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Effects of food web structure and resource subsidies on the patterns and mechanisms of temporal coherence in a tropical coastal lagoon: an experimental mesocosm approach

Efeitos da estrutura da teia trófica e de subsídios de recursos nos padrões e mecanismos de coerência temporal em uma lagoa costeira tropical: uma abordagem experimental em mesocosmos

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Abstract: Aim: The study of the patterns and mechanisms of temporal coherence of ecological variables among lakes has become an important area of limnology. However, no study to date has experimentally tested whether and how resource subsidies and food web configuration affect the patterns and mechanisms of temporal coherence of limnological variables. We conducted a field mesocosm experiment to test the following hypotheses: (*i*) nutrient enrichment would reduce the temporal coherence of system variables; (*ii*) fish predation would enhance the temporal coherence of system variables; and (*iii*) the strength of temporal coherence decreases from physical (water transparency), to chemical (dissolved oxygen concentration [DO]) to biological variables (total zooplankton biomass). **Methods:** For 11 weeks, we manipulated fish presence and nutrient (N and P) concentration in a 2 × 2 factorial design in sixteen within-lake enclosures installed in a tropical coastal lagoon. Coherence was estimated by pair-to-pair Pearson's moment correlations of the temporal trajectories of each response variable among enclosures of the same treatment. **Results:** Fish presence only enhanced the temporal coherence of zooplankton biomass, whereas contrary to our expectations, nutrient addition enhanced the temporal coherence of [DO]. The strength of the individual effects of fish and nutrients on temporal coherence was affected by variable identity, but this variation did not occur in a consistent pattern across variables. However, the interactive effects of fish and nutrients on the temporal coherence of the three variables monitored were not statistically significant. **Conclusions:** Our results indicate that local factors, such as fish presence and nutrient availability, may affect the temporal coherence of several system variables, but these effects are better predicted by the strength of direct interactions between the local factor and the variable than by the identity of the variable itself. We conclude that eutrophication and overfishing may alter the coupling of spatial and temporal dynamics of some ecosystem variables.

Keywords: eutrophication, temporal synchrony, stability, shallow lakes, fish, predation.

Resumo: Objetivos: Estudos sobre os padrões e mecanismos de coerência temporal de variáveis ecológicas entre lagos têm se tornado um tema importante na limnologia. Até o momento, nenhum estudo testou se e como a oferta de recursos e a configuração da teia trófica afetam os padrões e mecanismos da coerência temporal de variáveis limnológicas. Nós conduzimos um experimento de mesocosmos em campo durante 11 semanas para testar as seguintes hipóteses: (*i*) a adição de nutrientes reduz a coerência temporal de variáveis ecossistêmicas; (*ii*) a predação por peixes potencializa a coerência temporal de variáveis ecossistêmicas e (*iii*) a coerência temporal é mais forte para variáveis físicas (transparência da água), intermediária para variáveis químicas (concentração de oxigênio dissolvido [OD]) e fraca para variáveis biológicas (biomassa zooplanctônica total). **Métodos:** Nós manipulamos a presença de peixe e a adição de nutrientes inorgânicos (N e P) em um desenho fatorial 2 × 2 em dezesseis mesocosmos instalados em uma lagoa costeira tropical. A coerência foi estimada por correlações de Pearson par-a-par das trajetórias temporais de cada variável resposta entre os mesocosmos de um mesmo tratamento. **Resultados:** A presença de peixes aumentou significativamente apenas a coerência temporal da biomassa zooplanctônica, e, contrário às nossas expectativas, a adição de nutrientes aumentou a coerência temporal da [OD]. A intensidade dos efeitos da presença de peixe e da adição de nutrientes sobre a coerência temporal foi afetada pela identidade da variável monitorada, mas não em um padrão consistente. No entanto, a interação da presença de peixe e adição de nutrientes não afetaram a coerência temporal de nenhuma variável monitorada. **Conclusões:** Nossos resultados indicam que a predação de peixes e a disponibilidade de recursos podem afetar significativamente padrões de coerência temporal, mas tais efeitos dependerão mais de efeitos diretos do fator local sobre a variável do que da identidade da própria variável. Concluímos que a eutrofização e a sobrepesca podem interferir no acoplamento da dinâmica espaço-temporal de algumas variáveis limnológicas.

Palavras-chave: eutrofização, sincronismo temporal, estabilidade, lagos rasos, peixes, predação.

