UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE PESQUISAS HIDRÁULICAS

REGULADORES DA DINÂMICA DAS COMUNIDADES PLANCTÔNICAS E ÍCTICA EM ECOSSISTEMAS LÍMNICOS SUBTROPICAIS

LÚCIA HELENA RIBEIRO RODRIGUES

Tese submetida ao Programa de Pós-Graduação em Recursos Hídricos e Saneamento Ambiental da Universidade Federal do Rio Grande do Sul como requisito parcial para a obtenção do título de Doutor em Recursos Hídricos e Saneamento Ambiental.

Orientador: David da Motta Marques

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Porto Alegre, agosto de 2009

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“... Jamais desista de si mesmo.

Jamais desista das pessoas que você ama.

Jamais desista de ser feliz,

pois a vida é um espetáculo imperdível, ainda que se

apresentem dezenas de fatores a demonstrarem o contrário.

Pedras no caminho?

Guardo todas,

um dia vou construir um castelo..."

Fernando Pessoa

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RESUMO

As comunidades mudam no tempo e espaço em função de pressões decorrentes da estrutura do habitat e disponibilidade de recursos. O entendimento das relações ecológicas e interações das comunidades são essenciais para o manejo com objetivo de melhorar a qualidade da água através de interferências na cadeia trófica aquática e na dinâmica do ecossistema através de modelagem ecológica. O presente estudo foi desenvolvido em dois sistemas límicos subtropicais no extremo sul do Brasil: banhados temporários ('campos de cultivo de arroz') e um grande lago raso, lagoa Mangueira. O objetivo do trabalho nos banhados temporários constituiu-se em avaliar a dinâmica das comunidades planctônicas e íctica durante o desenvolvimento desses ecossitemas (um ciclo produtivo de cultivo de arroz). Nossos resultados evidenciaram um claro gradiente temporal direcionado pela disponibilidade de nutrientes no banhado temporário. Entretanto, as variáveis limnológicas não apresentaram nenhuma tendência espacial entre as estações amostrais. Através de regressão linear verificou-se correlação positiva entre clorofila *a*, nutrientes, biomassa zooplanctônica e, em especial, biomassa de copépodos. Por outro lado, biomassa de peixes e, particularmente, peixes planctívoros foram inversamente relacionados à concentração de clorofila *a*. Relações significativas entre o DOC com nutrientes, biomassa de plâncton e peixes foram igualmente identificadas ao longo do ciclo produtivo do arroz. Na lagoa Mangueira, sistema raso (z_{med} 3m), de 90 km de comprimento, o objetivo foi avaliar a distribuição espacial e temporal de plâncton e peixes em função da presença da macrófita emergente *Zizaniopsis bonariensis*. Além disso, foi verificada a existência de um gradiente longitudinal na lagoa e a estrutura da teia trófica do sistema. Análise de componentes principais e análise de redundância evidenciaram a presença de gradientes espacial (Norte/Sul) e temporal (sazonal) durante o estudo. Análise de similaridade (ANOSIM) aplicada às variáveis ambientais evidenciou diferenças significativas entre os extremos da lagoa (Norte e Sul). Transparência Secchi, DOC e clorofila *a* foram significativamente diferentes entre os pontos amostrais do Norte e Sul. Através de ANOVA verificou-se que os efeitos temporais sazonais são mais intensos no Norte da lagoa Mangueira. Com relação à estrutura da comunidade na lagoa Mangueira, a biomassa do bacterioplâncton, clorofila *a*, biomassa zooplanctônica e captura de peixes foram diferentes sazonalmente após a extração do efeito da estrutura de habitat, enquanto que no Sul apenas a clorofila *a* apresentou variação sazonal significativa. A estrutura de habitat (junto à *Z. bonariensis* e em água aberta) induziu diferenças significativas na concentração de clorofila *a* tanto no Norte como no Sul da lagoa Mangueira, após a extração dos efeitos decorrentes da sazonalidade. A captura de peixes também foi influenciada pela estrutura de habitat no Norte, após a extração do efeito sazonal. Análise de similaridade (ANOSIM) aplicada à comunidade de peixes também demonstrou diferenças significativas entre o Norte e o Sul da lagoa Mangueira, embora diferenças entre as áreas vegetadas e águas abertas não tenham sido verificadas. Biomassa dos peixes, número de capturas e riqueza específica foram diferentes entre os pontos amostrais. Baseado nas razões de $\delta^{13}C$ and $\delta^{15}N$ identificou-se a estrutura trófica da lagoa, bem como a posição trófica de espécies de peixes e as fontes de carbono do sitema. Análise de isótopos estáveis de nitrogênio permitiu a identificação de dois níveis tróficos de peixes na lagoa Mangueira. Macrófitas emergentes e perifíton foram identificadas como importantes fontes de carbono que sustentam a estrutura trófica do sistema. Análise de grupamento a partir de dados de $\delta^{13}C$ e $\delta^{15}N$ e de conteúdo estomacal identificou um arranjo perfeitamente filogenético entre as espécies de peixes analisadas, refletindo que, em sentido amplo, nichos alimentares são compartilhados por espécies taxonomicamente relacionadas. A dinâmica trófica da espécie de peixe dominante na lagoa, *Oligosarcus jenynsii* foi também analisada. Foram identificadas mudanças sazonais e ontogenéticas na dinâmica alimentar da espécie, evidenciando a grande plasticidade trófica associada com uma estratégia oportunista, característica de espécies carnívoras generalistas. As informações obtidas neste estudo permitiram identificar grande heterogeneidade espacial e claro gradiente longitudinal na lagoa Mangueira, tanto de fatores bióticos quanto abióticos, com reflexos na distribuição e abundância de plâncton e peixes. De posse destas informações foi possível alcançar um entedimento sobre a estrutura atual do sistema, bem como os direcionadores da sua dinâmica. A abordagem direcionada neste trabalho sobre o entendimento da estrutura atual de um lago raso subtropical possibilita futuros estudos na área da modelagem ecológica. A dinâmica das comunidades abordadas neste estudo vem subsidiar a parametrização de um modelo ecológico, com capacidade de estabelecer prognósticos, tendo como contorno, estressores naturais e antrópicos.

Palavras chave: banhados temporários, lago raso, macrófitas emergentes, dinâmica de nutrientes, gradiente espacial, gradiente temporal, dinâmica do plâncton, dinâmica dos peixes, análises isotópicas, cadeia trófica, arranjo filogenético, mudanças ontogenéticas, modelagem ecológica.

ABSTRACT

Biological communities change in time and space following driving pressures from differences in habitat structure and resource availability. Understanding the ecological role and interactions within aquatic community is essential for any management action trying to improve water quality by interferences in lake food web, ecosystem dynamics and modeling. The present study was carried out in two freshwater systems in Southern Brazil: an irrigated rice field and in a large shallow system, Mangueira Lake. The goal of this study in temporary wetlands was to evaluate the plankton and fish dynamics during a productive cycle. Our results evidenced a temporal gradient by nutrients availability in the temporary wetland studied. However, the limnological variables did not display any horizontal pattern among sampling stations. Linear regression showed a positive relationship between chlorophyll *a* and nutrients, zooplankton biomass and copepod biomass. In contrast, fish biomass and planktivorous fish biomass were inversely related to chlorophyll *a*. Statistically significant relationships between DOC with nutrients, plankton and fish biomass were also identified during the rice production cycle. In Mangueira Lake, a shallow system (z_{med} 3m) and 90 km long, the goal was to evaluate the spatial and temporal distribution of plankton and fish biomass as a function of the presence of the emergent macrophytes *Zizaniopsis bonariensis*. We also analyzed the existence of longitudinal gradient in lake and the food web structure in system. The PCA and RDA analyses showed the temporal (seasonal) and spatial (North/South) gradient during the study. Analysis of similarity (ANOSIM) applied to environmental variables showed significant differences between sampling sites (North and South). Secchi transparency, DOC and chlorophyll *a* were significantly different in North and South sampling sites. ANOVA results showed that season effects are stronger in the Northern sampling site. Concerning the community structure in the Mangueira Lake, bacterioplankton biomass, chlorophyll *a*, zooplankton biomass and fish captures were different seasonally after extracting the habitat structure effect, while in the Southern sampling site only chlorophyll *a* presented a seasonal significant variation. Habitat structure (by *Z. bonariensis* stands and open water samples) induced significant differences in chlorophyll *a* both in North and South samples after extracting seasonal effect. Fish captures do also responded to habitat structure in the North, after extracting the season effect. Analysis of similarity (ANOSIM) applied to fish community also showed significant differences between North and South, although no significant differences between vegetated and open water zones was observed. Fish biomass, number of captures, and richness were different between sampling sites. Based on the $\delta^{13}C$ and $\delta^{15}N$ ratios and analysis of stomach content of fish species, we provide also a description of food web structure, trophic positions of fish species and primary producers of system. Analysis of nitrogen isotope ratios yielded two fish trophic levels in Mangueira Lake. Emergent macrophytes and periphyton were important carbon source that sustain the food web structure of the system. Cluster analysis of $\delta^{13}C$ and $\delta^{15}N$ values and stomach content yielded a perfect phylogenetic arrangement of species. This result reflects that major feeding niches are shared by taxonomically related species. The feeding dynamics of the dominant fish species, *Oligosarcus jenynsii* was analysed by using analyses of stomach contents and stable isotopes signature. Seasonal and ontogenetic change in the feeding biology of *O. jenynsii* was identified, showing the high feeding plasticity, in addition to an opportunistic strategy of this generalist carnivore species. This study allows identifying a large spatial heterogeneity and clear longitudinal gradient both in biotic and abiotic factors, reflecting fish and plankton distribution and abundance. The evaluated parameters are intended to feed a mathematical model for the Mangueira Lake, looking for predictable scenarios from natural and anthropogenic stressors.

Key words: temporary wetland, shallow lakes, emergent macrophytes, nutrient dynamic, spatial gradient, temporal gradient, plankton dynamic, fish dynamic, isotopic analysis, food web, phylogenetic arrangement, ontogenetic changes, ecological modelling.

SUMÁRIO

APRESENTAÇÃO

Este trabalho foi desenvolvido junto ao Programa de Pós Graduação em Recursos Hídricos e Saneamento Ambiental da Universidade Federal do Rio Grande do sul, sob orientação do Professor David da Motta Marques.

O trabalho apresentado nesta Tese de Doutorado integra o Programa de Pesquisas Ecológicas de Longa Duração (PELD) *Sistema Hidrológico do Taim – Sítio 7*, (www.peld.ufrgs.br) financiado pelo Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). O PELD é composto por uma rede de sítios selecionados dos principais ecossistemas brasileiros e tem como foco a pesquisa integrada.

O Estado do Rio Grande do Sul possui um sistema único de água doce. Paralelamente ao Oceano Atlântico, a planície costeira do Estado é composta pela seqüência de lagoas em uma faixa de aproximadamente 640 km de extensão. Este sistema é basicamente compreendido por lagunas, lagoas costeiras de água doce e grandes lagoas interiores, apresentando canais e banhados de água doce que atuam como intercomunicadores. Este complexo sistema hídrico é peculiar, devido as suas características geomorfológicas, hidrológicas, climáticas e ecológicas.

Neste contexto, se insere o Sistema Hidrológico do Taim, Sítio 7 do PELD/CNPq, que inclui a Lagoa Mangueira como um dos seus mais importantes sub-sistemas. Promover a manutenção, organização e funcionamento dos ecossistemas brasileiros, gerando informação e subsídios para avaliação da diversidade física e biológica são objetivos do PELD/CNPq. Em especial no Sistema Hidrológico do Taim, identificar flutuações espaciais e temporais nas comunidades aquáticas considerando influências antrópicas e aspectos hidrodinâmicos é fundamental para se alcançar uma gestão integrada do sistema, considerando os usos múltiplos da lagoa Mangueira.

Dois aspectos importantes foram abordados nesta tese, visando uma melhor compreensão dos processos do sistema do Taim. Primeiro, a necessidade de compreender os processos e fatores reguladores da dinâmica das comunidades (plâncton e peixes) na lagoa Mangueira, e em um banhado temporário de campo de arroz. O segundo aspecto abordado refere-se à compreensão do fluxo de energia numa lagoa subtropical, a partir de análise isotópica de produtores e consumidores, identificando a estrutura trófica vertical e as fontes de carbono que sustentam o sistema.

A tese está estruturada na forma de capítulos. A primeira parte está composta por uma introdução geral (capítulo 1) e nos capítulos 2 a 5 serão apresentados os manuscritos elaborados a serem submetidos para publicação. Assim, o capítulo 2 refere-se ao papel dos nutrientes na dinâmica do plâncton e da ictiofauna durante um ciclo produtivo de cultivo de arroz. O capítulo 3 apresenta as mudanças sazonais na dinâmica das comunidades planctônicas e dos peixes, com foco na distribuição espacial e temporal destes organismos em função da presença de macrófitas emergentes na lagoa Mangueira.

No capítulo 4 serão apresentados os resultados da composição isotópica dos produtores primários e consumidores da lagoa Mangueira, baseado nas taxas de $\delta^{13}C$ e $\delta^{15}N$ de plantas, invertebrados e peixes. A dinâmica alimentar sazonal de uma espécie de peixe dominante na lagoa Mangueira (*Oligosarcus jenynsii*) a partir de análises de conteúdo estomacal e isótopos estáveis será apresentada no capítulo 5. Uma discussão geral e as conclusões são apresentadas, respectivamente, nos capítulos 6 e 7.

1. INTRODUÇÃO

1.1 Dinâmica de lagos rasos, banhados e campos de arroz (*'rice fields'*)

Lagos, rios, reservatórios e áreas alagadas são fontes permanentes de água para o abastecimento público, agricultura e indústria, além de sustentarem uma grande diversidade de organismos (Tundisi, 1999). A grande maioria dos lagos no mundo são pequenos e rasos (Downing *et al.* 2006), e configuram-se como importante recurso natural em áreas densamente habitadas na América do Sul.

A planície costeira do Rio Grande do Sul apresenta um grande número de lagos rasos que se originaram no quaternário, como conseqüência de regressões e transgressões marinhas, moldados posteriormente por processos de erosão fluvial, deposição marinha e movimentos da plataforma continental (Schäfer, 1988; Holz, 1999). Na região, o vento é o fator que, em especial, influencia a composição do material em suspensão na coluna d'água (Schwarzbold & Schäfer 1984).

Nos sistemas lacustres, a vegetação e o vento são dois dos principais agentes responsáveis pelas alterações na hidrodinâmica. A ocorrência de vegetação, suas características e a forma como está espacialmente distribuída têm papel fundamental sobre o comportamento hidrodinâmico de lagos rasos. Além de oferecer uma grande resistência adicional ao escoamento, a vegetação, quando emergente ou flutuante, proporciona um efeito protetor contra a ação do vento sobre a superfície da água (Paz *et al*, 2005).

A dinâmica de ventos, por sua vez, exerce forte influência no transporte de sedimentos e ressuspensão de nutrientes, sendo a principal fonte de energia cinética capaz de produzir movimento da massa d'água (Millet & Cecchi, 1992). A ressuspensão de nutrientes aumenta a eficiência do fluxo de energia na cadeia alimentar, promovendo uma maior homogeneidade da coluna d'água (Jeppesen *et al.*, 1999).

Na região Sul do Brasil, as lagoas costeiras apresentam comumente sistemas de banhados associados (Schwarzbold & Schäfer, 1984). Ecossistemas de banhados são considerados ambientes de alta produtividade biológica, devido principalmente à presença de macrófitas aquáticas e suas interações com o meio físico e biótico (Mitch & Gosselink, 1993).

No extremo sul do Brasil, banhados naturais transformados em campos de arroz (*rice fields*) são freqüentes. Esses ecossistemas aquáticos temporários apresentam potencial de sustentar grande diversidade de vertebrados e invertebrados (Bambaradeniya, 2000; Lawler, 2001). Campos de cultivo de arroz apresentam limnologia complexa, caracterizada por rápidas mudanças físicas, químicas e biológicas. Apesar de compartilharem características com lagos rasos e banhados, tem dinâmicas próprias e incomparáveis em função da temporalidade (alternância das fases seca e inundada) e da interferência das constantes práticas agrícolas (revolvimento do solo e aplicação de insumos) (Bambaradeniya, 2000; Fernando, 2005).

1.2 Lagos rasos, macrófitas aquáticas e comunidade associada

Muitos aspectos do funcionamento e estrutura de lagos rasos dependem da presença das macrófitas aquáticas, tanto em ambientes temperados (Jeppesen *et al.*, 1997a; Scheffer, 1998; Søndergaard *et al.*, 2005), quanto em ecossistemas tropicais e subtropicais (Thomaz & Bini, 2003; Meerhoff *et al.*, 2003; Kruk *et al.*, 2009).

Macrófitas aquáticas desempenham importante papel na estruturação dos lagos rasos (Scheffer *et al.*, 1993; Meerhoff *et al.*, 2003), interferindo no sistema de várias formas: (1) reduzindo forças hidrodinâmicas e consequentemente diminuindo a ressuspensão de partículas (Barko & James, 1998; Horppila & Nurminen, 2001, 2003, 2005; James *et al.*, 2004) e aporte de fósforo do sedimento; (2) servindo de refúgio para espécies de zooplâncton de maior porte (Jeppensen *et al.*, 1997b) que predam algas fitoplanctônicas em altas taxas (Jeppessen *et al.*, 2005); (3) produzindo substâncias alelopáticas que reduzem ou inibem o crescimento de fitoplâncton (Wium-Andersen, 1987); (4) reduzindo a concentração de nutrientes disponíveis na massa da água em função de sua absorção foliar (Van Donk *et al.*, 1993, Thomaz *et al.*, 2007); (5) contribuindo para o aumento da heterogeneidade estrutural dos hábitats, influenciando a diversidade biológica, as relações interespecíficas e a produtividade do sistema (Van Donk and Van de Bund, 2001; Burks *et al.*, 2002; Meerhoff *et al.*, 2003; Romare *et al.*, 2003).

