that did not have regionalized dynamics (spatial synchrony) were *Ancistrus* sp., *Astyanax* sp. e, *Pimelodus ortmanni*, *R. branneri*, and *R. voulezi*. However, there were significant relationships between synchrony (chord transformed) and distance (see results below). These results indicate that the mean of all correlation coefficients is an unreliable species-specific measure of population synchrony (Hanski & Woiwod, 1993; Ranta *et al.*, 1999), especially for *R. branneri* and *R. voulezi*.

For nine species, the degree of synchrony was significantly correlated with distance among the sampling sites (Table 3). However, the negative relationship between synchrony ( $r_{ij}$  values) and distance ( $d_{ij}$ ) was more evident for those species that presented significant regionalized dynamics (Table 2 and Fig. 2).

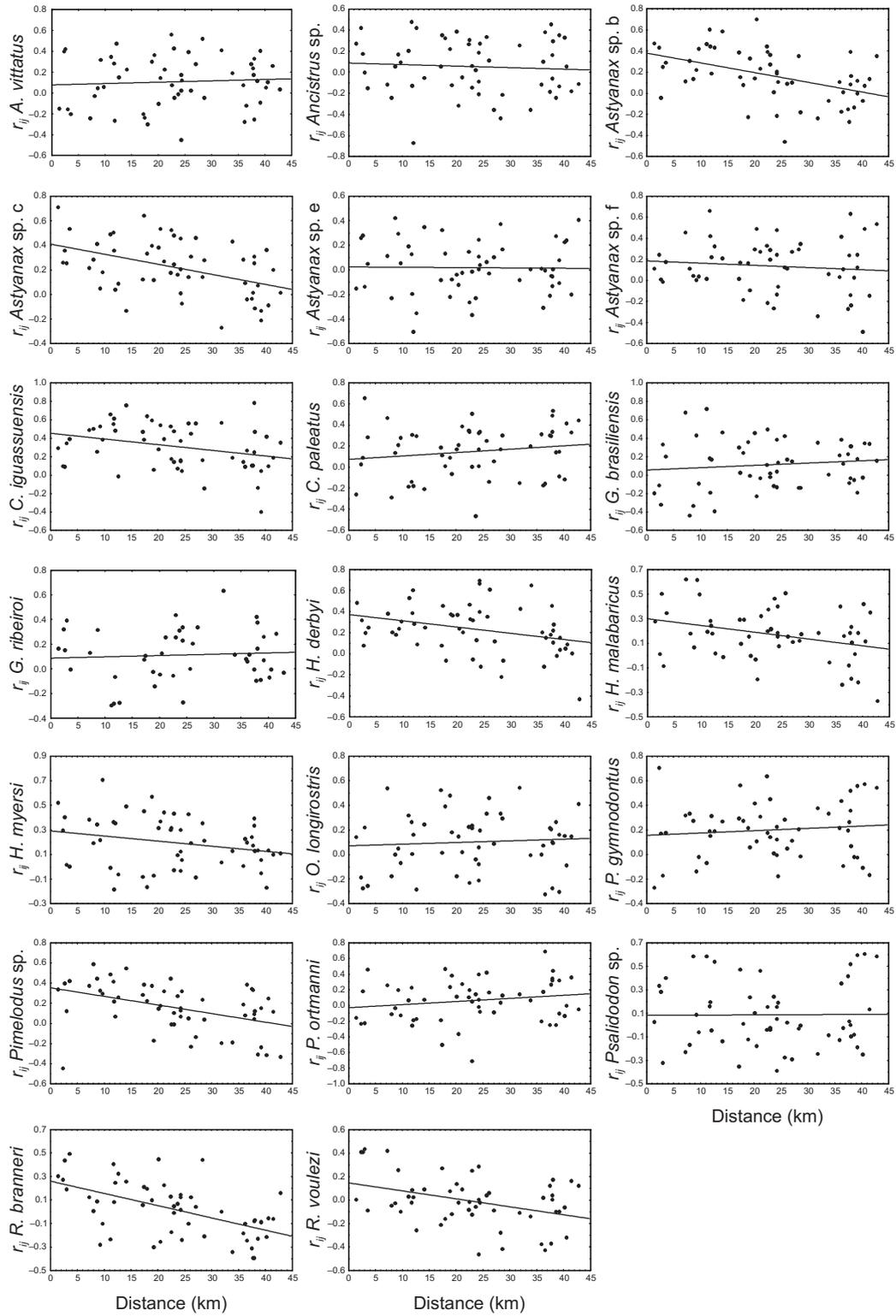
Spatial synchrony in air temperature dynamics was significant ( $CI_{95\%} = 0.30, 0.46$ ). The symmetric matrix associated with this variable (previously transformed into a chord distance matrix) was significantly related with the geographic distance matrix ( $m = 0.73$ ;  $p = 0.0001$ ). Thus, using the correlation coefficients, a clear decline in environmental synchrony with increasing distance between sampling sites was also observed (Fig. 3;  $y$ -intercept =  $0.79$ ).