1. Introduction

"Temporal coherence" refers to the degree of synchronicity among temporal trajectories of ecological units within a predefined realm (Magnuson et al., 1990; George et al., 2000). The temporal coherence of ecological variables is determined by local and regional factors that may influence the local dynamics of variables in similar ways (Kent et al., 2007). In aquatic sciences, the number of studies investigating the temporal coherence of environmental variables (i.e., biotic and abiotic) has increased in both temperate (Baines et al., 2000; George et al., 2004; Folster et al., 2005; Vogt et al., 2011) and tropical regions (Lansac-Toha et al., 2008; Caliman et al., 2010). The reason for this increased interest is associated with both fundamental and practical needs to consider lakes as dynamic ecological units that are connected and organized across a landscape, rather than spatially independent entities. From a more fundamental ecological view, limnologists are increasingly interested in knowing to what degree the dynamic properties of aquatic ecosystems are determined by large-scale regional factors or by local environmental factors (Lopes et al., 2011). From a more practical perspective, it will be important to know, under a global climate change scenario, whether and how the long-term behavior patterns of lakes will show common responses to environmental change across large geographic areas (Arnott et al., 2003). High temporal coherence would also be a fundamental premise justifying the extrapolation of results obtained in individual lakes to larger regions; this could considerably decrease the costs associated with monitoring a larger number of lakes (Stoddard et al., 1998). In addition, understanding patterns of temporal coherence and their mechanisms is important because it allows, in a regional context, decisions regarding management and environmental protection to be made based on functional aspects, rather than the structural ones usually employed.

Two general interrelated patterns have been observed in studies of the temporal coherence of lakes. The first is that temporally coherent patterns are strongest for physical variables, intermediate for chemical variables and weakest for biological variables (Livingstone and Dokulil, 2001; Kratz et al., 2003; Caliman et al., 2010). The second is the relatively weaker importance of individual local factors to determine temporal coherent patterns among lakes (Folster et al., 2005; Vogt et al., 2011), but see (Kling et al., 2000). The discrepancy of temporally coherent patterns among physical, chemical and biological variables has been attributed to differences in the number of processes that can affect such variables as well as to the sensitivity of these variables to broad-scale regional factors and/or more localized in-lake factors (Kratz et al., 2003). For example, physical variables such as water temperature are strongly affected by regional climate, which contributes to stronger coherent patterns among lakes across larger scales (Baines et al., 2000; Caliman et al., 2010). Water chemistry has also been shown to be temporally coherent for a myriad of variables (Folster et al., 2005), although to a lesser extent than physical properties because dissolved ions and other substances are also greatly affected by several local factors such as lake size and morphometry. Finally, biological variables are determined by an amalgam of controlling abiotic and biotic mechanisms, which make these variables more prone to be affected by multiple local factors (Baines et al., 2000) and subject to intrinsic species properties such as population growth rates and self-regulation (Hastings 1993). Local and intrinsic species properties, in turn, may interact in complex ways and exhibit asynchronous qualitative and quantitative variation across lakes. This complex interplay can affect the temporal trajectories of ecological variables in different directions, dampening the effects of local factors on temporal coherence (Kratz and Frost, 2000, and references therein).

However, the ecological knowledge that supports the aforementioned generalization comes from observational studies, which, although these studies were important to demonstrate the generality of temporally coherent patterns among lakes, they have weak power to rigorously test the strength and directions of the potential individual and interactive effects that local factors have on the temporal coherence of various limnological variables. Furthermore, spatial auto-correlation of local factors and larger-scale regional factors make it difficult to understand the relative importance of local and regional factors on temporal coherence. Finally, in a more applied context, individual local factors may represent the only suitable environmental factors that can be effectively managed. Therefore, understanding the consequences as well as the potentialities that individual representative local factors have on the patterns of temporal coherence among lakes may provide important knowledge for the conservation and/or restoration of lakes in a landscape context.