Entretanto, a maioria dos trabalhos realizados com foco no papel das macrófitas aquáticas relaciona-se às espécies submersas (Carpenter & Lodge, 1986; Jeppesen, *et al.*, 1997a,b; Mazzeo *et al.*, 2003; Meerhoff *et al.*, 2003; 2007; Kruk *et al.*, 2009), sem ênfase nas macrófitas emergentes (Nurminen & Horppila, 2002). Macrófitas emergentes desempenham papel fundamental regulando a ressuspensão do sedimento em lagos rasos e reduzindo a concentração de sólidos inorgânicos suspensos na água (Horppila and Nurminen, 2001, 2005; Nurminen & Horppila, 2002). As macrófitas aquáticas, principalmente as enraizadas, têm a habilidade de assimilar os nutrientes do sedimento e, através do efeito de bombeamento do sedimento para a coluna de água, podem prover grandes quantidades de matéria orgânica e nutrientes para o ecossistema (Mann & Wetzel, 1996). As macrófitas emergentes assumem grande dominância de cobertura vegetal em ecossistemas aquáticos, e a contribuição de carbono orgânico proveniente tanto das macrófitas aquáticas, quanto dos organismos associados, constitui um impacto significativo para o metabolismo de sistemas aquáticos (Wetzel, 1968; Wetzel & Ulehlová, 1971).

Associada aos estandes de macrófitas aquáticas existe toda uma comunidade biológica. As partes submersas das macrófitas formam um *habitat* complexo, composto de caules e raízes que são colonizados por algas e invertebrados. Este *habitat* representa um importante refúgio para invertebrados e peixes (Diehl & Eklov, 1995).

Para os peixes, os benefícios advindos da estruturação promovida pelas macrófitas variam conforme a espécie de peixe considerada, a fase ontogenética e a estratégia de vida. A estrutura da ictiofauna é afetada não apenas pela abundância e riqueza de espécies de macrófitas, mas também pela distribuição e composição dos estandes no ambiente (Agostinho *et al.*, 2003), bem como pela forma de crescimento e heterogeneidade estrutural das macrófitas (Weaver *et al.*, 1996).

1.3 Nutrientes e a cadeia trófica

A estrutura de um ecossistema é composta, em linhas gerais, por componentes abióticos (substâncias inorgânicas, compostos orgânicos, nutrientes) e bióticos (produtores e consumidores). Essas funções são essenciais para o entendimento da dinâmica dos ecossistemas, e podem ser analisadas através do fluxo de energia, das ciclagens de nutrientes, do padrão do desenvolvimento e da produtividade dos organismos em escala espacial e temporal (Overbeck, 2000).

Quanto ao fluxo de nutrientes nos sistemas aquáticos (especialmente C, P e N), estes são processados pelos produtores e transformados em matéria vegetal e microbiana. Durante o crescimento e especialmente após a morte dos organismos, compostos orgânicos são liberados no sistema, e mudanças na carga de nutrientes resultam também em mudanças na estrutura da comunidade de cada nível trófico (Jeppesen *et al.,* 2000).

Neste contexto, o metabolismo de um ecossistema compreende três etapas principais: produção, consumo e decomposição (Wetzel, 1993), sendo a cadeia trófica o resultado da interação entre as etapas deste metabolismo. Devido à presença das macrófitas, os processos que ocorrem na zona litoral de lagos rasos interferem na dinâmica da cadeia trófica (Jeppesen *et al.*, 1999). Contudo, os ecossistemas tropicais e subtropicais diferem dos lagos temperados nas características gerais das cadeias tróficas (Lazzaro, 1997). Os efeitos das macrófitas aquáticas nas interações tróficas são muito mais complexos em lagos tropicais e subtropicais, especialmente, devido a grande diversidade de macrófitas e a variedade de formas biológicas (Sondeergard *et al.*, 2000; Angeler *et al.*, 2003).

O entendimento dos processos que afetam a produtividade biológica nos diferentes níveis tróficos em lagos rasos relaciona-se basicamente aos aspectos de disponibilidade de recursos - controle ascendente (*bottom-up control*) ou o controle regulado pelo topo - controle descendente (*top-down control*). Assim, a teoria de cascata trófica em lagos, como ficou conhecida, é baseada em dois princípios:

1. Existe perda de energia entre níveis tróficos sucessivos;
2. A perturbação de um nível trófico terá conseqüências nos demais níveis tróficos.

Segundo Overbeck (2000), a transferência de energia de um nível trófico para outro é explicada, por exemplo, pela pressão que o zooplâncton exerce sobre o fitoplâncton e a predação dos peixes sobre o zooplâncton, sendo que cada transferência de um nível para outro se perde de 80 a 90% do potencial energético.

Macrófitas aquáticas podem interferir duplamente no controle do fitoplâncton. Através da redução da disponibilidade de nutrientes e/ou de substâncias alelopáticas (*bottom-up control*), ou pelo refúgio para o zooplâncton pelágico pastejador (*grazers*), permitindo um incremento de sua densidade, e conseqüentemente, um forte controle sobre a biomassa fitoplanctônica através da pressão de predação (*top-down control*) (Ferrão-Filho *et al*., 2009).

As macrófitas aquáticas, juntamente com o fitoplâncton e material alóctone, são componentes importantes para o desenvolvimento do bacterioplâncton em lagos (Saunders, 1980). O bacterioplâncton representa um componente chave nas cadeias tróficas de ambientes aquáticos, principalmente devido à extraordinária diversidade de suas vias metabólicas. O fato de serem capazes de processar substratos orgânicos e inorgânicos com grande eficiência e versatilidade faz com que as bactérias se tornem fundamentais na reciclagem da matéria e no fluxo energético desses sistemas (Lindstrom, 2001). Em razão de sua alta biomassa, o bacterioplâncton desempenha um papel fundamental na ciclagem de vários elementos nos ecossistemas aquáticos, constituindo importante ligação entre a matéria orgânica dissolvida e os níveis tróficos superiores (Farjalla *et al.,* 2004), além de representar excelente alimento para o zooplâncton.

A disponibilidade de nutrientes nos ecossistemas aquáticos é um dos fatores que atua mais diretamente sobre a dinâmica dos produtores (Tilman 1982; Reynolds, 1984; Sommer, 1988). Os principais elementos limitantes à produtividade fito-bacterioplanctônica são o carbono, o fósforo e o nitrogênio. A concentração de carbono nos ecossistemas aquáticos raramente é crítica, salvo em ambientes muito ácidos ou muito alcalinos, sendo o maior nutriente limitante para o bacterioplâncton (Bassoli & Roland, 2005). A importância do fósforo como nutriente limitante para o crescimento do fitoplâncton tem sido exaustivamente documentada para sistemas temperados (Huszar & Caraco, 1998; Oliver & Ganf, 2000), enquanto que o nitrogênio é indicado como principal nutriente limitante para os sistemas tropicais de água doce (Elser *et al.*

1990) em função das maiores taxas de desnitrificação a temperaturas mais elevadas (Lewis, 2002).

O zooplâncton é constituído por um conjunto extremamente variável de organismos cujos comportamentos biológicos são amplamente determinados por vários fatores ambientais, como predação, competição e recursos alimentares, além das variáveis abióticas, como temperatura, concentração de oxigênio dissolvido, flutuação do nível da água, vento e precipitação (Espindola & Niselli, 1996). Neste sentido, vale ressaltar a posição especial que o zooplâncton ocupa na cadeia alimentar, sendo a mais importante comunidade no controle *top-down* de algas em lagos (Scheffer, 1998). Além disso, devido a sua heterogeneidade de tamanho, diferentes grupos podem servir de alimento em diferentes estágios de vida para peixes ou mesmo para zooplâncton carnívoro (Jeppesen *et al.*, 1990).

Os peixes, capazes de provocar alterações no topo da cadeia alimentar, desempenham um importante papel na biocenose do lago, pois a presença e abundância de determinadas espécies determina a composição do plâncton presente no sistema e a quantidade de nutrientes (Straskraba & Tundisi, 2000). Alterações de topo de cadeia estão diretamente relacionadas ao efeito provocado pelos peixes bentívoros, geralmente dominantes sobre os demais peixes de lagos cuja turbidez é alta (Lammens, 1991). Por outro lado, a pesca sobre os peixes piscívoros pode amenizar a pressão sobre os planctívoros, bentívoros e onívoros, levando a uma redução da população de zooplâncton (Søndergaard *et al.*, 2000).

1.4 Fontes de matéria orgânica e posição trófica dos organismos (Análise isotópica)

Conforme mencionado anteriormente, o entendimento da dinâmica dos ecossistemas pode ser compreendido através do fluxo de energia. Neste sentido, as fontes de matéria orgânica que mantêm as cadeias alimentares e a determinação da posição trófica dos organismos correspondem, atualmente, às duas questões mais freqüentemente abordadas em estudos de ecologia trófica em ecossistemas aquáticos. Interações tróficas e utilização de recursos têm sido inferidas através de observações diretas ou de análises do conteúdo estomacal. Entretanto, o material ingerido pode não necessariamente representar o item assimilado, enquanto outros componentes da dieta podem estar subestimados devido a sua rápida digestibilidade (Jepsen, 1999).

Marcadores biogeoquímicos naturais correspondem a uma das alternativas para traçar o fluxo de energia e nutrientes entre os consumidores, e como resultado, uma ampla variedade de trabalhos utilizando isótopos estáveis tem emergido nos últimos anos (Hobson & Wassenaar, 1999). Entre os marcadores biogeoquímicos naturais, notadamente o $\delta^{13}C$ e o $\delta^{15}N$ são utilizados para a observação da ecologia trófica dos organismos e sua inter-relação nos ecossistemas. O uso combinado de isótopos estáveis de carbono ($\delta^{13}C$) e nitrogênio ($\delta^{15}N$), têm se revelado como eficiente ferramenta para o entendimento do fluxo de energia e nutrientes no sistema (Vander-Zanden *et al.*, 1997).

A assinatura isotópica de um organismo representa um sinal integrado desde a fotossíntese, os caminhos da fixação do dióxido de carbono e a transferência de energia nos ecossistemas (Ziegler & Fogel, 2003). Por outro lado, o $\delta^{15}N$ pode ser fracionado consistentemente ao longo das teias tróficas, oferecendo a possibilidade de inferir sobre a posição dos consumidores nessas teias (Benedito-Cecílio *et al.,* 2002). Neste contexto, o conhecimento sobre a incorporação de carbono e nitrogênio na cadeia trófica de lagos rasos subtropicais, com ênfase nos peixes, contribui para a compreensão de como se processa o fluxo de energia nestes sistemas.

1.5 Hipóteses

1.5.1 Hipótese geral

A estrutura das comunidades aquáticas (composição, riqueza, abundância) sofre variações espaciais e temporais. As pressões ambientais relacionadas a estas variações estão relacionadas às oscilações sazonais de variáveis ambientais, a eventos climáticos pontuais e à estruturação física do próprio ambiente.

1.5.2 Hipóteses específicas

- Comunidades planctônicas e íctica em sistemas límnicos são reguladas pela disponibilidade de recursos (nutrientes e luz).
- Macrófitas emergentes desempenham efeito estruturador na abundância e distribuição espacial das comunidades planctônicas e íctica na lagoa Mangueira.
- A lagoa Mangueira apresenta um gradiente longitudinal de variáveis limnológicas.
- As fontes de carbono que sustentam os sistemas límnicos e a posição trófica dos organismos são bem determinadas através da análise de isótopos estáveis de carbono ($\delta^{13}C$) e nitrogênio ($\delta^{15}N$).
- Variações ontogenéticas na dieta de peixes são refletidas na assinatura isotópica.

1.6 Objetivos

1.6.1 Objetivo geral

Avaliar os fatores reguladores da dinâmica das comunidades planctônicas e íctica em sistemas límnicos subtropicais permanentes e temporários, em escala espacial e temporal, identificando o papel estruturador de macrófitas aquáticas emergentes, dos parâmetros abióticos, da disponibilidade de recursos e das interações entre organismos.

1.6.2 Objetivos específicos

- Avaliar o papel dos nutrientes na dinâmica das comunidades planctônicas e íctica durante um ciclo produtivo de cultivo de arroz;
- Identificar a dinâmica da comunidade associada ao desenvolvimento de um banhado temporário;
- Identificar padrões de distribuição das comunidades aquáticas em função da presença de macrófitas emergentes na lagoa Mangueira;
- Avaliar o efeito estruturador de macrófitas emergentes na distribuição espacial das comunidades planctônicas e íctica na lagoa Mangueira;
- Analisar a existência de um gradiente longitudinal na lagoa Mangueira;
- Analisar a composição isotópica dos produtores primários e consumidores da lagoa Mangueira;
- Determinar fontes primárias de carbono e posição trófica dos peixes da lagoa Mangueira;
- Descrever a estrutura da teia alimentar da lagoa Mangueira.
- Descrever a dinâmica alimentar sazonal de uma espécie dominante de peixe da lagoa Mangueira.

1.7 Área de Estudo: Sistema Hidrológico do Taim, funções e uso da água

1.7.1 Lagoa Mangueira

A Lagoa Mangueira é um corpo d’água raso, com profundidade média de 3 m e área aproximada de 820 km^2 (Fig.1). A Lagoa faz parte do Sistema Hidrológico do Taim, localizado entre o Oceano Atlântico e a Lagoa Mirim, ao sul do Estado do Rio Grande do Sul, entre os municípios de Santa Vitória do Palmar e Rio Grande (32°20' e

33°00' S e 52°20' e 52°45'). Todo o sistema tem uma área de 2.254 km^2, incluindo a Estação Ecológica do Taim (ESEC-Taim).

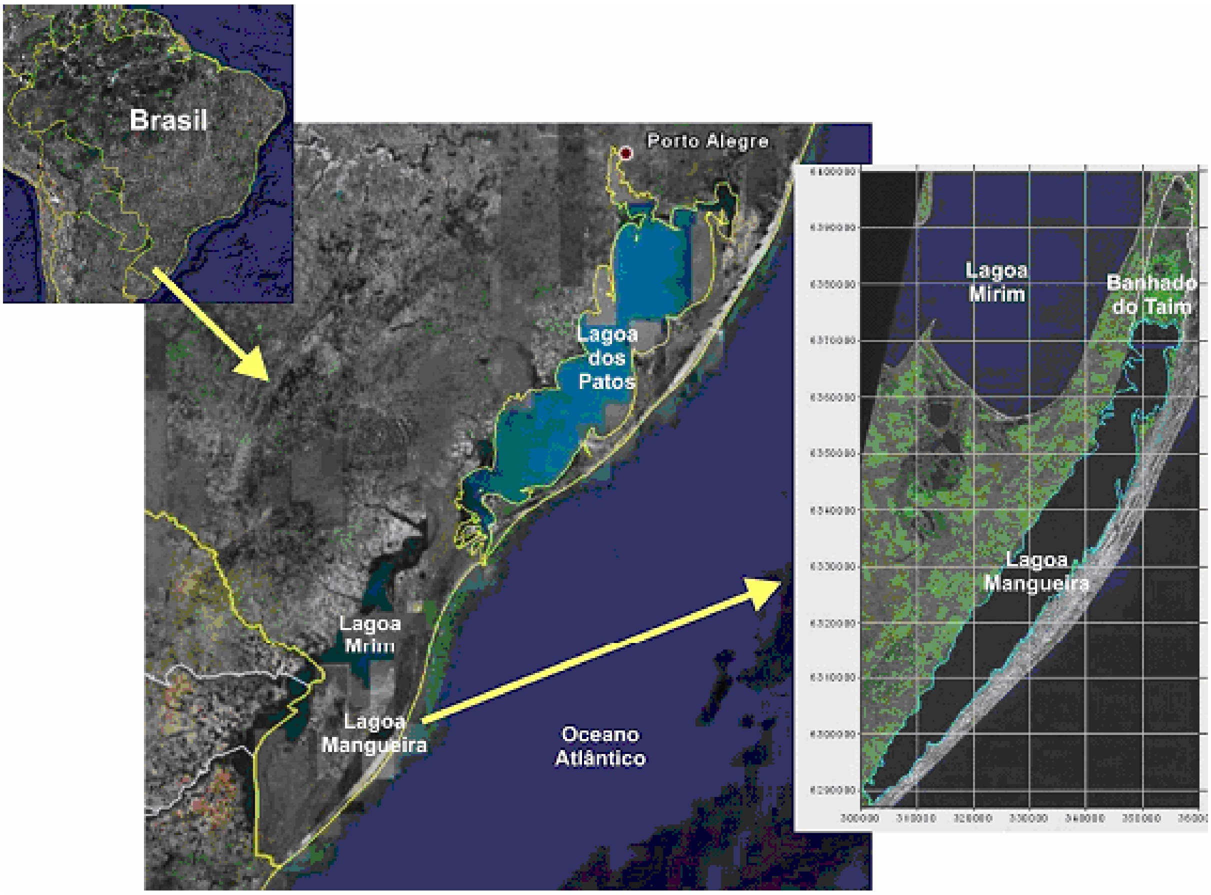

Figura 1. Localização do Sistema Hidrológico do Taim e delimitação da Lagoa Mangueira e Banhado do Taim sobre composição colorida RGB da imagem de satélite (Fonte: Google Earth e Landsat 5 TM, WGS 84, UTM-22S).

A região de inserção do Sistema Hidrológico do Taim é parte de uma série de áreas alagáveis que se estendem dos arredores das cidades de Pelotas e Rio Grande até o Uruguai, caracterizada por banhados e lagoas de água doce. Associada com o clima subtropical (Cfa; Koöppen, 1936), esta região se distingue de outras áreas alagáveis existentes no Brasil.

O SHT é complexo e pode ser dividido em três diferentes subsistemas: (a) Subsistema Norte, composto pela lagoa Caiubá, lagoa das Flores e o banhado do Maçarico, com um total de 387 km^2; (b) Subsistema Banhado, caracterizado por baixas velocidades superficiais, devido à existência de densos estandes de macrófitas aquáticas, com uma área total de 270 km^2; e (c) Subsistema Sul, formado pela Lagoa Mangueira e sua bacia de contribuição, com uma área de 1.597 km^2 (Villanueva, 1997).