The relationships between population synchrony and environmental synchrony were assessed using data from those species with significantly regionalized dynamics (Table 2) or those with a significant relationship between population synchrony and geographical distance (Table 3). For seven species, the Mantel test indicates a significant relationship between population synchrony and environmental synchrony matrices (*Astyanax* sp. b, *Astyanax* sp. c, *H. derbyi*, *H. myersi*, *Pimelodus* sp., *R. branneri*, *R. voulezi*; Table 3).

According to multiple regression analysis, regression coefficients for maximum growth rate and population variability were not significant. Thus, population synchrony was uncorrelated with both explanatory variables (Table 4). Multicollinearity problems were not detected in this analysis.

## DISCUSSION

Synchrony values for the fish assemblage analyzed in this study were inferior to those obtained in other studies (Sutcliffe *et al.*, 1996; Myers *et al.*, 1997; Lande *et al.*, 1999). As fish dispersal is generally highly constrained over large areas, especially in the Iguaçu River, we could expect fish to show less synchrony than other groups (Grenouillet *et al.*, 2001). In addition to the clear distinction of taxonomic groups as well as the life-histories and ecosystems analyzed, all of which produce intrinsic ecological differences, various other characteristics may explain the variation in the degree of spatial synchrony detected. Among these characteristics, the following two may be considered important: number of local populations (Ylikarjula *et al.*, 2000) and both temporal (Thompson & Page, 1989) and spatial (Hanski & Woiwod, 1993) scales analyzed.



**Fig. 2** — Relationship between population synchrony and distance for the 20 species analyzed in this study (see results of the Mantel test in Table 3). Species names are inserted.

TABLE 1

Species ranks, mean abundance (expressed in individuals/1,000 m<sup>2</sup> net/24 hours), and standard deviations for the 20 most abundant species in the Segredo Reservoir. Mean = arithmetic mean of the temporal means obtained in the 11 sampling sites. Standard deviation = arithmetic mean of the temporal standard deviations estimated in the 11 sampling sites. For both statistics, minimum and maximum values are reported.

Species	Ranks	Means			Standard deviation	
		Mean	Min.	Max.	Min.	Max.
<i>Apareiodon vittatus</i>	7	11.99	2.89	30.39	4.26	41.17
<i>Ancistrus</i> sp.	20	2.16	0.05	3.79	0.19	7.51
<i>Astyanax</i> sp. b	2	119.13	72.77	204.07	45.73	182.93
<i>Astyanax</i> sp. c	1	131.89	26.18	302.56	33.59	301.91
<i>Astyanax</i> sp. e	17	3.50	0.20	9.55	0.49	10.07
<i>Astyanax</i> sp. f	5	21.58	3.36	46.66	4.81	50.73
<i>Crenicichla iguassuensis</i>	11	8.90	2.00	16.23	2.77	30.73
<i>Corydoras paleatus</i>	10	9.99	0.49	69.67	1.03	149.90
<i>Geophagus brasiliensis</i>	14	4.51	1.38	11.85	2.18	18.89
<i>Glanidium ribeiroi</i>	16	3.58	0.00	13.53	0.00	45.67
<i>Hypostomus derbyi</i>	9	10.34	0.10	37.63	0.48	70.93
<i>Hoplias malabaricus</i>	8	10.89	4.15	18.36	4.04	19.51
<i>Hypostomus myersi</i>	3	37.38	0.65	169.06	1.07	187.37
<i>Oligosarcus longirostris</i>	6	12.87	5.93	26.83	5.70	26.07
<i>Psalidodon gymnodontus</i>	13	5.35	0.39	13.60	1.12	17.08
<i>Pimelodus ortmanni</i>	15	4.04	0.16	17.20	0.32	22.23
<i>Pimelodus</i> sp.	4	28.67	7.09	50.07	14.51	51.21
<i>Psalidodon</i> sp.	12	6.09	0.49	27.38	0.97	32.95
<i>Rhamdia branneri</i>	18	3.31	0.86	5.73	1.04	6.30
<i>Rhamdia voulezi</i>	19	2.74	1.55	4.18	1.51	4.72

In the present study, the number of locations is comparable, or even greater, than those considered in similar research (e.g., Ranta *et al.*, 1997; Shanker & Sukumar, 1999). The spatial scale also seems adequate in view of the fact that the sampling sites were widely distributed. The influence of the relatively few months analyzed ( $n = 24$ ), which may have jeopardized detection of correlations was, however, minimized by the first-differencing technique. According to Thompson & Page (1989)

and Pyper & Peterman (1998), if high frequency (i.e., rapid changes in CPUE) components of variability are the dominant source of covariation, then first-differencing may be useful because it should increase covariation and the statistical power to detect it by removing low frequency variability that obscures the detection of that covariation. Thus, it may be assumed that the available data was generally adequate for estimating the degree of spatial synchrony.