Inland aquatic ecosystems have been heavily impacted by cultural eutrophication and the trophic downgrading of their food webs originating from overfishing or the extirpation of top predators (Smith and Schindler, 2009; Estes et al., 2011). These impacts may be even worse in tropical coastal lagoons because of their distribution amidst densely populated areas and the absence of stringent environmental laws in most tropical countries, which makes these ecosystems particularly susceptible to the influence of human activities (Esteves et al., 2008). Eutrophication and the extinction of predators, alone or in combination, may severely alter the structure of aquatic food-webs, with important repercussions for the temporal dynamics and stability of populations, communities and ecosystem-level processes (Carpenter et al., 1985; Worm et al., 2002). Nutrient enrichment may alter the growth rates of organisms and destabilize interspecific interactions, generally leading to chaotic oscillatory behavior in populations and food web properties (Deangelis et al., 1989; Persson et al., 2001). On the other hand, predators are credited with dampening explosive growth or dominance in prey populations (Morin and Lawler, 1995), which may synchronize prey population variability (Ims and Andreassen, 2000). Therefore, local factors, such as nutrient enrichment and predation by fish, may have contrasting effects on the temporal coherence of aquatic communities and on the processes and environmental conditions that directly or indirectly rely on them.

In this study, we present the results of a field experiment carried out in a tropical coastal lagoon that was designed to test the individual and interactive effects of local factors (nutrient enrichment and fish predation) on the temporal coherence of physical (water transparency), chemical (dissolved oxygen concentration [DO]) and biological (total zooplankton biomass) variables. The experiment lasted for 11 weeks and was conducted in sixteen *in situ* enclosures, which provide real-life setting while maintaining experimental controllability. In this study, we aimed to test the hypothesis that the strength of temporal coherence decreases from physical, to chemical to biological variables (Caliman et al., 2010). We also predicted that (*i*) nutrient enrichment would reduce the temporal coherence of system variables; and (ii) fish predation would enhance the temporal coherence of system variables.

2. Methods

2.1. Experimental site

This study was conducted in Cabiúnas Lagoon, located at Restinga de Jurubatiba National Park, Rio de Janeiro, Brazil (22° 15’ S, 41° 40’ W) (Figure 1A). Cabiúnas is a distrophic freshwater coastal lagoon with a surface area of 0.35 km^2 and a mean depth of 2.0 m. The water is humic (13 mg C L^{-1} of dissolved organic carbon, DOC) and slightly acidic (pH 6.3) and has an average annual temperature of 23.6 °C (Caliman et al., 2010). During the study period, the mean total phosphorus and nitrogen concentrations of the water were 1.5 µM and 20 µM, respectively. The mean phytoplankton biomass estimated by chlorophyll-a (Chl-a) was 30 µg L^{-1}, and the mean Secchi disk depth was 0.6 m.

2.2. Enclosures and experimental design

The experiment was conducted over an eleven-week period using sixteen cylindrical, transparent polyethylene (thickness 0.6 mm) enclosures that were 2.0 m in diameter and 2.4 m tall (Figure 1B, C). The enclosures were equipped with iron rings at the top and bottom for structural stability and to attach floaters (top) and sediment anchors (bottom). All enclosures were open at the bottom to allow fish access to benthic food. However, to prevent fish from escaping without separating the sediment from the water column, nylon netting with a 1-cm