A Lagoa Mangueira e o Banhado do Taim estão hidrológica e sinergeticamente relacionados, havendo a ocorrência do efeito de seiche nas extremidades norte e sul em função da forte ação de ventos que predominam nos sentidos NE e SO. O banhado do Taim se caracteriza por um maciço de vegetação aquática emergente. Portanto, além de servir como sumidouro ou reservatório para partículas inorgânicas e nutrientes solúveis, serve também como fonte de compostos orgânicos dissolvidos e particulados (seston) que são exportados para a Lagoa Mangueira (Motta Marques *et al.*, 1997).

Devido à peculiaridade climática, edáfica e morfológica da planície costeira, onde está inserido o SHT, os banhados e lagoas costeiras de água doce estão associados à cultura do arroz irrigado (*Oriza* sp.). A cultura de *Oriza* sp. nesta região é altamente tecnificada, no que tange às práticas agrícolas em si, e usa quantidades substanciais de água para manter a cultura.

Para o Sistema Hidrológico do Taim como um todo, o consumo de água na época de irrigação pode atingir o valor de 110 m^3.s-^{1} (Tucci *et al.*, 2002), sendo que o ecossistema mais afetado devido ao intenso bombeamento de água (estruturas com capacidade individual de até 11 m^3.s-^{1}) é a Lagoa Mangueira. A intensa extração de água da Lagoa Mangueira ocorre durante o verão, quando naturalmente o nível da Lagoa tende a diminuir em função dos baixos índices de precipitação. Após o plantio, a água utilizada retorna enriquecida por nutrientes e matéria orgânica para a Lagoa (Motta

Marques *et al.*, 1997). Isto representa um potencial aumento do grau de trofia do sistema, capaz de promover alterações nas comunidades aquáticas em curto prazo.

1.7.2 Banhados temporários (‘campos de arroz’)

Neste estudo foram utilizadas duas quadras de cultivo de arroz (cultivar BR-IRGA 410), localizadas no município de Santa Vitória do Palmar, nos arredores do Sistema Hidrológico do Taim. As áreas apresentavam predomínio de solo arenoso ou argiloso, sendo, por isso, denominadas Área Arenosa, com 4 ha, e Área Argilosa, com 1 ha (Fig. 2). A técnica de cultivo empregada foi plantio direto. As quadras amostrais situam-se a aproximadamente 17 km de distância do ponto de captação da água, a Lagoa Mangueira.

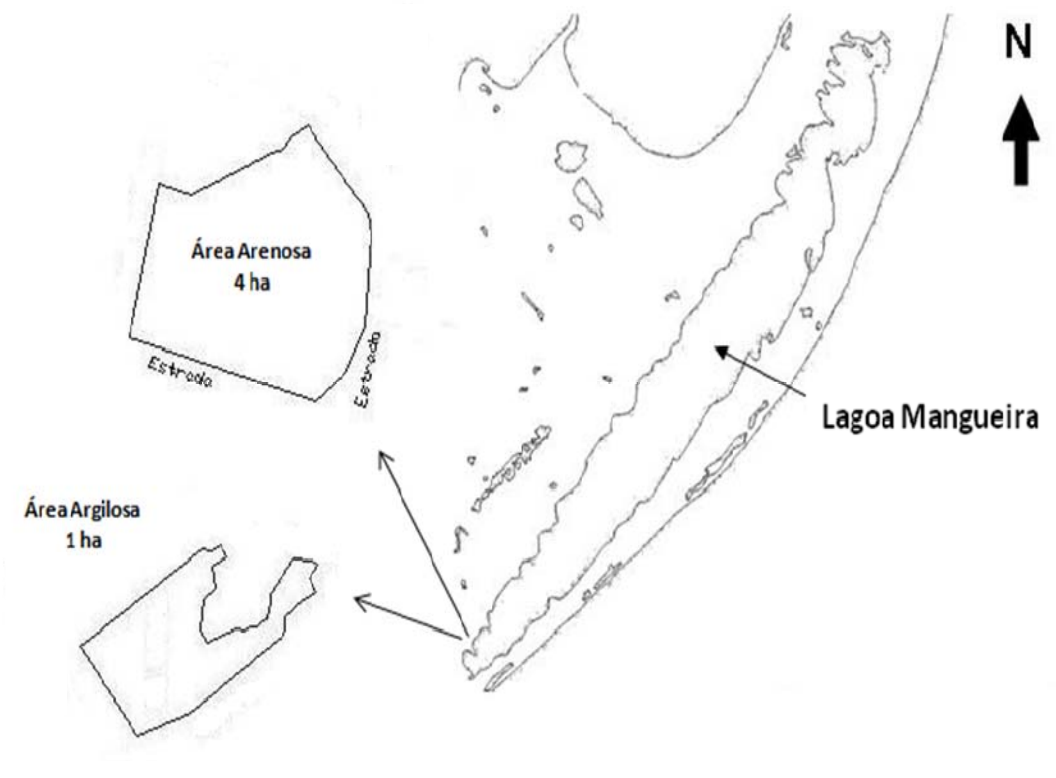

Figura 2. Localização dos banhados temporários (‘campos de arroz’) e da Lagoa Mangueira.

2. Dynamics of plankton and fish communities in a subtropical temporary wetland (rice fields)

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ABSTRACT

Rice fields are temporary wetlands that harbor many of the same species that breed in natural temporary ponds. These systems present a complex limnology, characterized by rapid physical, chemical and biological changes. The trophic structure of communities can be seen as the partitioning of biomass into different levels. It is basically determined by available resources and primary productivity but is also regulated by feedbacks from higher trophic levels, which in turn affect resource availability. In light of these concepts, we hypothesized that availability of nutrients (P, N, C) play an important role in the biomass planktonic and fish dynamics in a temporal gradient. The present study was carried out in an irrigated rice field in Southern Brazil. The goal of this study was to evaluate the role of the nutrients in the plankton and fish dynamics during a productive cycle, based on the autecology of the communities related to their adaptations to environmental temporal changes. The principal components analysis (PCA) results indicated a temporal gradient driven by nutrients availability, grouping four sampling periods during a productive cycle. ANOVA showed temporal differences of the limnological parameters during the development of rice fields production cycle. Linear regression showed a positive relationship between chlorophyll *a* and nutrients, zooplankton biomass and copepod biomass. In contrast, fish biomass and planktivorous fish biomass were inversely related to chlorophyll *a*. Statistically significant relationships between DOC with nutrients, plankton and fish biomass were also identified.

Key words: Chlorophyll *a*, zooplankton, fish, nutrients, temporary wetlands.

INTRODUTION

Irrigated rice fields are integrant part of the landscape of the tropical and subtropical regions. They are temporary wetlands that harbor many individulas of the same species that breed in natural temporary ponds (Roger 1996, Lawler 2001). Therefore the rice agro-ecosystem has the potential to help sustain the regional biodiversity of many invertebrates and vertebrates. Similar to natural areas of wetlands, rice cultivation provides a habitat mosaic of temporary and more permanent waters (Bambaradeniya 2000, Lawler 2001). These systems present a complex limnology, characterized by rapid physical, chemical and biological changes (Bambaradeniya 2000). The higher degree of environmental heterogeneity in the rice field ecosystem, operating on a temporal scale, may be a major contributing factor to its rich and varied biodiversity (Bambaradeniya *et al.* 2004). There is a full and diverse complements of aquatic organisms in rice fields, from bacteria and algae to fungi and higher plants, as well as all fauna groups from Protozoa to fishes, and others (Fernando 1993, 2005).

The organisms that live in these types of heterogenic habitats need therefore, to be very well adapted to these rapidly changing conditions, including the loss of water during the dry season (Bambaradeniya *et al*. 2004). The survival of such organisms depends largely on exceptional physiological tolerance or effective immigration and emigration abilities (Williams 1987). Furthermore, compared to other temporary freshwaters, the organisms in rice fields have to cope with various agronomic practices, which make its prevailing conditions more complicated (Bambaradeniya 2000, Bambaradeniya *et al*. 2004).

Limnologically, the rice field is characterized by its temporary nature, and the high flux of organic material both allochthonous and autochthonous. The changes from wet to dry conditions causes rapid demineralization of organic matter and both aerobic and anaerobic activity can be intense at times (Fernando 2005). With flooding, the remineralization of organic matter and first biological processes of wet phase are initiated. The temperatures are high and there is an abundance of nutrients. The outcomes of impacts of nutrient dynamics are reflected in community structure and interactions within the food web (Vakkilainen *et al*. 2004).

The availability of nutrients has an essential role in the control of the composition and biomass of phytoplankton communities (Reynolds 1997). Nitrogen and phosphorus loading determine many features of aquatic systems (Reynolds 2006). A consensus has emerged that nutrients remain very important in shallow systems, but the extent to which their potential influence may be realized is very much a function of food web structure and how it can be modified by nutrient loading. The rice field released inoculums of planktonic bacteria and phytoplankton into the water column, where they most likely use available nutrients and DOC (Kobayashi *et al*. 2008).

The present study was carried out in an irrigated rice field in Southern Brazil. This is one of the regions more vulnerable by rice fields in Brazil, considering the existence of great culture areas. The Taim Hydrological System, which it makes border with these areas of culture, has two eventually conflicting functions: (1) conservation, through the Taim Ecological Station; and (2) the supply of water for rice production. In recent decades, the Taim system has undergone an unregulated manipulation, irrigation and outflow control for conservation, of its hydrological signature and its present situation no longer represents natural conditions (Crossetti *et al*. 2007).

The goal of this study was to evaluate the role of the nutrients in the plankton and fish dynamics during a productive cycle, based on the autecology of the communities related to their adaptations to environmental temporal changes.

METHODS

Study site

The study was carried out in two irrigated rice fields of Santa Victoria do Palmar county, Southern Brazil (Fig. 1). The regional climate is subtropical without a dry season (Cfa type; Köppen 1936) with an average annual temperature of 16ºC and precipitation between 1800 and 2200 mm. The areas presented sandy or clay soil predominance, thus defined: Area 1 (A1) - Sandy, with 4 ha (Lat S 33.2885º; Lon W 53.0925º), and Area 2 (A2) - Clay, with 1 ha (Lat S 33.2872º; Lon W 53.0886º).

Sampling and field measurements

Considering the water flow through the rice field, in each sampling area (A1) and (A2), sampling was carried out in the inlet (I), in the central area (C) and in the outlet (O). The sampling program was performed from January/2006 to March/2006, with four collections 20 days apart, covering the entire water cycle of rice production. The first sampling (period 1) was performed just after the rice field inundation;

samplings two and three (periods 2 and 3) in the mid cycle, and the last sample just one day before the rice field draining (period 4).

Water temperature, dissolved oxygen and pH were measured with a multi-parameter probe (Yellow Spring model YSI 6920). Water samples for chemical analysis and chlorophyll *a* were collected at the surface, with a bottle (1 L). Zooplankton samples were made by filtering 10 liters of water through plankton net (65 µm mesh size) and fixed with formaldehyde (4%). Fish captures were made overnight (15h) by using tree *minnow traps* for each sampling point. Fish were preserved with formaldehyde (4%).

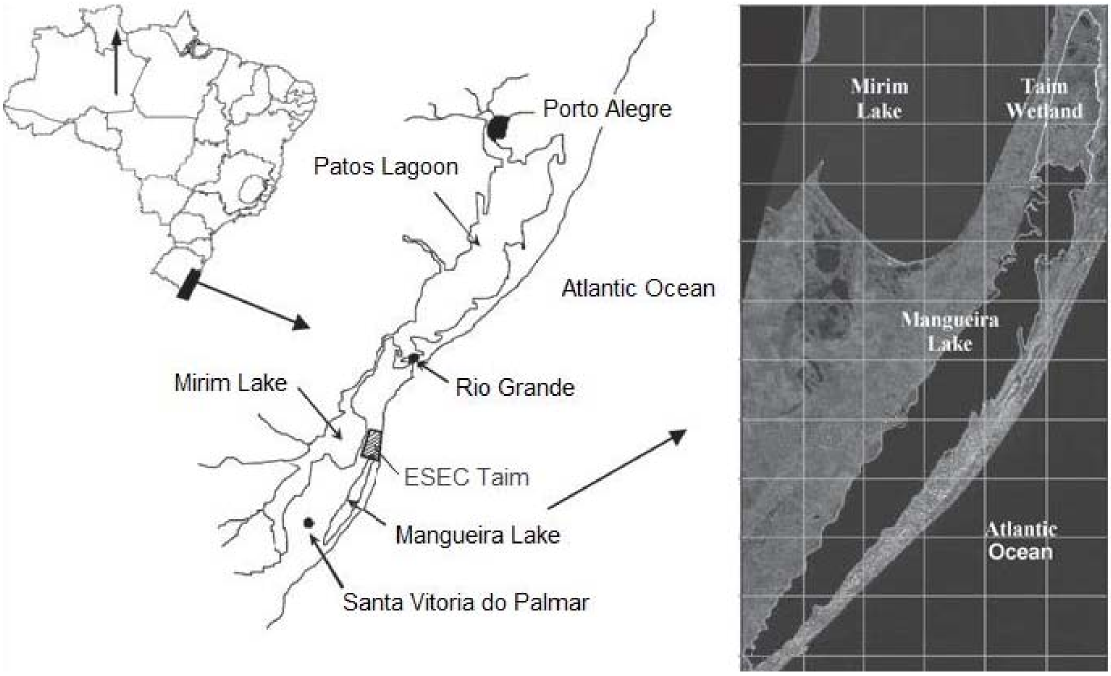

Figure 1. Localization of Santa Vitoria do Palmar, situated in the South of Brazil.

Sample analysis

Nutrients analysis - total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN), and nitrate (NO_3^-) - were analysed according to Mackereth *et al.* (1989). Dissolved organic matter (DOM) was analysed by spectrophotometric method (Strome and Miller 1978). Total solids analysis was estimated according to APHA (1999) and soluble reactive silicon (SRSi) was measured by photometric method using commercial kit (Si Merck Spectroquant® kit to silicate - sulfuric acid). Carbon analysis (dissolved organic - DOC and dissolved inorganic - DIC) were performed using a total organic carbon (TOC) analyzer (Shimadzu VCPH).

Chlorophyll *a* was extracted from GF/F filters into 90% ethanol (Jespersen and Christoffersen 1987) and measured by spectrophotometric method (APHA 1999). Quantitative analysis for zooplankton was performed using a Sedgwick-Rafter chamber (APHA 1992). Zooplankton biomass was estimated through bio-volume by applying the closest geometric formulae (Bottrell *et al.* 1976, Dumont *et al.* 1975, Ruttner-Kolisko 1977, Malley *et al.* 1989). Fish were identified and measurements of the standard length (centimeters) and total weight (grams) of each individual were performed.

Statistical Analysis

The principal components analysis (PCA) was performed using PC-ORD program version 4.0 (McCune and Mefford 1999). This analysis was undertaken to determine spatial and temporal changes of physical and chemical conditions. A two-way ANOVA test and linear regression (Statview ver. 5.0) were used to compare of the limnological parameters among sampling stations and sampling dates. A simple regression (Statview 5.0) was used to identify possible relationships among nutrients (P, N, C), planktonic biomass (chlorophyll *a*, zooplankton) and fish biomass, after $\log_{10}$ transformation.

RESULTS

Limnological scenario

During the study period, both rice fields, A1 (*sandy*) and A2 (*clay*), presented similar values of temperature and pH. Dissolved oxygen concentrations were on average higher in rice field A1 (8.2 mg L^{-1}) in relationship to A2 (6.6 mg L^{-1}) (Tab. 1). The concentrations of nutrients and chlorophyll *a* were highest in the beginning of the culture, just after the rice field inundation, and went decaying throughout the productive cycle where they were the lowest.

The principal components analysis (PCA) evaluated the main trends between limnological variables in the rice fields (Fig. 2). The PCA using 13 abiotic variables explained 75.9% of the data variability in the first three axes (axis 1= 51.6%; axis 2= 13.0%; axis 3= 11.3%). The most important variables for axis 1 ordination were TP (-0.92), N-NO_3^- (-0.89), organic matter (-0.85), total solids (-0.83), SRP (-0.82), DIC (0.74), SRSi (-0.73), chlorophyll *a* (-0.71), water temperature (0.67) and DOC (-0.67). In regard to axis 2, the most important variables for its ordination were TN (-0.73) and dissolved oxygen (0.52). The PCA results indicated a temporal gradient driven by nutrients availability (Fig. 2).

On the negative side of axis 1, sampling units for the period 1 were correlated with the highest values of dissolved nutrients (SRP, N-NO_3^-, SRSi), TP, total solids, organic matter and chlorophyll *a*, whereas on its positive side the sampling units for the period 4 were ordered with higher values of temperature and DIC. On the negative side of axis 2, all the sample units for the period 3 were ordered with higher concentration of total nitrogen, and on the positive side, the sample units for the period 2 were correlated with higher values of dissolved oxygen. Moreover, PCA revealed a homogeneous behaviour between sampling stations and the environmental variables in this system.

Sampling stations were grouped by sampling periods, with no evident horizontal gradient (Fig. 2).

ANOVA showed temporal differences (*P*<0.05) of the limnological parameters during the development of rice fields production cycle. Linear regressions showed that SRSi, ST, OM, DOC, TP, SRP, Chla, TN and $N^{-}NO_3^{-}$ presented decreasing trends (*P*<0.05), while DIC presented an increasing trend (*P*=0.05) throughout the productive cycle of the rice field. A spatial gradient was not identified by ANOVA or regression analysis.

Community structure

A total of 74 zooplankton species was identified (Tab 2). Copepods were predominant in biomass during the study period (3969.1 $mg.m^3$), followed by cladocerans (1360.2 $mg.m^3$). Rotifers (294.4 $mg.m^3$) and protists (123.8 $mg.m^3$) were the less important representatives in the community biomass (Fig. 5). In the group of the rotifers, the genus *Lecane* was the most representative, in special the species *Lecane bulla* (Gosse, 1851); *L. cf. papuana* (Murray, 1913) and *L. cf. inermis* (Bryce, 1892). For the cladocerans, *Moina minuta* Hansen, 1899; *Macrothrix triserialis* Brady, G.S. 1886 and *Ceriodaphnia cornuta* Sars (1885) were the most representatives species. *Eucyclops serrulatus* (Fischer, 1851) was the most abundant specie of copepods.