TABLE 2

Spatial synchrony means, standard deviations (SD), minimum values (Min), maximum values (Max), and 95% confidence intervals (CI) estimated for each species ( $k = 55$  cross-correlations values for each species).

Species	Means	SD	Min.	Max.	CI ( $\pm 95\%$ )
<i>Apareiodon vittatus</i>	0.11	0.24	-0.45	0.56	0.041-0.173
<i>Ancistrus</i> sp.	0.02	0.27	-0.70	0.50	-0.058-0.088
<i>Astyanax</i> sp. b	0.17	0.25	-0.46	0.70	0.099-0.233
<i>Astyanax</i> sp. c	0.22	0.22	-0.27	0.71	0.161-0.279
<i>Astyanax</i> sp. e	0.02	0.21	-0.50	0.42	-0.040-0.075
<i>Astyanax</i> sp. f	0.14	0.25	-0.49	0.66	0.071-0.206
<i>Crenicichla iguassuensis</i>	0.31	0.24	-0.39	0.78	0.245-0.377
<i>Corydoras paleatus</i>	0.15	0.24	-0.46	0.65	0.084-0.215
<i>Geophagus brasiliensis</i>	0.11	0.26	-0.44	0.72	0.042-0.182
<i>Glanidium ribeiroi</i>	0.11	0.21	-0.29	0.63	0.050-0.177
<i>Hypostomus derbyi</i>	0.24	0.23	-0.43	0.70	0.172-0.297
<i>Hoplias malabaricus</i>	0.17	0.21	-0.37	0.62	0.115-0.232
<i>Hypostomus myersi</i>	0.20	0.21	-0.18	0.71	0.140-0.254
<i>Oligosarcus longirostris</i>	0.10	0.23	-0.32	0.55	0.038-0.166
<i>Psalidodon gymnodontus</i>	0.20	0.23	-0.27	0.70	0.138-0.261
<i>Pimelodus ortmanni</i>	0.06	0.27	-0.71	0.69	-0.009-0.137
<i>Pimelodus</i> sp.	0.16	0.24	-0.44	0.59	0.092-0.223
<i>Psalidodon</i> sp.	0.09	0.28	-0.39	0.61	0.013-0.166
<i>Rhamdia branneri</i>	0.02	0.23	-0.39	0.50	-0.042-0.083
<i>Rhamdia voulezi</i>	-0.01	0.21	-0.46	0.43	-0.070-0.048

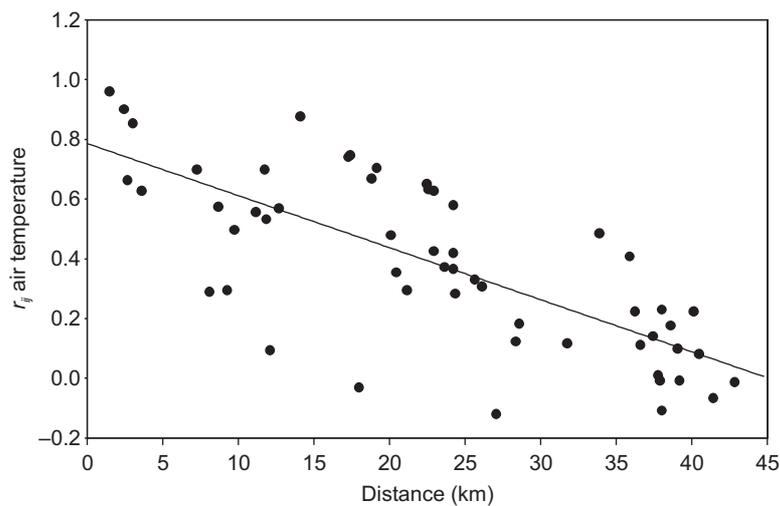


Fig. 3 — Relationship between geographic synchrony in air temperature and distance.

TABLE 3

Results of the Mantel test evaluating the relationship between spatial synchrony and geographical distance. Spatial synchrony matrices significantly related to geography distance were compared with environmental synchrony (air temperature). The values of the Mantel statistic and the significance levels (between parentheses) are presented.