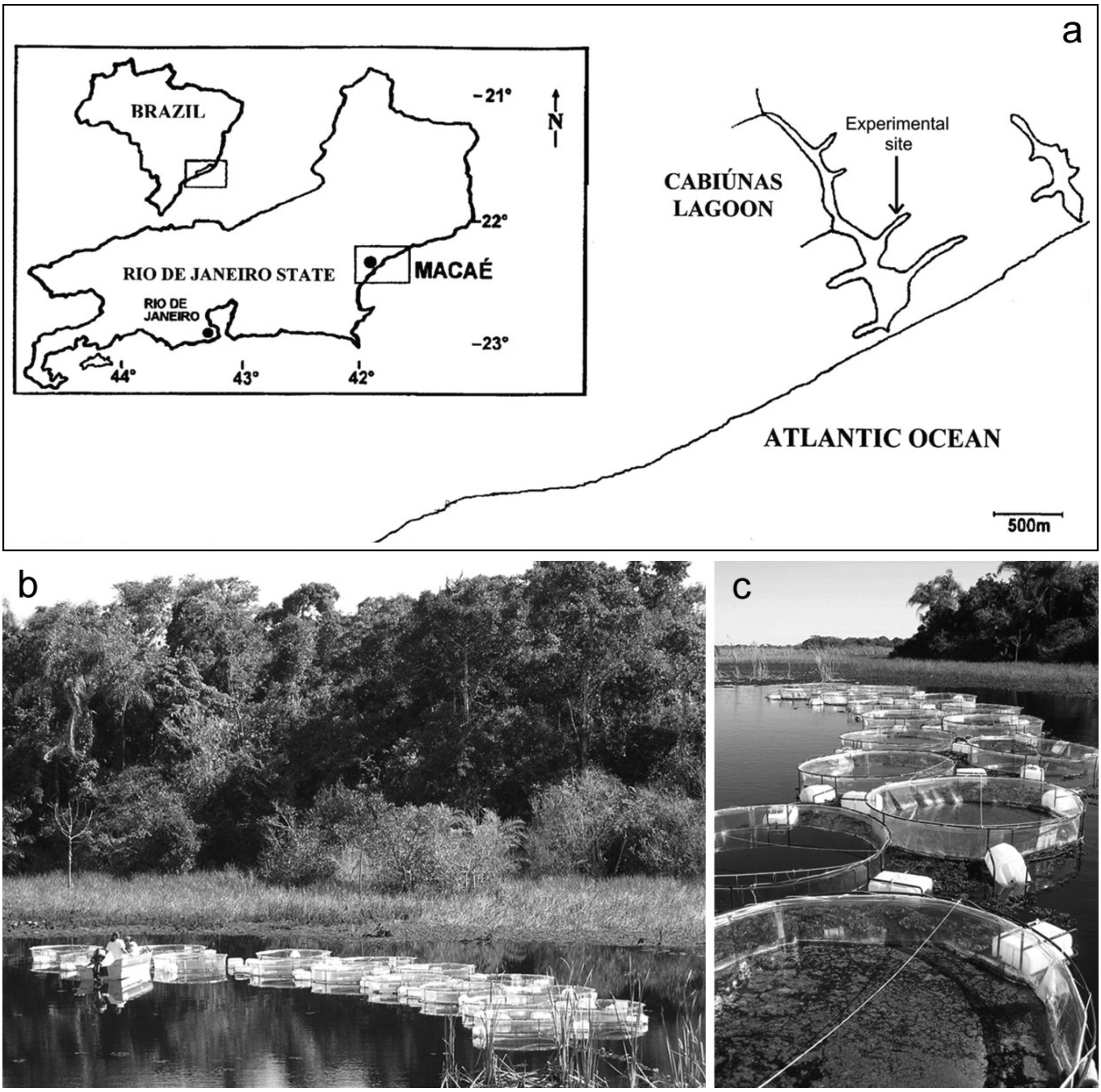

Figure 1. (a) Geographic location of Cabiúnas Lagoon in the Rio de Janeiro State, Brazil highlighting the experimental site (arrow). (b) The experimental site was near to the littoral region of the lagoon, but no macrophytes were included in enclosures. (c) Sixteen enclosures were installed adjacently to one another and experimental treatments were assigned in a block design.

mesh size was placed at the bottom of each enclosure and the bottom ring was pushed 0.1 m into the sediment. All enclosures were placed at a mean depth of ~2 m, so that the top ring of the enclosures reached 0.3 m above the water surface, protecting the enclosures against lagoon water ingression due to wave action. At this depth, the enclosed water volume was ~6,300 L.

The experimental design was a 2 × 2 orthogonal factorial combination of nutrients and fish (+/– nutrients and +/– fish). The treatments were "Control" (no fish or nutrient addition), "F" (only fish addition), "N" (only nutrient addition), and "N+F" (both fish and nutrient addition) and were replicated four times in a block design (1 treatment per block) (Figure 1C). This design allowed all experimental treatments and controls to be equally exposed to regional effects (i.e., climate, lagoon water temperature variation, sediment influence). Therefore, differences among treatments and the control could be safely attributed to the treatment effects.

2.3. Experimental setup

Experimental treatments were established one week after the enclosures were installed. This period allowed limnological conditions to stabilize after perturbations associated with installation. In the treatments with nutrient addition, the final concentrations of dissolved inorganic nitrogen (DIN - NH_4+NO_3) and phosphorus (DIP - PO_4) were kept constant throughout the experiment at 50 µM N (adjusted weekly with NH_4NO_3) and 10 µM P (adjusted weekly with KH_2PO_4 and K_2HPO_4), thereby maintaining a final N:P ratio of 5:1. Fish presence was manipulated by introducing 40 adult individuals of *Hyphessobrycon bifasciatus* Ellis 1911 (Characidae) into the enclosures, achieving a final density of 13 individuals m^{-2}, which is similar to that found in the littoral region of the Cabiúnas lagoon. Fish were caught near the experimental location with a net and were conditioned for 1 day in a fish tank-net inside the lagoon to allow for recovery from the stress associated with capture. Only active and healthy individuals were used in the experiment. Individual fish varied in size from 3 to 3.5 cm, and mass ranged from 0.3 to 0.5 g individual^{-1}. *H. bifasciatus* is an omnivorous fish that forages in both pelagic and benthic food webs and can feed on zooplankton, phytoplankton, periphyton and detritus (Guariento et al., 2010, 2011; Fonte et al., 2011). Fish mortality was low throughout the experiment (< 10%), as determined by daily enclosure inspections. The few fish that died were immediately replaced to maintain a constant fish density throughout the experiment.