The fish checklist resulted in 11 species, distributed in 7 families (Tab 3). The planktivorous fish as *Astyanax jacuhiensis* (Cope, 1894) (42.45%) and *A. eigenmanniorum* (Cope, 1894) (12.36%), and the piscivorous fish as *Hoplias malabaricus* (Bloch, 1794) (28.24%) and *Crenicichla lepidota* Heckel, 1840 (11.15%) were the most representative species in relation to biomass.

Table 1 Means and standard deviations of the limnological variables measured during the study.

	Sampling 1		Sampling 2		Sampling 3		Sampling 4	
Parameter	Sandy	Clay	Sandy	Clay	Sandy	Clay	Sandy	Clay
Water temperature (ºC)	22.1	21.2	27.2	26.3	23.8	22.8	26.3	27.4
pH	7.8±0.2	7.4±0.4	7.3±0.3	7.2±0.1	6.7±0.4	6.9±0.2	7.6±0.4	7.3±0.4
Dissolved Oxigen ($mg.L^{-1}$)	7.6	5.9	10.6	6.8	9.9	7.7	5.9	5.5
Total Solids ($mg.L^{-1}$)	310±102	274±96	238±20	247±12	221±10	211±11	201±61	201±17
DOM (UV_{DOC} - 254nm)	0.44±0.26	0.30±0.13	0.14±0.03	0.18±0.03	0.03±0.03	0.05±0.03	0.02±0.01	0.01±0.01
DIC ($mg.L^{-1}$)	19.66±4.4	24.79±4.5	21.82±2.3	28.32±3.5	25.47±2.5	26.38±1.1	27.74±2.8	29.19±3.2
DOC ($mg.L^{-1}$)	15.11±8.6	18.33±10.6	12.52±5.9	10.16±2.7	7.12±1.7	6.33±0.8	8.30±1.7	7.42±1.9
SRSi ($mg.L^{-1}$)	3.22±0.77	3.47±0.68	1.03±0.90	1.56±1.04	1.76±0.84	2.14±0.48	0.36±0.33	0.27±0.09
TP ($\mu g.L^{-1}$)	5.90±4.51	3.23±1.92	2.34±1.51	2.83±1.74	1.03±0.31	1.52±0.21	0.16±0.03	0.18±0.02
SRP ($\mu g.L^{-1}$)	2.82±1.31	1.21±0.88	1.30±0.88	1.25±0.90	0.14±0.03	0.18±0.03	0.03±0.02	0.02±0.01
TN ($\mu g.L^{-1}$)	100±20	170±70	40±20	40±10	30±20	20±10	20±10	10±5
N-NO_3 ($\mu g.L^{-1}$)	50±40	50±20	20±10	30±20	10±5	10±5	NQ	NQ
Chlorophyll *a* ($\mu g.L^{-1}$)	39.5±17.3	42.7±21.3	29.3±21.8	33.2±22.8	2.5±1.4	2.5±0.6	2.2±1.2	1.6±0.6

DOM, Dissolved Organic Matter; DIC, Dissolved Inorganic Carbon; DOC, Dissolved Organic Carbon; SRSi, Soluble Reactive Silicate; TP, Total Phosphorus; SRP, Soluble Reactive Phosphorus; TN, Total Nitrogen; N-NO3, Nitrate.

Linear regressions of log-transformed data demonstrated a positive relationship between chlorophyll *a* and nutrients (TP, SRP, $N^-NO_3^-$ and DOC), zooplankton biomass and copepod biomass (Tab. 4, Fig. 3). In contrast, fish biomass and planktivorous fish biomass were inversely related to chlorophyll *a* (Tab. 4, Fig. 3). Statistically significant relationships between DOC with nutrients (TP and SRP), plankton and fish biomass (Tab. 4, Fig. 4) were also identified.

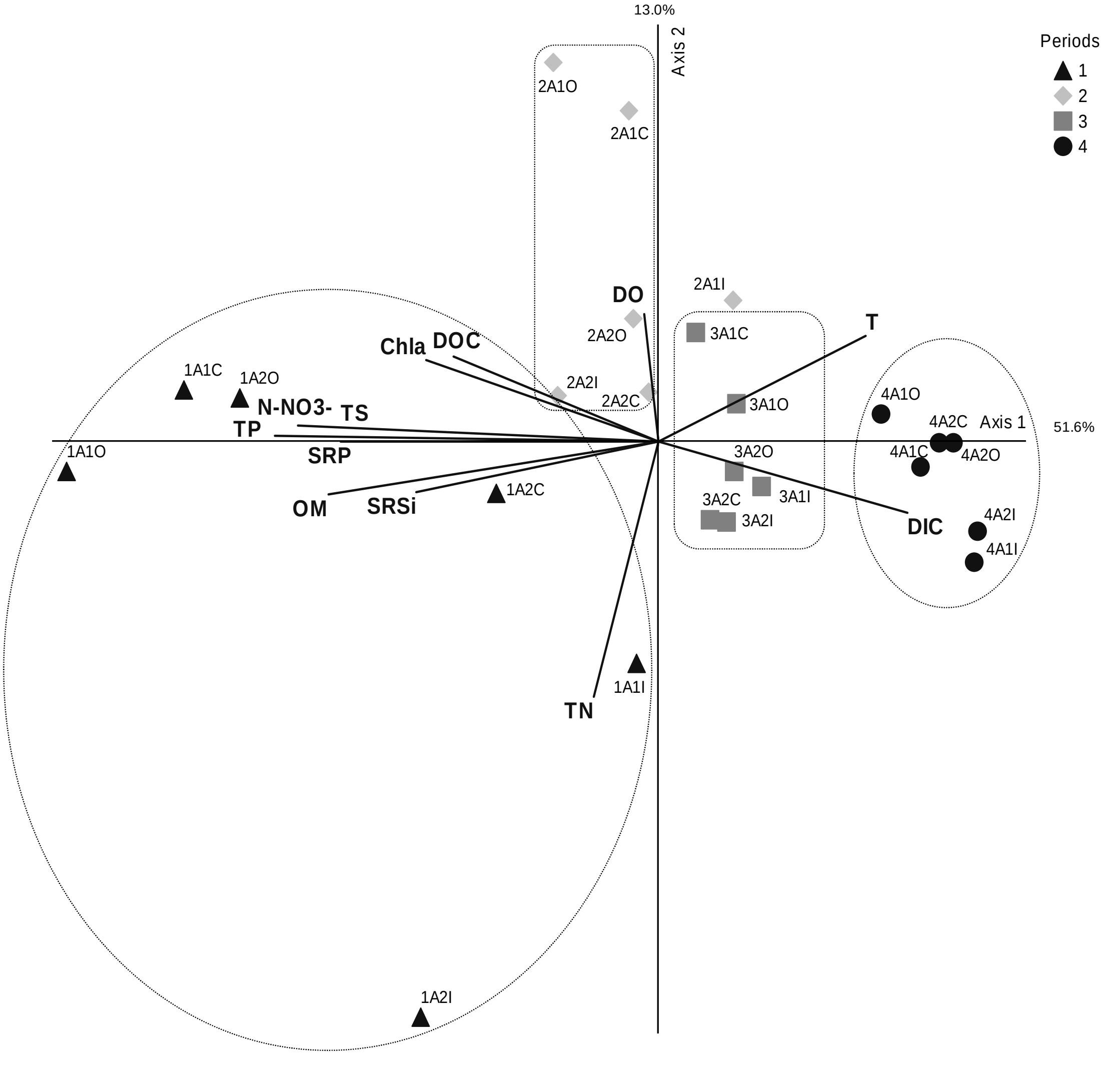

Figure 2. Results of the Principal Components Analysis (PCA) applied to environmental variables in rice fields in Santa Victoria do Palmar, Southern Brazil.

Sample units= sampling periods 1,2,3,4; A1= Sandy area; A2= Clay area; I= inlet; C= central point; O= outlet. T= water temperature; TP= Total Phosphorus; SRP= soluble reactive phosphorus; TN= Total Nitrogen; N-NO3= nitrate; SRSi= soluble reactive silicate; DIC= Dissolved Inorganic Carbon; DOC= Dissolved Organic Carbon; Chl a= chlorophyll *a*; TS= total solids; OM= organic matter.

Table 2 Zooplankton checklist of species captured during the study.

	Taxonomic group	
	Species	
Copepods	Cladocerans	Rotifers
Nauplii	Aloninae	*Asplanchna* sp.
Copepodits	*Alona cambouei*	*Brachionus* cf. *angularis*
Eucyclops serrulatus	*Alonella dentifera*	*Brachionus* cf. *bidentata*
Notodiaptomus incompositus	*Bosmina longirostris*	*Brachionus cf. calyciflorus*
	Bosminopsis deitersi	*Brachionus caudatus*
	Ceriodaphnia cornuta	*Brachionus patulus*
	Chydorus nitidulus	*Brachionus plicatilis*
	Chydorus sphaericus	*Brachionus quadridentata*
	Diaphanosoma spinulosum	*Cephalodella* sp.
	Dunhevedia odontoplax	*Conochilus* sp.
	Ephemeroporus hibridus	*Dipleuchlanis propatula*
	Ilyocryptus spinifer	*Euchlanis dilatata*
	Macrothrix trisserialis	cf. *Encentrum* sp.
	Moina minuta	cf. *Itura aurita*
	cf. Pleuroxus sp.	*Keratella cochlearis*
	Scapholeberis armata	*Keratella lenzi*
	Simocephalus serrulatus	*Keratella tropica*
		Lecane bulla
		Lecane cornuta
		Lecane curvicornis
		Lecane cf. *hornemanni*
		Lecane leontina
		Lecane luna
		Lecane lunaris
		Lecane ludwigii
		Lecane cf. *papuana*
		Lecane cf. *signifera*
		Lecane cf. sola
		Lecane cf. *stenroosi*
		Lecane quadridentata
		Lecane cf. *thienemanni*
		Lecane cf. *inermis*
		Lecane sp.1
		Lecane sp.2
		Lecane sp.3
		Lecane sp.4
		Lepadella sp.
		cf. *Lindia* sp.
		Lophocaris oxysternon
		Macrochaetus cf. *collinsi*
		cf. *Monommata* sp.
		Mytilina ventralis
		cf. *Notommata* sp.
		Platyas quadricornis
		Ploesoma truncatum
		Polyarthra vulgaris
		cf. *Proales* sp.
		cf. *Rotaria* sp.
		cf. Scaridium sp.
		Synchaeta stylata
		Testudinella patina
		Trichocerca cf. *bicristata*
		Trichocerca sp.1
		Trichocerca sp.2
		Trichotria tetractis

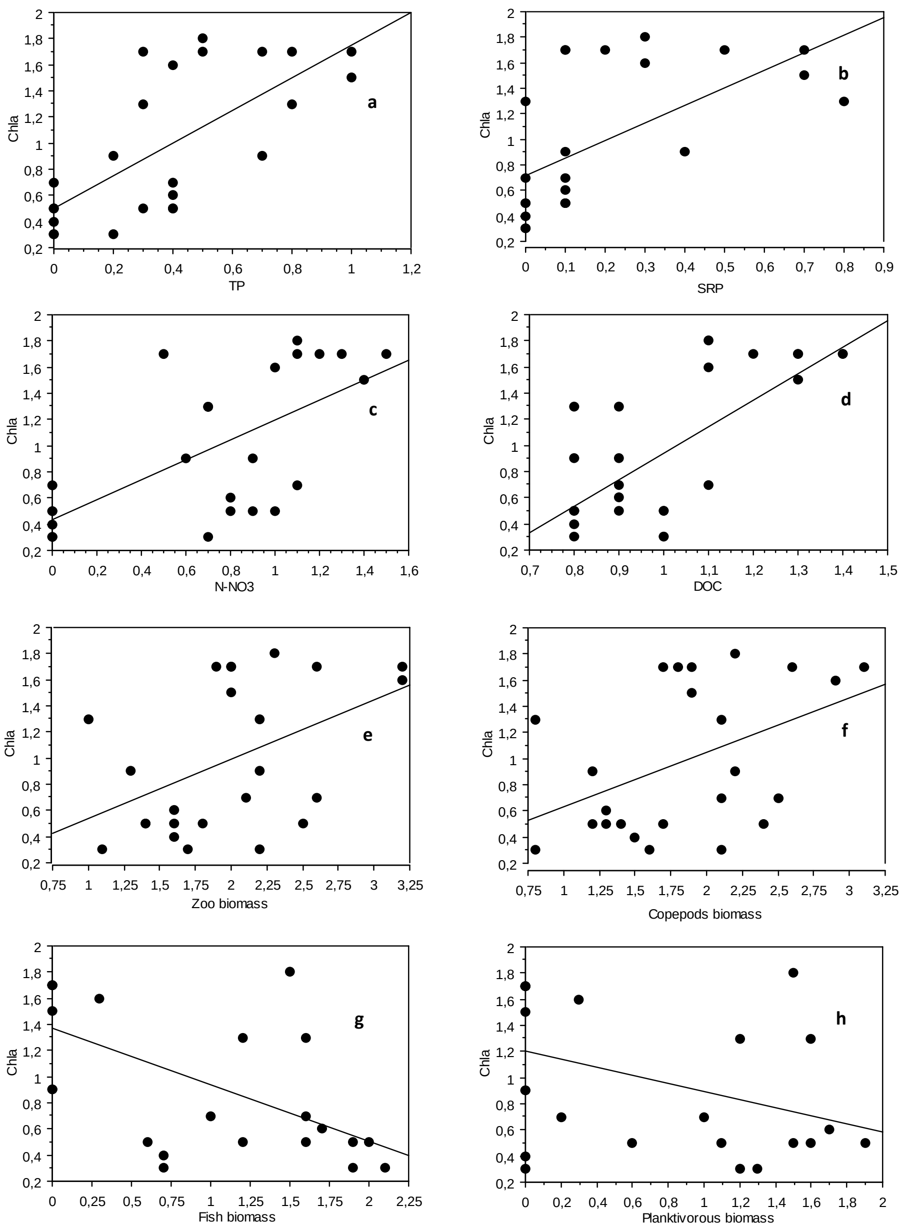

Figure 3. Relationship between chlorophyll *a* concentration (chl a) and the (a) total phosphorus concentration (TP); (b) soluble reactive phosphorus (SRP); (c) N-NO_3; (d) dissolved organic carbon (DOC); (e) zooplankton biomass; (f) copepods biomass; (g) fish biomass; (h) planktivorous biomass.

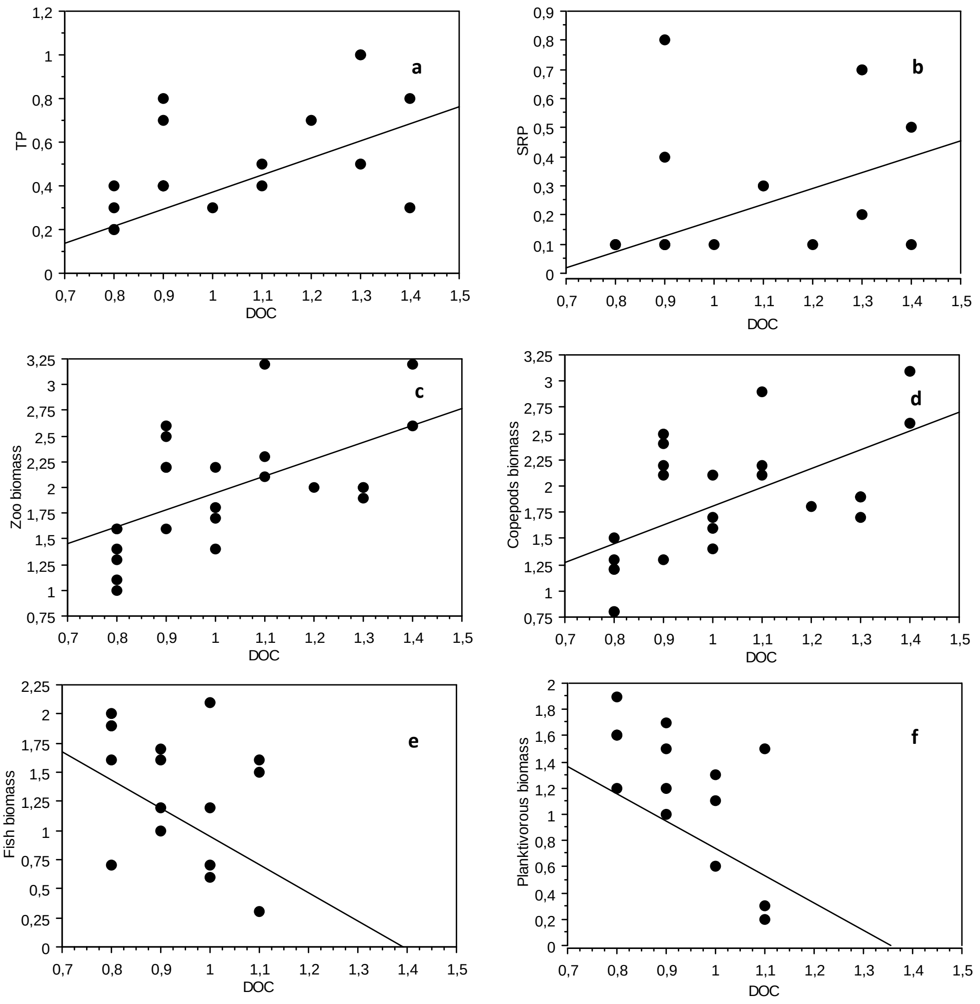

Figure 4. Relationship between (a) TP and dissolved organic carbon (DOC); (b) SRP and DOC; (c) zooplankton biomass and DOC; (d) copepods biomass and DOC; (e) fish biomass and DOC; (f) planktivorous biomass and DOC.

Table 3 Fish checklist of species captured during the study.