Species	Distance (km)	Air temperature °C
<i>Apareiodon vittatus</i>	-0.05 (p = 0.3865)	
<i>Ancistrus</i> sp.	0.07 (p = 0.2932)	
<i>Astyanax</i> sp. b	<b>0.45 (p = 0.0031)</b>	<b>0.45 (p = 0.002)</b>
<i>Astyanax</i> sp. c	<b>0.45 (p = 0.0052)</b>	<b>0.43 (p = 0.003)</b>
<i>Astyanax</i> sp. e	-0.05 (p = 0.3657)	
<i>Astyanax</i> sp. f	0.07 (p = 0.2823)	
<i>Crenicichla iguassuensis</i>	<b>0.29 (p = 0.0382)</b>	0.12 (p = 0.184)
<i>Corydoras paleatus</i>	-0.15 (p = 0.1439)	
<i>Geophagus brasiliensis</i>	-0.06 (p = 0.3306)	
<i>Glanidium ribeiroi</i>	-0.06 (p = 0.3673)	
<i>Hypostomus derbyi</i>	<b>0.28 (p = 0.0434)</b>	<b>0.40 (p = 0.0042)</b>
<i>Hoplias malabaricus</i>	<b>0.31 (p = 0.0217)</b>	0.12 (p = 0.1971)
<i>Hypostomus myersi</i>	<b>0.27 (p = 0.0395)</b>	<b>0.27 (p = 0.0275)</b>
<i>Oligosarcus longirostris</i>	-0.06 (p = 0.3675)	
<i>Psalidodon gymnodontus</i>	-0.09 (p = 0.2669)	
<i>Pimelodus ortmanni</i>	-0.19 (p = 0.0929)	<b>0.28 (p = 0.0253)</b>
<i>Pimelodus</i> sp.	<b>0.45 (p = 0.0017)</b>	
<i>Psalidodon</i> sp.	-0.02 (p = 0.4810)	
<i>Rhamdia branneri</i>	<b>0.55 (p = 0.0001)</b>	<b>0.42 (p = 0.0018)</b>
<i>Rhamdia voulezi</i>	<b>0.40 (p = 0.0027)</b>	<b>0.36 (p = 0.0067)</b>

TABLE 4

Results of a multiple regression analysis of population synchrony (intercept of the relationship between population synchrony and distance) regressed against population variability and maximum increase.

Variable	Partial coefficient	t	P	F	R <sup>2</sup>
Populational variability	0.11	0.45	0.66	0.59	6.57%
Maximum increase	0.27	1.08	0.29		

A decline in population synchrony between sites as the distance between them increases is the main pattern that emerges in the studies of spatially structured populations (Lande *et al.*, 1999; Koenig, 1999; Ranta *et al.*, 1999). This pattern was true for 9 of the 20 species analyzed in this study. Although interesting and with conservation biology implications (Hanski & Woiwod, 1993; Ranta *et al.*, 1999; Kendall *et al.*, 2000), the detection of decline in synchrony with increase in distance between locations is not sufficient to identify the main mechanism that engenders population synchronization. In fact, at least three processes may be discerned as causal agents of this pattern, i.e., (1) the presence of nomadic predators moving between areas containing high densities of prey ("predation" hypothesis); (2) dispersal (migration hypothesis), and (3) spatially correlated environmental stochasticity (Moran effect) (Koenig, 1999; Hudson & Cattadori, 1999; Kendall *et al.*, 2000).

In this study, the first two hypotheses listed above are less probable. For example, the migration hypothesis is doubtful since there are no large migrators in the Iguaçú river basin. Unlike the fish fauna of other rivers of the Paraná river basin, those developing in the Iguaçú River confront several obstacles (Suzuki & Agostinho, 1997; Júlio Jr. *et al.*, 1997).

The only genus registered that includes migratory species, such as those observed in other basins, was *Pimelodus* (Agostinho *et al.*, in press). However, there is no evidence that species of this genus in the Iguaçú basin present similar behavior. The predation hypothesis is also dubious in view of the fact that characteristic predators in the area of study are generally sedentary (*H. malabaricus*, *Rhamdia*, *Crenicichla*) or whose migrations are short (*O. longirostris*). In addition, except for *Astyanax* spp., species with significant relationships between synchrony levels and geographic distance were either not registered in the diet of piscivores or registered at very low frequencies. Even in the juvenile phases these species are not consumed with great frequency (Hahn *et al.*, 1997; Gealh & Hahn, 1998).

We can expect the synchronizing effect of temperature (mainly driven by region-wide climatic factors) to be more important for fish, which are poikilotherms, than they are for homeotherms (Grenouillet *et al.*, 2001). Thus, temporal dynamics of the environment (spatially correlated) are the most

probable explanation for the patterns detected in this study.

In addition, a positive relationship between maximum population increase and spatial synchrony, expected according to the migration hypothesis, was not found. In this way, the evaluation of the model proposed by Hanski & Woiwod (1993) also demonstrates that patterns of spatial synchrony for fish assemblages in the Segredo Reservoir are probably caused by environmental stochasticity. It can be concluded from this study that, although estimated degrees of synchrony for the species analyzed are lower in relation to other studies, they may be detected in a relatively short time scale, in a recently-formed environment, and in a comparatively high number of species.

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