2.4. Sampling and analysis

Sampling started 1 week (hereafter 1st week) after the establishment of experimental treatments (to guarantee that aquatic communities inside the enclosures had some time to begin responding to fish and nutrient additions), and enclosures were resampled after 2, 3, 4, 5, 6, 7 and 11 weeks, resulting in 77 days of experimental duration. Water transparency of each enclosure was estimated with a Secchi disk which gives a reliable and integrative measures of variation in water color and turbidity (Padial and Thomaz, 2008). Depth-integrated water samples were collected weekly from each enclosure by integrating individual water samples collected at depths of 10, 70, and 140 cm from the water surface with a van Dorn bottle. We used integrated water samples for assessment of DIN and DIP concentrations in each enclosure. The nitrate concentration was measured by flow injection analysis (FIA) after persulfate oxidation and nitrate reduction in a cadmium column with post-nitrite determination (APHA, 1989). The ammonium concentration was measured according to Solorzano (1969). Soluble reactive phosphorus was measured using the ammonium-molybdate method according to Golterman et al. (1978). The [DO] was measured at depths of 10, 70, and 140 cm from the water surface at noon with an oxymeter (YSI 85). Depth-integrated [DO] was obtained by averaging [DO] from the three depths. Zooplankton was sampled by vertical hauls of 1.6 m with a net with a 65-µm mesh size. Zooplankters were counted either in a Sedgewick-Rafter chamber under a microscope (rotifers, nauplii, cladocerans and meroplanktonic larvae) or in open chambers under a stereomicroscope (copepodites and adult copepods). Zooplankton biomass was estimated by weighing 20 individuals of each species (Mettler UMT2 microbalance), except for rotifers, whose biomass was obtained as average values from Ruttner-Kolisko (1977). The total zooplankton biomass was obtained by multiplying mean zooplankter weights by respective species density in the sample.

2.5. Statistical analysis

To verify the efficacy of the experimental nutrient addition, we used two-factor (fish and nutrient) repeated measures analysis of variance

(RM-ANOVA followed by contrast analysis as a post-hoc test) to test for differences in DIN and DIP concentrations. We used Log_{10}-transformed DIN and DIP data for all sampled weeks in the RM-ANOVAs. We also conducted RM-ANOVAs to test for the effects of experimental block (random factor) on Secchi disk depth, [DO] and total zooplankton biomass.

We first measured the temporal coherence of each variable by calculating the pair-to-pair Pearson's moment correlation coefficients between the enclosures of a given treatment. Before we performed Pearson's correlation, we tested for normality of each variable with Kolmogorov-Smirnov's test. The degree of temporal coherence was assumed to be the magnitude of the correlation coefficient ($r_{pearson}$) (Baines et al., 2000; George et al., 2000). For each treatment (Control, F, N and F+N), a total of 6 pair-to-pair correlations were possible for a given variable due to the 4 different enclosures for each treatment. To test for the individual and interactive effects of fish and nutrients on the temporal coherence of each system variable, we calculated the average Pearson's correlation coefficients and the 95% confidence intervals (± 95% CI) for each treatment. Confidence intervals were estimated by a bootstrapping technique with 9,999 iterations. This randomization-based analysis circumvents the problem of dependence among the correlation coefficients calculated from all possible pair-to-pair enclosures' time series within a given treatment (Caliman et al., 2012). The aforementioned statistical analyses were performed using the software STATISTICA version 8.0 for windows (StatSoft, 2007). A significance level of $P = 0.05$ was used for all analyses.