Family Species
Anablepidae
Jenynsia multidentata (Jenyns, 1842)
Curimatidae
Cyphocharax voga (Hensel, 1870)
Erythrinidae
Hoplias malabaricus (Bloch, 1794)
Characidae
Astyanax eigenmanniorum (Cope, 1894)
A. jacuhiensis (Cope, 1894)
H yphessobrycon luetkenii (Boulenger, 1887)
Oligosarcus robustus Menezes, 1969
Callichthyidae
Corydoras paleatus (Jenyns, 1842)
Cichlidae
Gymnogeophagus rhabdotus (Hensel, 1870)
Crenicichla lepidota Heckel, 1840
Poeciliidae
Cnesterodon decemmaculatus (Jenyns, 1842)

Table 4 Results of linear regressions describing relationships between chlorophyll *a*, zooplankton biomass, fish biomass and phosphorus (TP and SRP) (dependent variable) and abiotic/biotic factors.

Dependent variable	Independent variable	R^2	F	P
Chlorophyll *a*	TP	0.49	21.14	< 0.001
	SRP	0.36	12.62	0.002
	N-NO_3	0.43	16.84	< 0.001
	DOC	0.53	24.81	< 0.001
	Zooplankton biomass	0.22	6.08	0.022
	Copepod biomass	0.20	5.56	0.028
	Fish biomass	0.37	13.02	0.002
	Planktivorous biomass	0.15	4.01	0.050
TP	DOC	0.25	7.34	0.013
SRP		0.20	5.43	0.029
Zooplankton biomass		0.33	10.95	0.003
Copepod biomass		0.35	12.00	0.002
Fish biomass		0.39	13.85	0.001
Planktivorous biomass		0.34	11.49	0.003

TP, Total Phosphorus; SRP, Soluble Reactive Phosphorus; N-NO3-, Nitrate
DOC, Dissolved Organic Carbon.

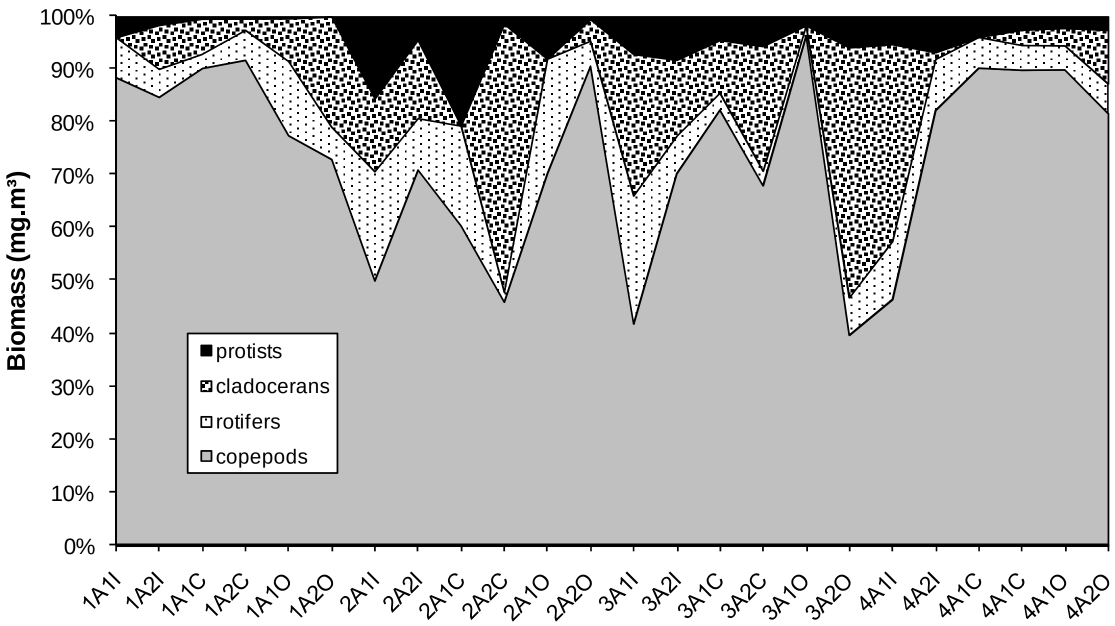

Figure 5. Zooplankton biomass in the studied rice fields.

(Sample units = sampling periods 1,2,3,4; A1= Sandy area; A2= Clay area; I= inlet; C= central point; O= outlet).

DISCUSSION

Our results evidenced a temporal gradient by nutrients availability in the wetland rice fields studied. However, the limnological variables did not display any horizontal pattern among sampling stations. In general the aquatic phase of a rice field is temporary and seasonal (Fernando 1993). These systems can be considered as a modified marsh ecosystem. However, agronomic practices change the natural physical, chemical and biological conditions making them less favorable for some organisms but also temporary more favorable for others (Heckman 1979).

Four distinct periods during the development of these ecosystems were identified following the results of the PCA. The first period was characterized by the highest concentrations of nutrients, in the initial phase of the culturing, following the overflow period. The second and third periods were characterized as transition periods when modifications on the physical structure of the systems were gradual, when rice macrophytes are in the growth phase, and nutrient concentrations are decreasing. The fourth period was characterized by high concentrations of DIC, probably due to transformation of DOC, and by the highest temperatures, considering that this period of the culturing cycle coincided with the end of the summer.

The nutrient decreasing tendency observed throughout the study could be associated to the incorporation of these nutrients by the rice macrophytes, and/or by the sediment during the productive cycle, or by the phytoplankton metabolism according to the results of the PCA and regression analyses. Organisms which survive in this environment have a wide tolerance limits for these rapid changes and take advantage of the abundant food, low competition and little predation (Fernando 1993). The concentrations of dissolved inorganic nutrients and DOM such as DOC in wetlands, like rice fields, are generally higher than those recorded in lakes and reservoirs (Wetzel 2001).

Autochthones sources of DOC are related to the phytoplankton, to the aquatic macrophytes, and to the periphyton (Farjalla *et al.* 2004). On the other hand, DIC was a relevant variable indicated by the PCA in the final phase of the productive process (period 4), and it is indirectly related to the fish biomass since it was negatively related to DOC. In environments with a large fluctuation of the DOC content, such as rice fields, the photoxidation of DOC to inorganic carbon is mediated by UVA, UVB, and PAR and results in the production of DIC (Granéli *et al.* 1998). This is one of the hypotheses for the fluctuation of DOC and DIC observed in the present study

Effects on phytoplankton, through bottom-up, nutrient-mediated processes in lakes, are well understood. Phosphorus and nitrogen or both are usually relatively scarce in temperate regions and therefore become limiting to algae in many water bodies

(Gibson 1971). An increase in nutrients, through a myriad of bottom-up mechanisms, can increase the phytoplankton biomass until another factor becomes limiting (Williams and Moss 2003).

The deficiency of phosphorus is commonly observed in rice fields (Fernando *et al.* 2005). In the present study, TP and SRP showed a tendency to decrease, being incorporated in the metabolism of the ecosystem, especially in the phytoplankton, since the highest concentrations of chlorophyll *a* in the initial phase of the cycle were associated to the highest concentrations of TP and SRP. It was observed in the present study, a positive relationship between chlorophyll *a* and TP, and SRP and $N^{-}NO_3^{-}$. Considering the N:P ratio, according to Sondergaard *et al.* (1999), environments limited by N present a TN:TP <9, while P is considered limiting when TN:TP > 22. In this study, the mean value of TN:TP was 42, indicating that the system could be P limited for the phytoplankton growth. Even though the ratios indicate limitation, the biomass of the phytoplankton presented a positive correlation with P, which does not indicate growth limit.

The shift from a dry to a wet environment observed in rice cultures is probably a key factor for the composition of the zooplankton community. This shift probably favors organisms that present survivorship and reproduction strategies, such as dormancy, and production of resistant eggs that are deposited on the sediment e will quickly hatch when conditions are favorable. Non-encysted dormancy was observed for copepod species, especially late stages of copepodite, while rotifers and cladocerans are known for the production of resistant eggs. *Eucyclops serrulatus*, the copepod species with highest contribution for the zooplankton biomass, is recognized by Nandini and Sarma (2007) as very tolerant to extreme environmental conditions, such as the chemical and physical dynamics observed in rice cultures.

The relationship between chlorophyll *a* and nutrients, as well as between chl *a* and zooplankton biomass is extensively studied (e.g. Jeppesen *et al.*, 1997, Vakkilainen *et al.* 2004, Reynolds 2006). Correlation (Currie 1990) and regression analysis (Basu and Pick 1996) indicated a positive significant relationship between chl *a* and zooplankton biomass. This relationship is evident since the increase of the phytoplankton biomass is directly related to the availability of nutrients. When the phytoplankton takes up phosphorus, this will rapidly increase its biomass in the system, allowing the increase of the zooplankton biomass due to a higher availability of food. This increase in zooplankton biomass was clear when the regression results confirmed a positive relationship, particularly copepod biomass, the most representative group.

The positive relationship between chl *a* and copepods presented in our study confirm the importance of these large crustaceans grazers in controlling algal biomass, already verified in Vakkilainen *et al.* (2004). The tradicional equilibirium theory of food chain dynamics and its modifications emphasises the control of lower trophic levels by consumers, and predicts that effects of nutrient enrichment are transferred into biomass at the top trophic level and even-numbered levels below it (Vakkilainen *et al.* 2004).

Our results revealed a negative relationship between chl *a* concentrations and fish biomass and between fish biomass and DOC, in special with planktivorous fish biomass. These observations suggest a positive relationship between fish biomass and DIC, whereas without a statistically significance. Highest concentrations of DIC are associated to the final phase of the rice productive cycle. In this phase, the system is more “mature” and presents a higher spatial structure promoted by the growth of the rice macrophytes. When the fish enter the culture areas they find more structured habitats and a high abundance of food, considering the high zooplankton biomass. This will reflect in a high permanence time of these fish in the fields, and consequently in a high capture rate and biomass observed in the middle and at the end of the culture cycle.

In synthesis, our data had evidenced the important role of the availability of nutrients (P, N, C) in the biomass planktonic and fish dynamics in a temporal gradient. DOC proved to be an element key in the system. These results contrast top-down and bottom-up effects regulating along a temporal gradient (cycle of rice production) the primary production in the wetland rice field.

ACKNOWLEDGMENTS

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3. Driving factors of the plankton and fish distribution in a subtropical lake (Mangueira Lake, Southern Brazil)

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ABSTRACT

Biological communities change in time and space following driving pressures from differences in habitat structure and resource availability. In this study we have analyzed changes in the seasonal dynamics of plankton and fish communities in a subtropical lake during one year. We have focused on the spatial and temporal distribution of plankton and fish biomass as a function of the presence of the emergent macrophytes *Zizaniopsis bonariensis*. Mangueira Lake is a large shallow oligo-mesotrophic system. Its average depth is 3 m, being 90 km long, with a maximum width of 11 km and presenting an area about 820 km^2, in Southern Brazil. The lake main axis in the North-East to South-West direction, aligned with the more frequent winds. Analysis of similarity (ANOSIM) applied to environmental variables showed significant differences between sampling sites (North and South), but not significant differences in the habitat structure (by *Z. bonariensis* and open water). Secchi transparency (P <0.001), DOC (P=0.03) and chlorophyll *a* (P<0.001) were significantly different in North and South sampling sites. ANOVA results showed that season effects are stronger in the Northern sampling site. Bacterioplankton biomass (P=0.036), chlorophyll *a* (P=0.043), zooplankton biomass (P=0.049) and fish captures (P=0.044) were different seasonally after extracting the habitat structure effect, while in the southern sampling site only chlorophyll *a* presented a seasonal significant variation (*P*=0.045). Habitat structure (by *Z. bonariensis* stands and open water samples) induced significant differences in chlorophyll *a* both in North (*P*=0.004) and South samples (*P*=0.042) after extracting seasonal effect. Fish captures do also responded to habitat structure (*P*=0.017) in the North, after extracting the season effect. Analysis of similarity (ANOSIM) applied to fish community also showed significant differences between North and South, although no significant differences between vegetated and open water zones was observed. Total biomass (*P*=0.01), number of captures (*P*<0.001), and richness (*P*=0.01) were different between sampling sites. Redundancy Analysis (RDA) by using 5 abiotic variables and plankton biomass explained 97.4% of data variability in the first two axes (axis 1=92.3%; *P=0.005*). The RDA showed that copepod nauplii, copepod cyclopoid and *Conochilus coenobasis* (Rotifer) biomass were strongly correlated with low depths. The RDA analyses also confirmed the temporal (seasonal) and spatial (North/South) gradient, as observed in the PCA analyses.

Key-words: Bacterioplankton, chlorophyll *a*, zooplankton, fish, Shallow lake, Redundancy analysis, Spatial and Temporal Gradient.

INTRODUCTION

Studies of fish-zooplankton interactions and its effects on phytoplankton and bacterioplankton are crucial for understanding the functioning of an aquatic ecosystem. The structure of the fish community in a lake, however, strongly regulates their effects in the whole ecosystem (Jeppesen *et al.* 1997b). Fish, due to their mobility and flexible feeding behavior, link the littoral, benthic, and pelagic habitats in a much more significant manner than was historically considered, affecting nutrient transport and predator-prey interactions (Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002).

Biological communities change in time and space as result of habitat structure, resource availability among with other factors (Grenouillet *et al*. 2002). To identify the factors driving the distributional pattern of lake organisms it is important to understand the whole system a mosaic of habitats, especially the littoral zone (Lodge *et al*. 1988, Chick and McIvor 1994).

The structuring effects of aquatic plants in the littoral zone of lakes, with influences in the entire lake ecosystem, have been widely recognized (Carpenter and Lodge 1986, Jeppesen *et al*. 1997a, Meerhoff *et al*. 2007). However, most studies have focused on submerged macrophytes (Meerhoff 2003, Mazzeo *et al*. 2003, Teixeira-de-Mello *et al*. 2009), instead of emergent species (Dieter 1990, Horppila and Nurminen 2001, 2005).

Also, several works have focused on the structure of shallow lakes communities in temperate areas (Carpenter and Lodge 1986, Moss 1990, Jeppesen *et al*. 1997b, Teixeira-de Mello *et al*. 2009), although a tropical and subtropical ecosystem may presents greater complexity both in structure and trophic interactions (Lazzaro 1997, Teixeira-de Mello *et al*. 2009).

In a complex systems comprised of shallow lakes, a wetlands and wetland-lakes, such as the Taim Hydrological System (THS), the hydrodynamics and the hydrological signature could also play an important role driving the structure of biological communities. The Taim Hydrological System has two main conflicting functions: (1) biological conservation of an important landscape, through the Taim Ecological Station; and (2) the supply of water for rice production. In recent decades, the Taim ecosystem had undergone an unregulated manipulation and its present hydrological cycle no long represents natural conditions (Crossetti *et al.* 2007). Over this same period, the biological communities may have undergone changes in such an extent that may be difficult to evaluate. Whether influenced by human or natural stressors, alteration in the Taim Hydrological System includes stabilization and changes in the inundation period, as well as increases and reductions in inundation amplitude (Motta Marques and Villanueva 2001). In this study we have analyzed changes in the seasonal dynamics of plankton and fish communities in a subtropical lake of Taim Hydrological System. We have focused on the spatial and temporal distribution of fish, zooplankton, bacterioplankton and chlorophyll *a* concentration as a function of the structuring effect of the emergent macrophyte *Zizaniopsis bonariensis*. We also analyzed the existence of longitudinal gradient in Mangueira Lake.

MATERIAL AND METHODS

Study site

The study was carried out in a large shallow (oligo-mesotrophic and max. depth 6m) coastal lake, named Mangueira. It is situated along the Atlantic Ocean, Southern Brazil (33º31’22”S 53º07’48”W) (Fig.1) and has 90 km in length and 3-10 km in width. This ecosystem was originated from the last glaciation on the southeast coast of South America (during the Pleistocene ~5,000 years ago). The lake main axis in the North-East to South-West direction, following the more frequent winds. The Northern and Southern extremes of the lake establish an important interface with the Taim wetlands.

Sampling and field measurements

Limnological and biological data were collected immediately outside of *Zizaniopsis bonariensis* stands (=Vegetated Zones) and adjacent open water (=Unvegetated Zones), distant ~ 500 meters. The samplings were performed seasonality, from winter of 2006 to autumn of 2007, in two sampling points - North (N) and South (S) (Fig. 1).

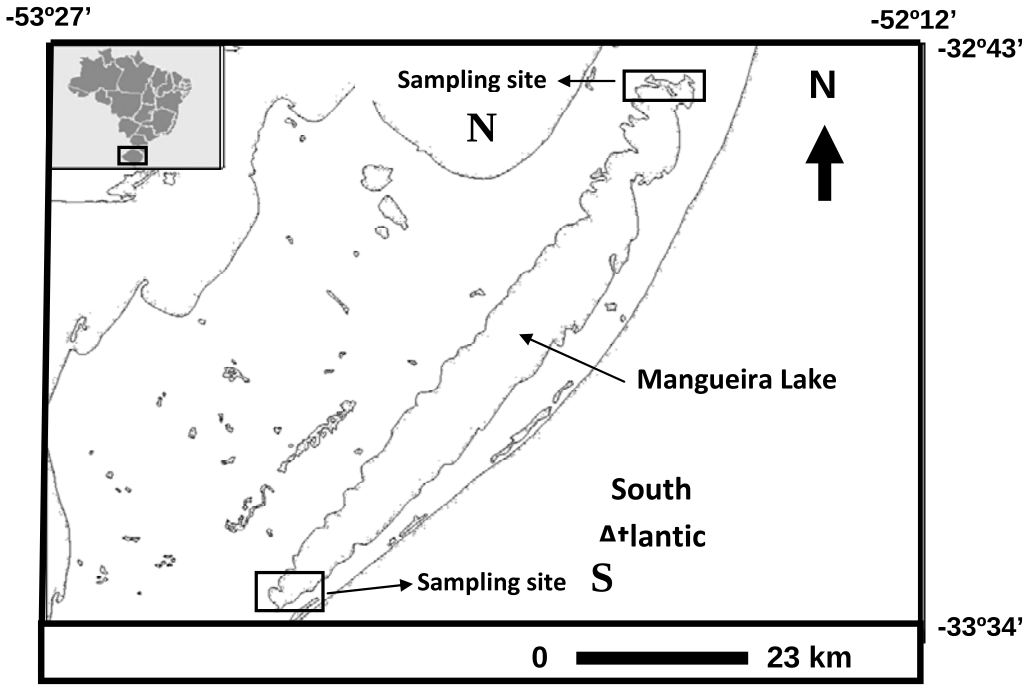

Figure 1. Mangueira lake, coastal lake in Rio Grande do Sul state, Southern Brazil.