We calculated "temporal coherence effect sizes" to test whether the strength of the individual and interactive effects of fish and nutrient enrichment on the temporal coherence of each variable depended on the system variable identity. We computed the effect sizes with the log response ratio, defined as the natural logarithm (ln) of all of the individual Pearson's correlation coefficients for each treatment ($n = 6$ for F, N or F+N) divided by all individual Pearson's correlation coefficients of the control. These calculations, for a given treatment and variable, resulted in a distribution of 36 individual effect sizes. We then calculated the cumulative effect sizes from the average of this distribution and its bootstrapped 95% CI using 9,999 iterations. The log response ratio is the most widely used metric for calculating effect sizes and is intuitive for estimating the proportional difference between treatments (Hedges et al., 1999).

3. Results

The nutrient addition was successful at establishing significant differences among the treatments with regard to the concentrations of DIN and DIP during the eleven-week experiment (RM-ANOVA; Table 1). The mean concentrations of DIN and DIP in the treatments that received the addition of nutrients (N and N+F) were 7.4× and 60× greater than the non-amended treatments (Control and F), respectively (Table 1). Furthermore, no significant effects of the experimental block were observed for the Secchi disk depth, [DO] and total zooplankton biomass ($F_{3,\,10} = 1.73$, P = 0.22; $F_{3,\,10} = 1.07$, P = 0.40; $F_{3,10} = 0.30$, P = 0.81, respectively). These results indicate that possible spatial heterogeneity among enclosures was not a confounding factor for the results of the experiment and that "regional" effects affected all experimental enclosures similarly.

Differences in the temporal coherence between nutrient and control treatments were only significant for [DO] (Figure 2B). This result shows that nutrient-enriched enclosures were most coherent for [DO], but no difference was observed for Secchi disk depth (Figure 2A) or zooplankton biomass (Figure 2C). Regarding the temporal coherence between the fish and control treatments, the zooplankton biomass variable was most coherent in enclosures where fish were introduced (Figure 2C). Neither the coherence of Secchi disk depth (Figure 2A) nor [DO] (Figure 2B) in the fish treatment was significantly different from that of the control. Coherence between the control and the F+N treatments was not different for any of the variables tested (Figure 2), although for the

Table 1. Average concentrations of dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) in the water column of the experimental enclosures. The results are the mean (± SD) of weeks 2 through 11. Different letters above the mean values represent significant differences (RM-ANOVA with Contrast Analysis as a post-hoc test, $P<0.05$).

	Control	Fish	Nutrient	Fish+Nutrient
DIN (µM)	3.6^{a} (4.1)	3.9^{a} (1.2)	30.8^{b} (3.5)	24.7^{b} (5.5)
DIP (µM)	0.1^{a} (0.1)	0.1^{a} (0.1)	5.9^{b} (0.8)	6.1^{b} (1.5)

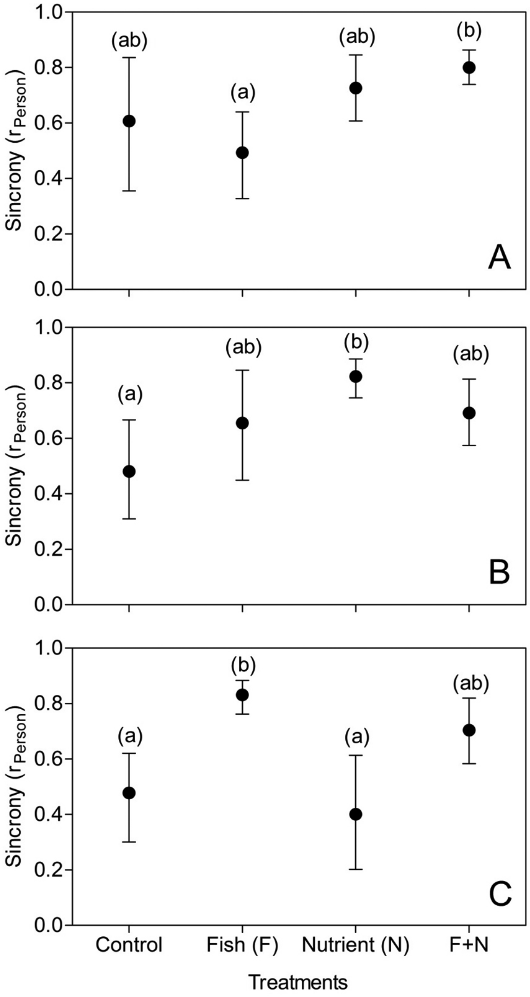

Figure 2. Individual and interactive effects of fish and nutrient addition on the temporal coherence of (a) Secchi disk depth (i.e., water transparency); (b) dissolved oxygen concentration; and (c) total zooplankton biomass. Data points are the averaged Pearson's correlation coefficients (*n* = 6) calculated from all possible pair-to-pair correlations among the enclosures (*n* = 4) of a given treatment. Error bars show the bootstrapped 95% CI estimated with 9,999 iterations. Different letters indicate that treatments are significantly different from one another (i.e., their 95% CIs do not overlap).

Secchi disk depth, the interactive effect increased the temporal coherence in comparison to the fish treatment (Figure 2A).

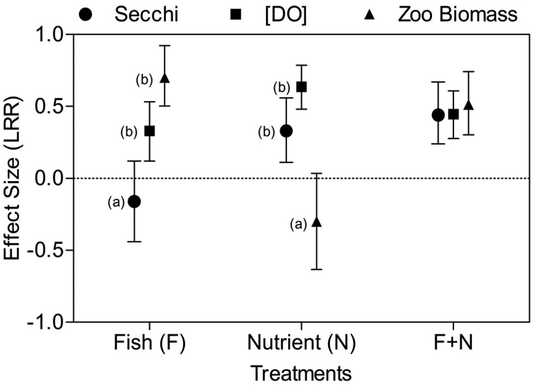

Figure 3. Strength of the individual and interactive effects of fish (F) and nutrient addition (N) on the temporal coherence of physical (Secchi disk depth), chemical ([DO]) and biological (total zooplankton biomass) variables. The strength of the treatment effects was estimated by effect size, calculated as the log (ln) response ratio between all Pearson's correlations of treatments and the control. Positive and negative values indicate that treatments increase or decrease, respectively, the temporal coherence of a given variable compared to the control. Error bars show bootstrapped 95% confidence intervals (constructed with 9,999 iterations). The magnitude of the effects of a given treatment differs among variables if the 95% CIs of the effect sizes do not overlap. Symbols marked by different letters are significantly different from one another.

There were differences among the individual and interactive effects of nutrients and fish on the strength of the temporal coherence of all variables, but these differences showed no consistent pattern with regard to the identity of the variables (Figure 3). The strength of the nutrient effect on temporal coherence was higher for Secchi disk depth and [DO], but the difference between these two variables was not statistically significant. However, the strength of the nutrient effect on the temporal coherence of zooplankton biomass was statistically weaker than for Secchi disk depth and [DO]. The strength of the fish effect on the temporal coherence of Secchi disk depth was significantly lower than [DO] and zooplankton biomass (Figure 3), but no significant difference was observed between [DO] and zooplankton biomass. Finally, the strength of the interactive F+N effect on temporal coherence did not vary significantly among the variables tested.

4. Discussion

To the best of our knowledge, this is the first experimental study to test general questions about temporal coherence in lakes. Contrary to most findings in the literature, which generally report medium to low coherence in temporal patterns among tropical lakes (Lansac-Toha et al., 2008; Caliman et al., 2010), we found a strong pattern of temporal coherence considering all variables and treatments together (grand mean of the correlation coefficient $r \approx 0.62$). This finding can be explained by the physical proximity of the within-lake enclosures and the relatively shorter experimental duration compared to those reported in observational studies, which guaranteed a high similarity of ecological conditions among enclosures of a given treatment. However, despite the high similarity in the "regional" ecological conditions among enclosures (i.e., regional climate, lagoon water temperature variation and sediment characteristics), we observed significant quantitative and qualitative variation in patterns of temporal coherence associated with our experimental manipulation. These results indicate that for some variables, the effects of the alterations to fish presence and nutrient enrichment were consistently strong enough not to be masked by the overall control of the "regional" factors.

Overall, we found no support for the general hypothesis that the strength of temporal coherence decreases from physical to chemical to biological variables. However, our results partially supported our predictions about the effects of fish presence and nutrient enrichment on the temporal coherence of the three measured variables. We observed that the strength of individual local factors on temporal coherence depended on the identity of the variable but not in a consistent pattern. The prediction that nutrient enrichment would decrease the temporal coherence of variables was not confirmed, and the presence of fish only increased the temporal coherence of zooplankton biomass. In addition, the interactive effects of both local factors had no significant effect on the temporal coherence of any variable, and the strength of the interactive effects between nutrient enrichment and fish presence was also unaffected by variable identity. This result may indicate that the generally weak control attributed to individual local factors can emerge from quantitatively antagonistic or "noisy" interactions among individual local factors that reciprocally mask their individual effects on temporal coherence, even when such individual effects exist (Kratz and Frost, 2000). This result is an important first step toward applying knowledge about the temporal coherence of system variables in the large-scale management of lakes (Stoddard et al., 1998). Because inland aquatic systems have been altered by the simultaneous effects of multiple stressors (Christensen et al., 2006; Bozelli et al., 2009), it may be difficult to understand and associate the changes in the temporal dynamics of lakes with any isolated human-mediated perturbation (Arnott et al., 2003; Woodward et al., 2010).