Water temperature, dissolved oxygen and pH were measured with a Multiparameter Water Quality Sonde (YSI 6600). Transparency was estimated with a Secchi disk and depth with a handheld sonar system. Water samples for chemical analysis were collected using a water column sampler, extracting the entire water column from surface to two meters. After homogenizing, a sub-sample were stored and conserved following appropriate protocols (Mackereth *et al.* 1989; Jespersen and Christoffersen 1987; APHA 1999)

For bacterioplankton analysis, sub-samples of 9 mL were fixed with 1 mL of formaldehyde (4%). Zooplankton samples were obtained by filtering 20 liters of water column through plankton net (65 µm mesh size) and fixed with formaldehyde (4%). Fish captures were made overnight (15h) by using multiple-mesh gillnets (5, 6.25, 8, 10, 12.5, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65 and 70mm of mesh size, modified EU Standard), each sampling unit with triplicate. Sampled fish were stored in formaldehyde (4%).

Sample and data analysis

Total phosphorus (TP) and total nitrogen (TN) were analysed according to Mackereth *et al*. (1989). Total solids analysis was estimated according to APHA (1999) and carbon analysis - dissolved organic (DOC) and dissolved inorganic (DIC) - were measured by total organic carbon (TOC) analyzer (Shimadzu VCPH). Chlorophyll *a* was extracted from GF/F filters into 90% ethanol (Jespersen and Christoffersen, 1987) and measured by spectrophotometric method (APHA 1999).

Bacterioplankton biomass was estimated through biovolume after morphotype identification (Hobbie *et al*. 1977) by applying the closest geometric formulae (Norland 1993, Kepner and Pratt 1994, Massana *et al*. 1997), through an images analyzer CMEIAS (Liu *et al*. 2001).

Quantitative analysis for zooplankton was performed using a Sedgwick-Rafter chamber (APHA 1992). Zooplankton biomass was calculated through biovolume, by applying the closest geometric formulae (Bottrell *et al*. 1976, Dumont *et al*. 1975, Ruttner-Kolisko 1977, Malley *et al*. 1989).

In laboratory fish were identified to species, measured (total length, to nearest mm) and weighed with a semi-analytical balance (to nearest 0,01g). The fish species were grouped according to feeding habits (functional guilds) after stomach content analysis. Frequency of occurrence (%) was used to identify ontogenetic change on feeding habits. Each species was assigned to a feeding guild as: mainly invertebrate (MI), mainly fish (MF), detritus (D), invertebrates and fish (IF), planktivorous and invertebrates (PI) and omnivorous (OV), adapted of Sánchez-Botero *et al.* (2008). For feeding preference guilds, fish was analyzed as biomass.

Fish community structure was estimated for each sampling unit according to total specimens collected (N), species richness (S), Shannon diversity index (H'), and Shannon equitability (Evenness, E) (Krebs 1989). The software package Species Diversity and Richness 3.0 (Henderson and Seaby 2002) was used to estimate diversity parameters.

Statistical Analysis

Ordinations analyses were performed using the software PC-ORD version 4.0 for Windows (McCune and Mefford 1999) and CANOCO version 4 (ter Braak and Šmilauer 1998). Detrended correspondence analysis (DCA) for species abundance parameters and environmental data was used to determine whether linear or unimodal ordination methods should be applied (ter Braak and Šmilauer 1998). For the ordination analysis, the abiotic data were transformed by $\log_x + 1$.

Principal components analysis (PCA) was undertaken to determine spatial and temporal changes of physical and chemical conditions. Redundancy analysis (RDA) was used to examine the relationships between the plankton community and environmental variables (ter Braak and Šmilauer 1998). The significance of environmental variables to explain the variance of functional groups data in the RDA was tested using Monte Carlo simulations with 199 permutations (ter Braak and Šmilauer 1998).

Analysis of similarity (ANOSIM) was applied to identify dissimilarity between environmental variables and attributes of fish community in both habitat structure (vegetated and unvegetated zones) and sampling site (North and South). Bonferroni correction was applied in the analysis of Bray-Curtis similarity through PAST statistical software version 1.72 (Hammer *et al.* 2001).

ANOVA (two-way) test was used to compare the effect of the habitat structure and seasons in different sampling site, and the effect of sampling site and seasons in different habitat structure for plankton and fish communities.

RESULTS

Physical and chemical scenario

Our results showed considerable spatial (North-South) and temporal (seasonal) variation in limnological parameters of the Mangueira Lake, nevertheless similar values for environmental variables were measured on *Z. bonariensis* stands and in open waters (Table 1). Nutrient dynamics were driven by the season, mainly for total nitrogen (TN) and total phosphorus (TP). Total nitrogen and total phosphorus were generally low in both sampling sites but with increased concentration in the summer (Table 1). Total nitrogen ranged from 0.23 $mg.L^{-1}$ to 1.68 $mg.L^{-1}$ in the South and from 0.26 $mg.L^{-1}$ to 1.53 $mg.L^{-1}$ in Northern Mangueira Lake. Total phosphorus ranged from 0.02 $mg.L^{-1}$ to 0.11 $mg.L^{-1}$ in South and from 0.03 $mg.L^{-1}$ to 0.08 $mg.L^{-1}$ in North. DOC presented lower values in the North of the study area, averaging 16.13 ± 3.40 $mg.L^{-1}$ and 20.13 ± 2.75 $mg.L^{-1}$ respectively (Table 1). Secchi transparency showed highest values in the Southern sampling site (South average transparency = 1.15 m; North average transparency = 0.45 m).

Table 1 Limnological variables measured of the Mangueira Lake during the study period.

Parameter	Winter 2006				Spring 2006				Summer 2007				Autumn 2007			
	North_UZ	North_VZ	South_UZ	South_VZ	North_UZ	North_VZ	South_UZ	South_VZ	North_UZ	North_VZ	South_UZ	South_VZ	North_UZ	North_VZ	South_UZ	South_VZ
Water temperature (ºC)	14.8	14.8	13.5	13.5	17.0	17.0	16.0	16.0	26.0	26.0	24.8	24.8	12.7	12.7	12.4	12.4
Dissolved Oxigen (mg.L^{-1})	10.3	10.3	11.9	11.9	9.9	9.9	9.8	9.8	9.9	9.9	8.6	8.6	9.1	9.1	8.6	8.6
pH	8.1	8.1	8.1	8.1	7.9	7.9	7.8	7.8	7.6	7.6	7.3	7.3	7.9	7.9	7.6	7.6
Depth (m)	1.7	1.7	1.8	1.8	2.0	2.0	2.1	2.1	1.3	1.3	1.6	1.6	1.0	1.0	1.5	1.5
Secchi transparency (m)	0.7	0.7	2.0	2.0	0.2	0.2	1.0	1.0	0.4	0.4	0.8	0.8	0.5	0.5	0.8	0.8
Total Solids (mg.L^{-1})	390	393	160	163	311	317	187	191	438	442	363	369	139	143	110	114
DOC (mg.L^{-1})	20.7	20.3	17.9	17.2	19.2	15.0	23.0	25.3	14.0	15.0	18.0	21.0	12.0	13.0	20.0	19.0
DIC (mg.L^{-1})	23.5	24.1	18.8	15.9	27.0	28.0	24.5	24.9	27.7	27.0	16.1	16.7	19.0	19.0	14.0	13.0
TP (mg.L^{-1})	0.042	0.047	0.018	0.020	0.067	0.076	0.032	0.036	0.040	0.062	0.083	0.114	0.028	0.032	0.040	0.038
TN (mg.L^{-1})	0.478	0.407	0.233	0.318	0.948	0.874	0.941	0.902	1.498	1.530	1.617	1.682	0.256	0.313	0.295	0.311
Chlorophyll *a* (μg.L^{-1})	5.7	8.8	3.5	4.6	8.1	13.7	0.5	2.6	9.0	14.5	2.7	3.3	5.4	11.4	1.8	2.7

North and South = sampling sites; UZ, Unvegetated Zone; VZ, Vegetated Zone; TP, Total Phosphorus; TN, Total Nitrogen; DOC, Dissolved Organic Carbon; DIC, Dissolved Inorganic Carbon.

Analysis of similarity (ANOSIM) applied to environmental variables showed significant differences between sampling sites (North and South), but not significant differences in the habitat structure (by *Z. bonariensis* and open water). Secchi transparency (R=0.43, *P* <0.001), DOC (R=0.22, *P*=0.03) and chlorophyll *a* (R=0.67, *P*<0.001) were significantly different in North and South sampling sites.

The principal components analysis (PCA) evaluated the main trends between limnological variables in the Mangueira Lake showing temporal (Fig. 2a) and spatial (Fig. 2b) gradients. By using 11 abiotic variables, the PCA explained 84.9% of data variability in the first three axes (axis 1= 37.1%; axis 2= 27.1%; axis 3= 20.7%). The most important variables for axis 1 ordination were temperature (0.87), Secchi (-0.69), TS (0.70), TP (0.82), TN (0.87) and pH (-0.76). Axis 2 was related mainly to DO (-0.70), DIC (0.69) and depth (-0.71); wears for the axis 3 chlorophyll *a* (0.84) and DOC (-0.80) were the more relevant parameters. Axis 1 showed a temporal gradient, axis 2 was related to deep, reflecting lake water level, and the axis 3 divides clearly North and South samples, indicating a spatial gradient.

Biotic data

Seasonal variation of chlorophyll *a*, bacterioplankton biomass, zooplankton biomass and fish biomass by sampling site could be observed though figure 3.

Parameters of fish diversity by sampling unit are described in Table 2. ANOVA results (Table 3) showed that season effects are stronger in the Northern sampling site. Bacterioplankton biomass (*P*=0.036), chlorophyll *a* (*P*=0.043), zooplankton biomass (*P*=0.049) and fish captures (*P*=0.044) were different seasonality after extracting the habitat structure effect, while in the Southern sampling site only chlorophyll *a* presented a seasonal significant variation (*P*=0.045).

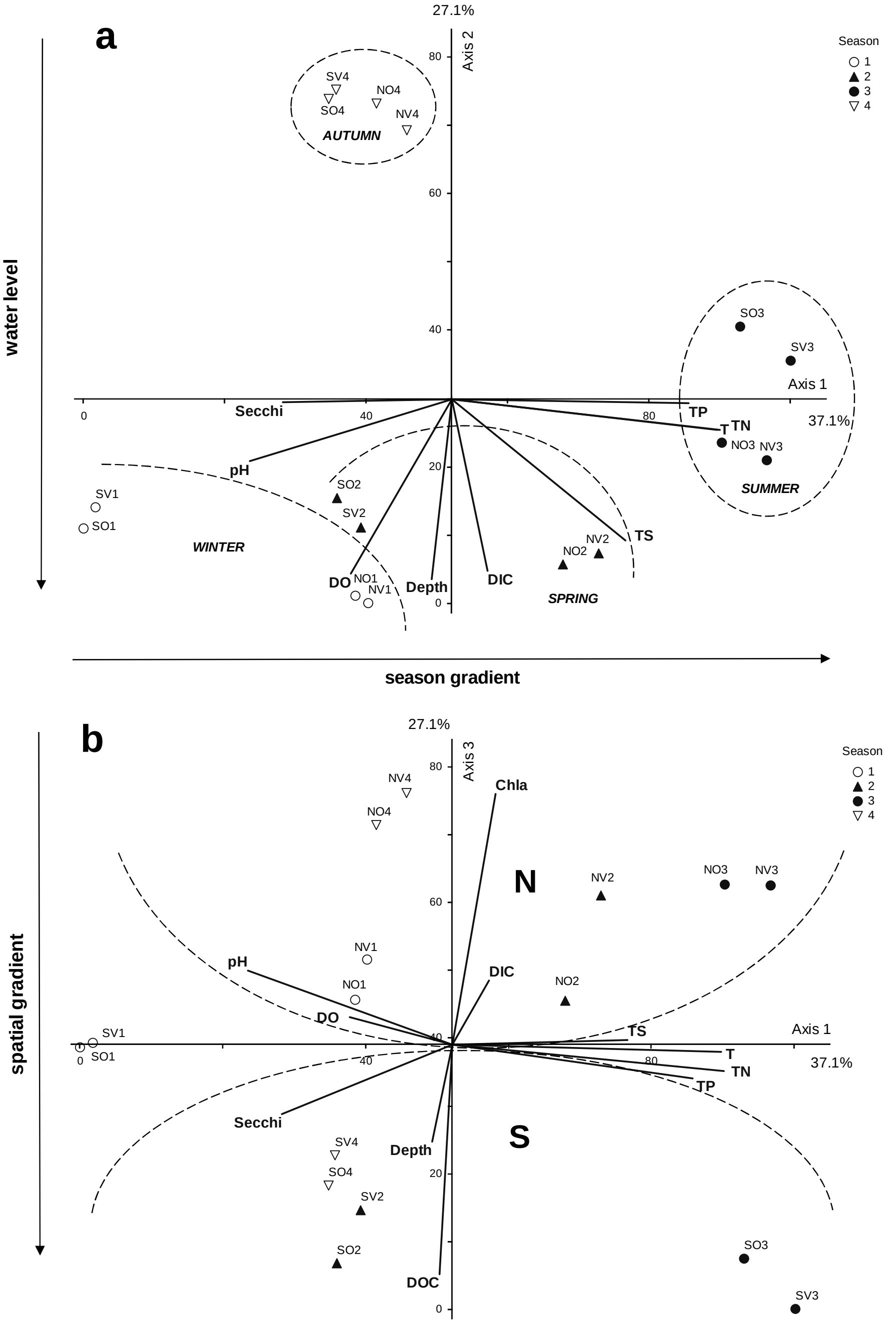

Figure 2. Scores derived from the principal components analysis (PCA) applied to environmental variables in the Mangueira Lake: axis 1 and 2 (a); axis 1 and 3 (b).

Sampling site = North (N); South (S).
Habitat structure = Vegetation (V) = *Zizaniopsis bonariensis* stands; Open water = (O).
Seasons = 1 = winter; 2 = spring; 3 = summer; 4 = autumn.
T = water temperature; TP = total phosphorus; TN = total nitrogen; TS = total solids; DOC = dissolved organic carbon; DIC = dissolved inorganic carbon; DO = dissolved oxygen; Chla = chlorophyll *a*.

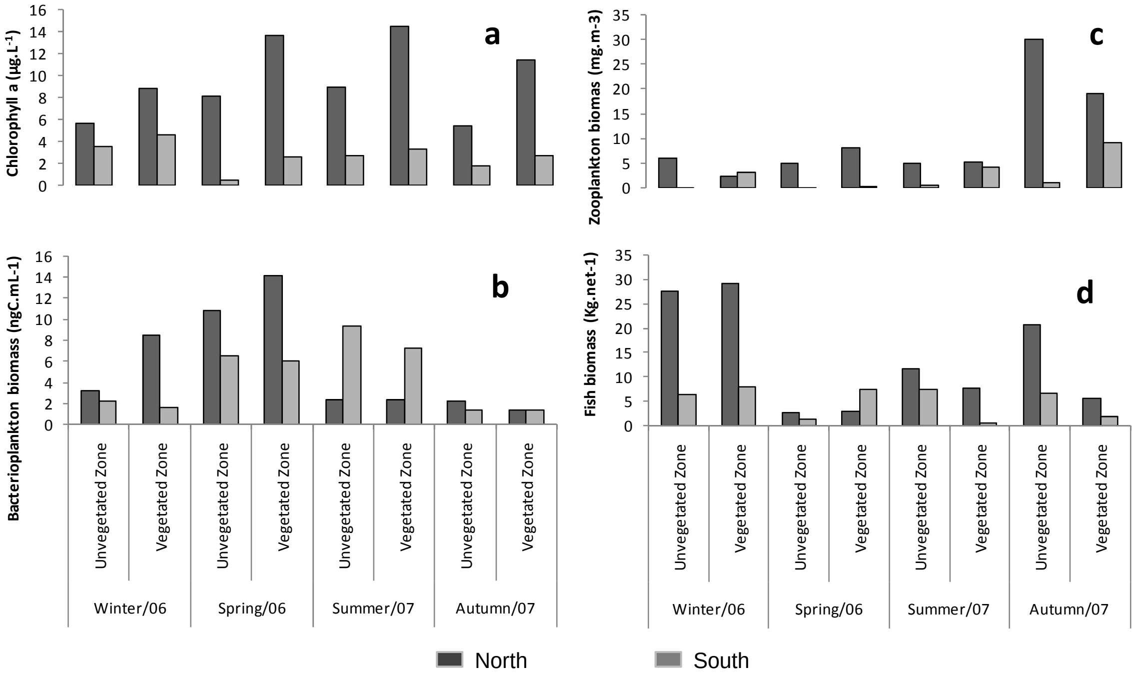

Figure 3. Chlorophyll *a* (a), bacterioplankton biomass (b), zooplankton biomass (c) and fish biomass (d) in the Mangueira lake during the study.

Habitat structure (by *Z. bonariensis* stands and open water samples) induced significant differences in chlorophyll *a* both in North (*P*=0.004) and South samples (*P*=0.042) after extracting seasonal effect. Fish captures do also responded to habitat structure (*P*=0.017) in the North, after extracting the season effect.

By comparing sampling site (North-South) without the effect of seasonal variability, it was identified differences in chlorophyll *a* concentration both in open water (*P*=0.029) and by *Z. boneriensis* stands (*P*=0.012). Fish captures (*P*=0.009) and fish biomass (*P*=0.040) were also different between sampling sites, without season effect in open water. In vegetated zone (by *Zizaniopsis bonariensis* stands) chlorophyll *a* (*P*=0.012) and zooplankton richness (*P*=0.023) presented differences.

Table 2 Attributes of fish community (total biomass, captures, Shannon diversity index (H'), Shannon equitability (E) and richness (S) in the Mangueira lake during the study.

Season	Sampling site	Habitat structure	Total biomass	Captures	H'	E	S
Winter_2006	Northern	Unvegetated zone	29275.0	262	2.03	0.72	17
		Vegetated zone	32702.0	351	1.46	0.52	17
	Southern	Unvegetated zone	6990.0	83	1.75	0.68	13
		Vegetated zone	8021.0	53	2.10	0.87	11
Spring_2006	Northern	Unvegetated zone	9623.0	343	1.79	0.62	18
		Vegetated zone	5127.0	370	2.07	0.70	19
	Southern	Unvegetated zone	1675.0	164	2.06	0.80	13
		Vegetated zone	10454.0	440	1.84	0.65	17
Summer_2007	Northern	Unvegetated zone	15098.0	200	1.88	0.68	16
		Vegetated zone	10485.0	291	2.43	0.78	23
	Southern	Unvegetated zone	8979.3	106	2.27	0.80	17
		Vegetated zone	449.5	34	1.77	0.85	8
Autumn_2007	Northern	Unvegetated zone	21778.1	297	1.84	0.74	12
		Vegetated zone	5619.2	382	1.48	0.71	8
	Southern	Unvegetated zone	6656.5	61	1.06	0.77	4
		Vegetated zone	2036.4	42	2.09	0.84	12

Analysis of similarity (ANOSIM) applied to fish community structure also showed significant differences between North and South, although not significant differences between vegetated and open water zones. Total biomass (R=0.17, P=0.01), number of captures (R=0.47, P<0.001), and richness (R=0.21, P=0.01) were different between sampling sites.

Detrended correspondence analysis (DCA) applied to plankton species indicated that gradient lengths of the first two axes (2.14 and 2.00 standard deviation units, respectively) were relatively short, and therefore linear ordination methods, as Redundancy Analysis (RDA), were appropriate.

RDA using 5 abiotic variables explained 97.4% of data variability in the first two axes (axis 1=92.3%; $P=0.005$). The most important environmental variables for axis 1 ordination were depth (-0.74) and TN (-0.33). Axis 2 was mainly related to TP (-0.34) (Fig. 4).

Table 3 Two way ANOVA results (P values) comparing the effect of the habitat structure (open water and by *Zizaniopsis bonariensis* stands), sampling seasons and sampling site (North and South) for plankton and fish communities in the Mangueira lake.

Northern Mangueira	Habitat structure without season effect	Seasons without habitat structure effect
Bacterioplankton biomass	0.272	***0.036***
Chlorophyll *a*	***0.004***	***0.043***
Zooplankton Biomass	0.425	***0.049***
Zooplankton Richness	0.473	0.447
Fish Captures	***0.017***	***0.044***
Fish Biomass	0.268	0.080
Fish Richness	0.689	0.162
Southern Mangueira	Habitat structure without season effect	Seasons without habitat structure effect
Bacterioplankton biomass	0.266	0.310
Chlorophyll *a*	***0.042***	***0.045***
Zooplankton Biomass	0.103	0.353
Zooplankton Richness	0.126	0.500
Fish Captures	0.660	0.261
Fish Biomass	0.838	0.925
Fish Richness	0.950	0.651
Unvegetated zone	Sampling site without season effect	Seasons without sampling site effect
Bacterioplankton biomass	0.920	0.340
Chlorophyll *a*	***0.029***	0.674
Zooplankton Biomass	0.167	0.458
Zooplankton Richness	0.850	0.738
Fish Captures	***0.009***	0.260
Fish Biomass	***0.040***	0.291
Fish Richness	0.122	0.130
Vegetated zone	Sampling site without season effect	Seasons without sampling site effect
Bacterioplankton biomass	0.147	0.170
Chlorophyll *a*	***0.012***	0.788
Zooplankton Biomass	0.182	0.136
Zooplankton Richness	***0.023***	0.995
Fish Captures	0.115	0.407
Fish Biomass	0.283	0.392
Fish Richness	0.320	0.609

Chlorophyll *a* concentration (Chla) (62.2%), Nauplii (Nau) (61.4%), Cyclopoid copepodit (C) (58.5%), *Conochilus coenobasis* (Cc) (57.2%), Bacterioplankton (Bac) (48.9%), *Centropyxis aculeata* (Ca) (31.3%) and *Bosmina longirostris* (Bl) (30.5%) were explained in the first four axes. The RDA showed that nauplii, *Conochilus coenobasis* and cyclopoid biomass were strongly correlated with low depths. The RDA analyses also confirmed the temporal (seasonal) and spatial (North/South) gradient, as observed in the PCA analyses.

Bacterioplankton was mainly of the Coccus morphotype in almost all samples (Fig. 5). Regular Rod and Curved Rod bacterioplankton morphotype were also present but less representative. A total of 55 zooplankton species was identified. No clear pattern of spatial or temporal change in zooplankton composition was verified even though South samples presented less group diversity sample by sample. Copepods were predominant in both sampling sites (60.71% in North and 64.63% in South) (Fig. 6), represented mainly by Cyclopoid copepodites and nauplii. Cladocerans (8.11% in North and 9.28% in South), rotifers (6.05% in North and 6.25% in South) and protists (6.49% in North and 10.54% in South) were presented with minor biomass abundance. Identified important species in biomass were *Conochilus coenobasis* Skorikov, 1914 (Rotifer), *Bosmina longirostris* (O.F. Muller, 1785) (Cladocera) and *Centropyxis aculeata* (Ehrenberg, 1838) (Protist).

Important differences in fish structure (abundance and richness) between the extremes of the Mangueira Lake were identified. A total of 3479 fish specimens were collected, with 2496 in the Northern and 983 in the Southern extremes of Mangueira Lake. Fish biomass was also highest in the Northern sampling site than in South. The checklist resulted in 35 species, distributed in 11 families (Table 4).

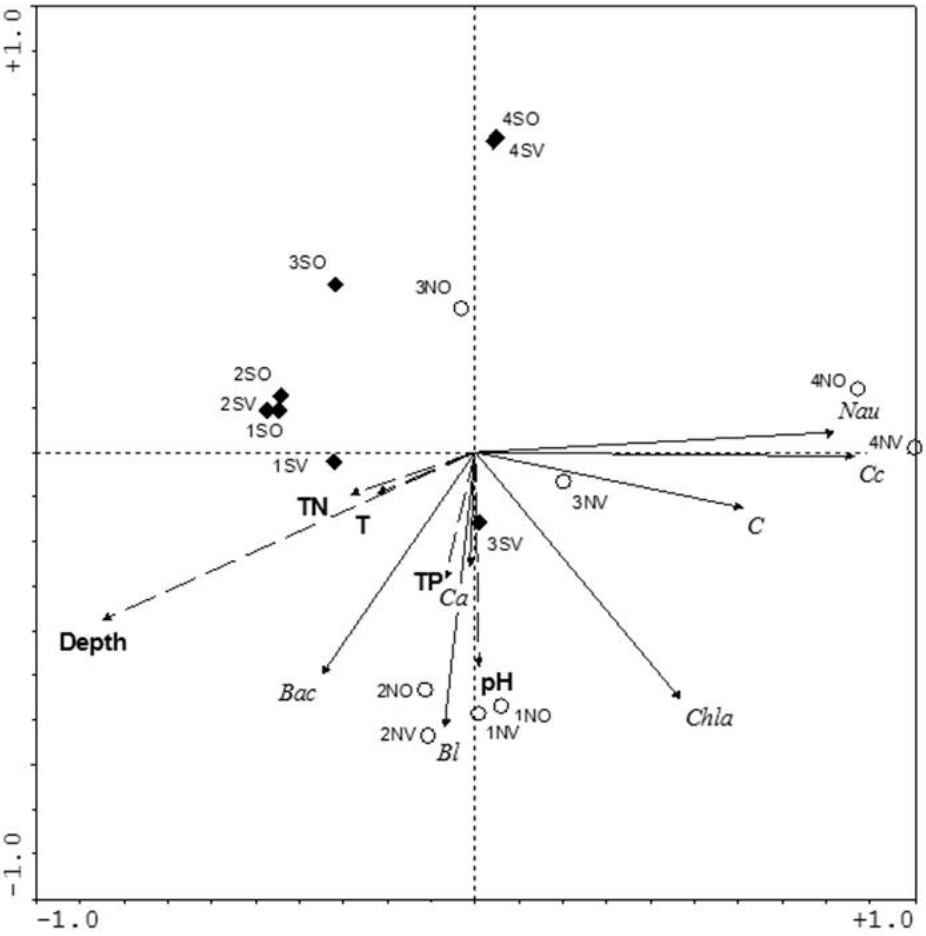

Figure 4. Triplot diagram for RDA of Mangueira Lake data, including limnological variables (explanatory variables), biotic data (dependent variables), sample units (sampling site and habitat structure) and seasons.

Limnological variables = T = temperature; TP = total phosphorus; TN = total nitrogen; pH; depth.

Biotic data = Chla = chlorophyll *a*; Nau = nauplii; C = Cyclopoid; Cc = *Conochilus coenobasis*; Bac = Bacterioplankton; Ca = *Centropyxis aculeata*; Bl = *Bosmina longirostris*.

Sampling site = North (N); South (S).

Habitat structure = Vegetation (V) = *Zizaniopsis bonariensis* stands; Open water = (O).

Seasons = 1 = winter; 2 = spring; 3 = summer; 4 = autumn.

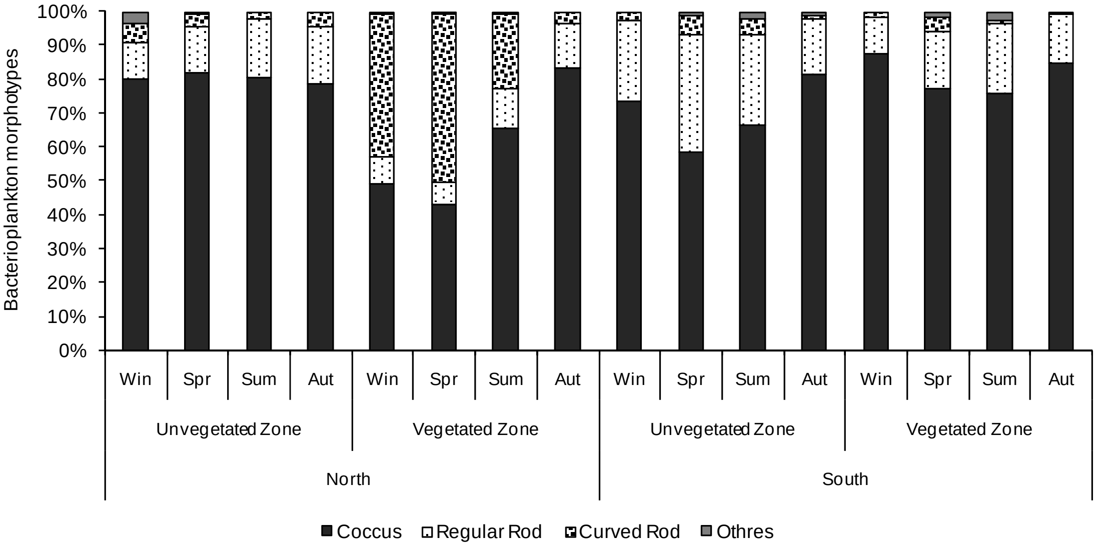

Figure 5. Biomass of bacterioplankton morphotypes in the Mangueira lake.

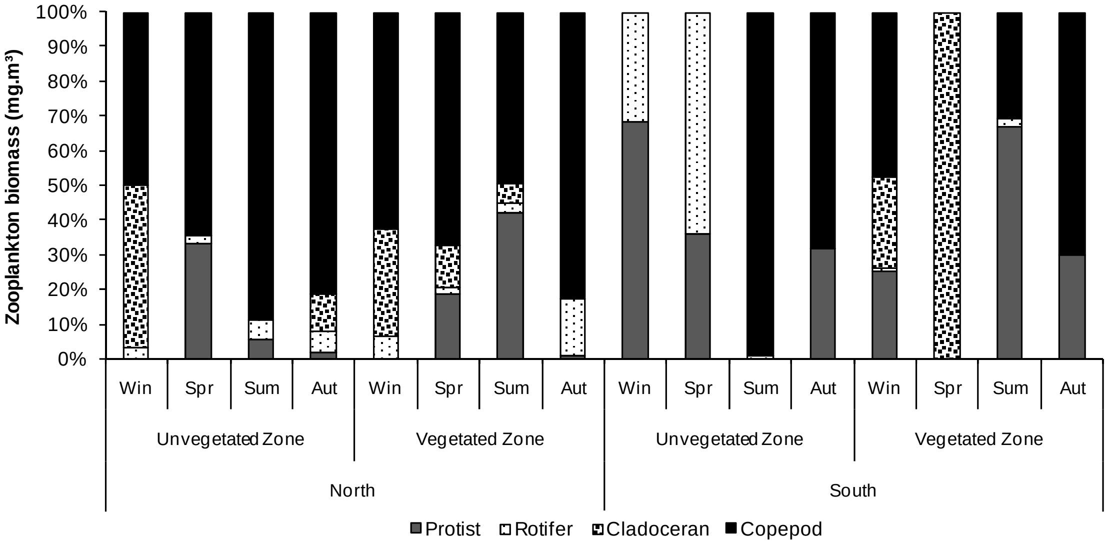

Figure 6. Biomass of zooplankton taxonomic groups in the Mangueira lake.

Table 4 Fish families and species captured in the Mangueira lake during the study and functional guild classifications for more abundant species (mainly invertebrate (MI), mainly fish (MF), detritus (D), invertebrates and fish (IF), other than planktivorous and invertebrates (PI) and omnivorous (OV)).

Family Species	Feeding Guilds
Clupeidae	
Platanichthys platana (Regan, 1917)	PI
Curimatidae	
Cyphocharax voga (Hensel, 1870)	D
Erythrinidae	
Hoplias malabaricus (Bloch, 1794)	MF
Characidae	
Astyanax eigenmanniorum (Cope, 1894)	OV
A. fasciatus (Cuvier, 1819)	OV
A. jacuhiensis (Cope, 1894)	OV
Astyanax sp.	OV
Bryconamericus iheringii (Boulenger, 1887)	PI
Charax stenopterus (Cope, 1894)	-
Cheirodon ibicuhiensis Eigenmann, 1915	-
Cyanocharax alburnus (Hensel, 1870)	PI
Hyphessobrycon bifasciatus Ellis, 1911	-
H. luetkenii (Boulenger, 1887)	OV
Oligosarcus jenynsii (Günther, 1864)	MI
O. robustus Menezes, 1969	MF
Auchenipteridae	
Trachelyopterus lucenai Bertoletti, Silva & Pereira, 1995	OV
Heptapteridae	
Pimelodella australis Eigenmann, 1917	-
Rhamdia quelen (Quoy & Gaimard, 1824)	OV
Callichthyidae	
Corydoras paleatus (Jenyns, 1842)	-
Hoplosternum littorale (Hancock, 1828)	-
Loricariidae	
Hisonotus taimensis (Buckup, 1981)	-
Hypostomus commersoni Valenciennes, 1836	-
Loricariichthys anus (Valenciennes, 1836)	-
Rineloricaria longicauda Reis, 1983	-
Anablepidae	
Jenynsia multidentata (Jenyns, 1842)	-
Atherinopsidae	
Odontesthes bonariensis (Valenciennes, 1835)	MI
O. humensis de Buen, 1953	MI
O. mirinensis Bemvenuti, 1995	MI
O. perugiae Evermann & Kendall, 1906	MI
O. retropinnis (de Buen, 1953)	MI
Cichlidae	
Crenicichla lepidota Heckel, 1840	MF
C. punctata Hensel, 1870	MF
Gymnogeophagus gymnogenys (Hensel, 1870)	-
G. rhabdotus (Hensel, 1870)	-
Geophagus brasiliensis (Quoy & Gaimard, 1824)	OV

Characiformes was the most representative order by number of captured specimens and biomass. *Oligosarcus jenynsii* (Günther, 1864) was the most abundant species as total captures (28%) and biomass (26%) in Northern Mangueira Lake. *Cyphocharax voga* (Hensel, 1869), although with low frequency of captures (8%), represented 24% of captured biomass in the Northern site. In Southern Mangueira Lake *Bryconamericus iheringii* (Boulenger, 1887) was the most representative specie as captures (29%), but with low biomass (3%) while *Odontesthes humensis* de Buen, 1953 was the most represented specie as biomass (23%), followed of *Hoplias malabaricus* (Bloch, 1794) (21%) and *O. jenynsii* (18%).

The more frequent fish species were classified as functional feeding guilds (Table 4). Figure 7 presents guild distribution by sampling site and season. High percentage of the mainly invertebrate eaters guild (38%), detritivorous (28%) and omnivorous (21%) were present in the Northern site, while mainly fish eaters were less frequent (13%). In Southern Mangueira Lake the trophic structure is similar, but with an inversion. An increased presence of mainly fish eaters (25%) and a decrease of detritivorous fish (16%) were identified, although mainly invertebrate eaters (41%) and omnivorous fish (19%) were present in similar frequencies.

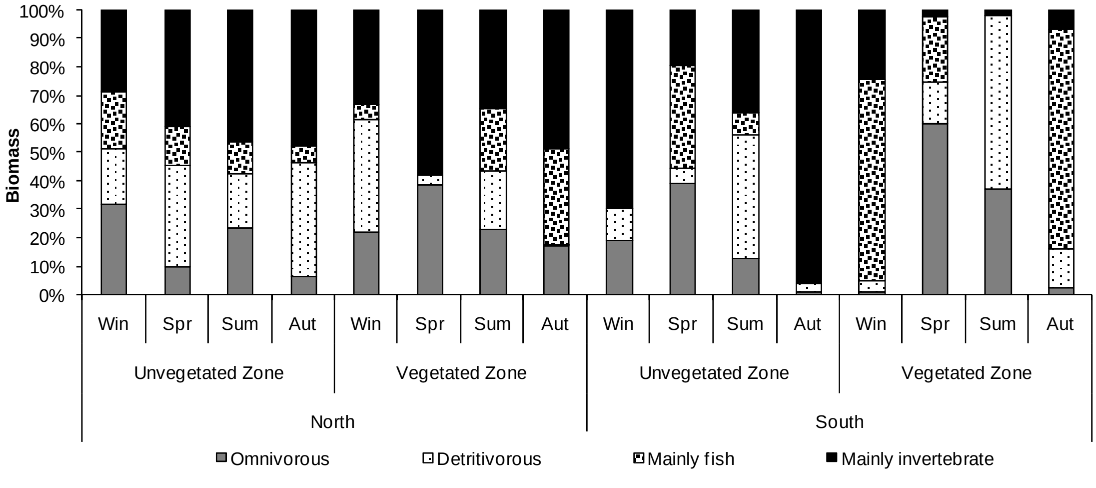

Figure 7. Fish guilds biomass in the Mangueira lake during the study.