We predicted that the individual effects of fish presence and nutrient addition would be opposite regarding the temporal coherence of variables, with fish presence increasing and nutrient addition decreasing the temporal coherence of variables. Compared to control, fish presence enhanced the temporal coherence only for zooplankton biomass, and nutrient addition increased, instead of decreasing, the temporal coherence of [DO]. In addition, based on previous work, we expected that the magnitude of the individual effects of each factor would be strongest for physical, intermediate for chemical and weakest for biological variables, a pattern also not supported by our results. Taken together, these results raise doubt about the generalization that the effects of temporal coherence are stronger in physical variables than on chemical and biological variables. In fact, Secchi disk depth, the physical variable we monitored in our study, was the only variable with a temporal trajectory that was not affected by the individual effects of fish presence or nutrient addition. Two non-mutually exclusive hypotheses may explain the apparent divergence of our results and the patterns described in the literature. First, it has been argued that physical variables are more temporally coherent than chemical and biological variables because physical variables are more strongly affected by large-scale regional factors, whereas chemical and biological variables may also respond to several in-lake factors. As we noted previously, although our experiment was conducted under natural field conditions, the isolation of the water column certainly simplified the community- and ecosystem-level processes occurring inside the experimental enclosures compared to the lagoon. This situation may have caused the environmental pathways and mechanisms that could affect the temporal trajectories of chemical and biological variables to be fewer and/or simpler inside the enclosures in comparison to the rest of the lagoon. Consequently, the functional discrepancies among physical, chemical and biological variables could be reduced.

Most of the generalizations in the literature consider water temperature as physical, dissolved ions as chemical and phytoplankton chlorophyll-*a* as biological variables. With respect to their functional attributes, these variables may differ substantially from the variables we monitored in our experiment, which may imply a weakness in classifying system variables into such large "functional" categories. We can easily detect such conceptual weaknesses if we consider the fact that light extinction in the water column, which can be roughly measured by the Secchi disk depth, may be affected by chemical (i.e., colored dissolved organic carbon - CDOC) and biological variables (i.e., phytoplankton biomass), which in turn may be affected by a larger number of mechanisms resulting from the effects of fish presence and nutrient enrichment. As was discussed previously (Kratz et al., 2003), the temporal coherence of a variable can be better predicted by relating the strength of the sensitivity of the variable to the causal links of the factor affecting the variable. It can be more straightforwardly assessed, for example, by verifying if the variable of interest responds to a given environmental factor directly or across multiple indirect interactions. For example, fish presence had a significant effect only on the temporal coherence of zooplankton biomass, most likely because fish predation acts directly on zooplankters, whereas fish effects on [DO] and water transparency are necessarily mediated by indirect interactions (e.g., via cascading effects on primary producers and heterotrophic microbes). On the other hand, nutrient addition may directly affect ecosystem-level processes such as phytoplankton primary productivity and microbial respiration, which in turn may have more pronounced effects on the temporal coherence of [DO] than on water transparency and zooplankton biomass that may also be affected by nutrients indirectly (e.g., via stimulation of microbial degradation of CDOC and growth of phytoplankton).

Irrespective of the peculiarities of our results, our study showed that fish presence and nutrient enrichment may significantly alter the temporal coherence of some system variables. This effect undoubtedly has important implications for the large-scale management (use and protection) of lakes. The impacts of human activities on ecosystems are assumed to occur simultaneously and to be highly localized (Comim et al., 2004; Huston, 2005) because the environmental pressure of human activities, in general, starts and strengthens as human populations spread over the landscape. Therefore, the effects of eutrophication and/or fish extinctions/introductions may be spatially structured, which indicates that monitoring programs would benefit from knowledge of temporal coherence patterns in lakes. However, it is important to consider that our conclusions rely on few, although ecologically diverse, environmental variables. Further experimental studies that monitor a larger number of environmental variables over larger temporal scales are necessary to comprehensively understand the effects of eutrophication and fish abundance on the patterns of temporal coherence in lakes.

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