The planktivorous guild was not important as captured biomass in both sites, although *B. iheringii* was a dominant species as number of captures in Southern Mangueira Lake.

DISCUSSION

Remarkable spatial (Northern-Southern) and temporal (seasonal) differences in water chemistry characteristics and between plankton and fish communities were observed in littoral zones of Mangueira Lake. The availability of nutrients has an essential role in the control of the biomass and composition of plankton communities (Reynolds 1997). Although nutrients analysis did not show differences in TP and TN concentrations between habitat structures and sampling sites, significant differences in chlorophyll *a* concentrations were observed when compared structure (by *Z. bonariensis* beds and open water) or sampling site (North and South). Concentrations of chlorophyll *a* were highest in vegetated zones in both North and South sampling sites, maybe due to periphyton and metaphyton associated to macrophyte beds.

A spatial gradient were clearly identified. The Southern sampling site was characterized by increased water transparency, less chlorophyll *a* concentration and more PVI (percent volume infested) of submerged macrophytes (Finkler-Ferreira 2009), maybe inhibiting phytoplankton and bacterioplankton production and producing more DOC. On the other hand, in the Northern sampling site there were increased chlorophyll *a* concentration, minor water transparency, absence of submerged macrophytes and increased total solids concentration, may be due to input of nutrients and organic matter from the Taim wetland.

Large oligo-mesotrophic lakes may be expected to tend towards autotrophy because of low DOC values, long water renewal times and weaker coupling to the terrestrial catchments (Bocaniov and Smith 2009). Autochthones sources of DOC are related to phytoplankton, aquatic macrophytes, and periphyton (Farjalla *et al*. 2004). This autochthon primary production is responsible for a considerable part of the DOC in aquatic environments (Wetzel 1992). Southern Mangueira presented larger biomass of submerged and free floating macrophytes, and this is one of the hypotheses for explain the increased DOC concentration in this samplings site.

A temporal (seasonal) gradient related to nutrient dynamics and depth was also found in the study. Seasonal differences are related to environmental factors, such as irradiance levels, temperature, and resource availability, especially nutrients and light (Wersal *et al*. 2006). Abiotic factors, such as wind, precipitation, turbidity, and the hydrological cycle are also critical factors affecting the seasonality in the tropics (Hart 1990, Mengistu and Fernando 1991).

The seasonal cycle of abiotic parameters of the Mangueira Lake were key factors driving the planktonic communities. During the spring, with increased water level (deep) and nutrient concentration in Northern Mangueira Lake, bacterioplankton presented increased biomass. In the summer, nutrient input from rice fields (Rodrigues *et al*., in prep.) reflected in increased bacterioplankton biomass but with no greater values of chllorophyll *a*.

Bacterioplankton and phytoplankton compete directly for nutrients, manly for phosphorus. Bacteria may have uptake advantages compared with phytoplankton because of greater surface area to volume ratios (Cottingham *et al*. 1997, Litchman *et al*. 2004). Thus, the algal growth can be severely restricted in the presence of bacteria when phosphorus is a limiting factor. This result suggests that heterotrophic bacteria may have been phosphorus limited, assuming that they were not carbon limited (Wetzel 2001).

Coccus was a predominant bacteria morphotype in extremes of Mangueira Lake, although curved rod morphotype presented increased biomass in North vegetated sites during the winter and spring. Large bacteria, as Coccus, are related to nutrient availability and DOC concentration, especially the labile fraction (Steinberger *et al.* 2002). More complex bacteria morphotypes, as Curved Rod, are related to the refractory fraction DOC with inputs from Taim wetland.

Differences in zooplankton biomass between sampling sites and habitat structure were found. In Southern Mangueira Lake larger zooplancton biomass were obtained on *Z. bonariensis* beds. Structured microhabitats seem to provide a variety of potential refuge for zooplankton from predators, favoring their diversity and density (Lansac-Tôha *et al.* 2003, Meerhoff *et al.* 2003). This same pattern was not identified in the Northern site probably due to increased water tubidity.

Copepods are the most abundant metazoans on the planet (Raymont 1980) and are the primary processors of photosynthetically fixed organic matter. Also, copepod nauplii of several species are capable of bacterivory, suggesting an important role in pelagic food webs (Roff *et al.* 1995). Cyclopoid copepodit was an important component of the zooplankton in this study. Many cyclopoids are associated preferentially with littoral vegetation. Velho *et al.* (2001) suggests that there is a gradient in which cyclopoids increase in richness and abundance from the open central water toward the shores. Our results suggest that nauplii, cyclopoids and *Conochilus coenobasis* were more frequent by *Z. bonariensis* beds, in shallow waters, maybe as a predation response for visual-feeding fish (Velho *et al.* 2001).

The fish fauna of Mangueira Lake was dominated by Characiformes as already described for South America by, Lowe-McConnell (1987) and Agostinho and Júlio Jr. (1999). Differences between Northern and Southern sites were also identified though fish community. Total fish biomass, number of captures and species richness presented high values in the Northern sampling site, maybe due to increased habitat complexity derived from lake-wetland interface and greater nutrient concentration also indicated by chlorophyll *a* concentration.

The spatial structure was also identified through frequency distribution of different feeding guilds. Mainly invertebrate eaters was the dominant feeding guild, as biomass, in both the Northern and Southern sampling sites of Mangueira Lake. North/South frequencies of omnivorous fish were quite similar in the 19-21% range, while planktivorous fish presented low captured biomass in both sites. However, it is interesting to note that the dominant main invertebrate eaters were different in both sides of Mangueira Lake. In the Northern sampling site *Oligosarcus jenynsii* was the dominant invertebrate eater, feeding mainly crustaceans (*Aegla sp.* and *Palaemonetes argentinus*). In contrast, the dominant invertebrate eater of Southern Mangueira Lake was *Odontesthes humensis*, consuming mainly mollusks (*Heleobia sp.* and *Corbicula sp.*). It was also observed an inversion related to frequencies of detritivorous and mainly fish eaters. Muddy sediments in the Northern Mangueira Lake may explain the relative abundance detritivorous (28%), wears sandy sediments and clear waters could be related to increased frequency of mainly fish eaters in the South, supposing easier prey detection. Secchi transparency and maximum lake depth were the most important factors structuring fish communities in floodplain lagoons of the Araguaia and Orinoco (Tejerina-Garro *et al*. 1998; Rodríguez and Lewis Jr. 1997). This pattern was related to differential predation pressures of visually oriented piscivores in clear water and piscivores adapted for low light in turbid lagoons.

In synthesis, Mangueira Lake is a long shalow lake with a clear longitudinal gradient, both of biotic and abiotic factors. Northern Mangueira Lake presents more turbid water, muddy sediments, increased nutrients and chlorophyll *a* concentration, and greater bacterioplankton, zooplankton and fish biomass. This longitudinal gradient could be related with two main driving pressures.

First, predominant winds from northeast to southwest (Fragoso Jr. *et al*. 2008), following the lake main axis, can move surface water trough Southern Mangueira Lake and provide a lot of energy to suspend fine sediments, as a result of a fetch that can reach 90 km. At the same time, fine sediments and associated nutrients are transported to North by bottom contra-currents, resulting in a Southern sandy bottom, clear water, and lower chlorophyll *a* concentration, with predictable consequences in the whole trophic cascade.

The second structuring pressure is the Taim wetland interface with Northern Mangueira Lake. Water flow from the wetlands can carry both particulate material and nutrients to Northern Mangueira Lake. Also, the structural complexity of the lake/wetland interface can also contribute to increase richness in all taxa resulting in a complex ecosystem.

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4. Can a food web structure emulate a phylogenetic tree in a subtropical shallow lake?

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ABSTRACT

Understanding the ecological role and interactions within a fish community is essential not only to manage fisheries, but also for any management action trying to improve water quality by interferences in a lake food web, ecosystem dynamics and modeling. In this study we analyzed the isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) of primary producers and consumers from a subtropical large lake. Based on the $\delta^{13}C$ and $\delta^{15}N$ ratios and analysis of stomach content of fish species, we provide a description of food web structure and trophic positions of fish species. Mangueira Lake, in Southern Brazil, is a shallow oligo-mesotrophic system. Its average depth is 3 m, being 99 km long, with a maximum width of 11 km and presenting an area about 820 km^2. Samplings were performed seasonality, from the winter of 2006 to autumn of 2007 in Northern side of Mangueira Lake. Analysis of nitrogen isotope ratios yielded two consumer trophic levels in Mangueira Lake. Isotopic signatures of primary consumer were compatible to producers, indicating a food web sustained by autochthonous carbon. *Cyphocharax voga* and Tetragonopterinae (*Astyanax* species and *Bryconamericus iheringii*), except by *Hyphessobrycon luetkenii* were all in the second trophic level, although with ample variation in nitrogen content. The Characids *Hyphessobrycon luetkenii* and *Oligosarcus* *jenynsii* and the silversides *Odontesthes aff. perugiae* and *O. humensis* were in the third trophic level. Cluster analysis of $\delta^{13}C$ and $\delta^{15}N$ values and stomach content yielded a perfect phylogenetic arrangement of species. Although convergent evolution pressures may approximate phylogenetically diverse species, it was not identified. When food items were classified inside larger groups by relative size and source (large-benthos, sediment-detritus, large-neritic, small-nerict), the combined analysis of isotopic signature and feeding preferences revealed a perfect phylogenetically structured arrangement. Despite initially unexpected, this result reflects that major feeding niches are shared by taxonomically related species.

Key-words: shallow lake, isotopic signature, trophic position, matching structures.

INTRODUCTION

Understanding the ecological roles and interactions within a fish community is essential not only to manage fisheries, but also for any process trying to improve natural water quality by interferences in a lake food web. The roles of fish in aquatic food webs are usually complex as they may occupy multiple trophic levels and consume varied food sources (Christensen & Moore 2009). Spatial and temporal differences in the abundance of consumers and of their food sources increase interspecific variability in any aquatic system, at the same time that ontogenetic diet shifts can induce intraspecific variability, affecting energy flow and top-down trophic regulation (Carpenter & Kitchell 1993, Vander Zanden *et al*. 2000, Post 2003).

Characterization of trophic levels and food web structure has been traditionally based on gut content analysis (GCA). Gut content analysis gives a “snapshot” of immediate feeding trends but may overlook variation between sampling periods

(Vander Zanden *et al*. 2000, Power *et al*. 2002, Clarke *et al*. 2005). While dietary analysis provides valuable taxonomic information on fish diets, they can be complemented by the analysis of stable isotope ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) to characterize food web structure and trophic interactions (Peterson & Fry 1987).

The use of stable isotope techniques in food web studies, particularly of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), have been used since the 1970s to provide information on the energy flow through an aquatic ecosystems (West 2006). The advantage of the stable isotope technique is that it integrates the diet over large time periods as a function of the turnover time of a specific tissue (Perga & Gerdeaux 2005), whereas stomach contents are only indicative of what the fish had eaten shortly before the capture. This methodological advantage is responsible by the increased use of stable isotopes to investigate the diet of fish in a wide range of environments (Harding *et al*. 2004; Thompson *et al*. 2005, Vizzini *et al*. 2005, Wissel & Fry 2005).

The combined analysis of carbon and nitrogen stable isotopes is a powerful tool for identifying the ultimate organic matter sources and trophic position of consumers (Michener & Schell 1994, Froneman 2001). Stable carbon isotopes fractionate very little in the food web, with around 1‰ enrichment in $\delta^{13}C$ per trophic level (Peterson & Fry 1987, Vander Zanden & Rasmussen 2001). Because of these low fractionation rate, stable carbon isotope values reflect the carbon source of their diets. The concentration of $\delta^{13}C$ in any consumer will be closely related to the $\delta^{13}C$ signature of the producer that constitute the main carbon source. Different physiological photosynthetic pathways (C_3 or C_4), specific growth rates, CO_2 concentration and pH levels can influence the $\delta^{13}C$ of plants at the base of a food web (Hecky and Hesslein 1995). As a result, there are differences in $\delta^{13}C$ values between organisms within a food web based on different sources of primary production. These differences are passed up in the food chain, indicating the origin of organic carbon in organisms at higher trophic levels (Hecky & Hesslein 1995).

In contrast, stable nitrogen isotopes are useful in determining the relative trophic position or an organism. Nitrogen isotopes consistently fractionate as ^{14}N is selectively eliminated while ^{15}N is incorporated into body tissues. Consequently, at each successive trophic transfer, $\delta^{15}N$ tissue values increase at a predictable rate, becomig "heavier" (Campbell *et al.* 2003).

Many studies quantified the average $\delta^{15}N$ difference between an animal and its food source as between 2.5 to 3.5‰ (DeNiro and Epstein 1981, Vander Zanden and Rasmussen 2001, Vanderklift and Ponsard 2003). Different fractioning values could be related to environment, taxonomic group and sampled tissue (Vanderklift and Ponsard 2003). Previous experimental studies by DeNiro and Epstein (1981), Minagawa & Wada (1984), Vander Zanden & Ramussen (1996) and Post (2002) suggested a fractionation value of approximately 3.4 ‰. Vander Zanden & Rasmussen (2001) found a value of 2.92 ‰, considering field $\delta^{15}N$ estimates and estimates from the laboratory. The meta-analysis of Vanderklift & Ponsard (2003) found 2.54 ‰ as a overall mean from 134 estimates of $\delta^{15}N$ compiled in different environments (natural and laboratory), taxonomic groups and tissues. However, for freshwater organisms, these authors recommend a fractionation value of 2.98‰.

Stable isotope analysis (SIA) has been used successfully in several aspects of aquatic ecology. Cabana and Rasmussen (1996), Vander Zanden & Rasmussen (1999) and Vander Zanden *et al.* (1999a, 1999b) used SIA to compare and define trophic food webs in aquatic environments. Post (2003) identified ontogenetic diet variations in largemouth bass (*Micropterus salmoides* L.) and found that an early shift to piscivory ultimately resulted in increased rates of growth and survival. Cunjak *et al*. (2005) and McCarthy & Waldron (2000) identified spatial and trophic feeding niches utilizing SIA to identify fish migrating from different areas within a watershed.

In this study we analyzed the isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) of primary producers and consumers from the Mangueira Lake (Southern Brazil). Based on the $\delta^{13}C$ and $\delta^{15}N$ ratios and analysis of stomach content of fish species, we provide a description of food web structure. We identified the production sources that sustain vertical trophic structure, the trophic positions of fish species and the matching phylogenetic structure.

METHODS

Study site

Mangueira is a large shallow lake, with average depth of 3 m, 90 km in length, 3-10 km in width and an area about 820 km^2. It is situated along the Atlantic Ocean, Southern Brazil (33º31’22”S 53º07’48”W) (Fig.1) and was originated from the last glaciation on the southeast coast of South America (during the Pleistocene ~5,000 years ago). In the Northern part, the lake has an interface with wetland, presenting dense beds of macrophytes. The lake main axis in the North-East to South-West direction, following the more frequent winds.

Field collection, sample processing for isotopic analysis and data analysis

The samplings were performed seasonality, from the winter of 2006 to autumn of 2007 in Northern side of Mangueira Lake. Representative organisms of the pelagic and littoral compartments of the food web were sampled. Macrophytes and macroinvertebrates were collected only in littoral zone, whereas zooplankton and fish were collected in both littoral and pelagic areas. Primary producers (macrophytes and periphyton - removed from the macrophytes), zooplankton, macroinvertebrates (*Palaemonetes argentinus* Nobili, 1901 and *Pomacea* sp.) and fish were collected and ice conserved for transport to the laboratory, where they were frozen (-18ºC).

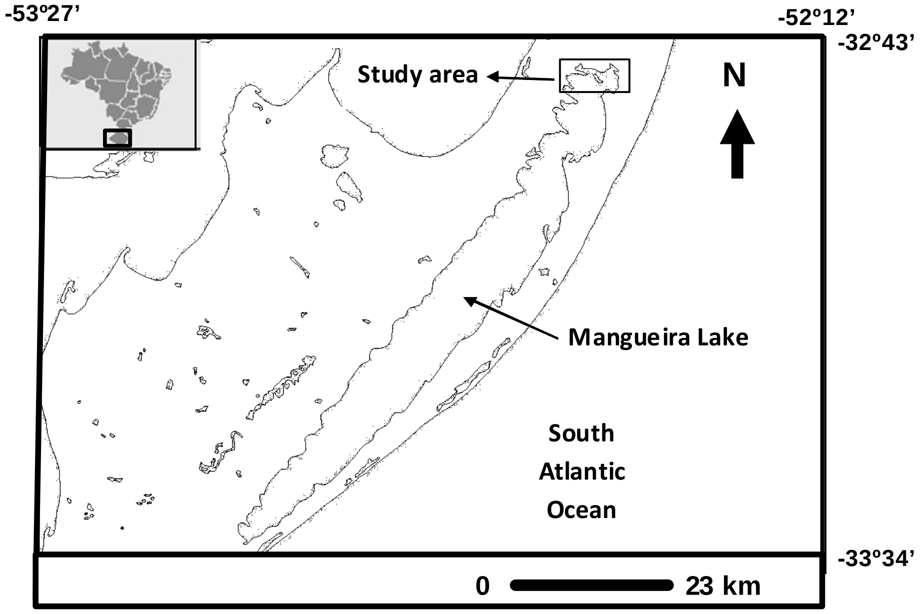

Figure 1. Mangueira Lake, coastal large lake in Rio Grande do Sul state, Southern Brazil.

Emergents macrophytes *Zizaniopsis bonariensis* (Balansa & Poitr.) Speg; *Scirpus californicus* (C.A. Mey) Steud and *Sagittaria montevidensis* (Cham. & Schltdl); and the submerged macrophytes *Egeria densa* (Planchon 1849); *Cabomba caroliniana* (A Gray 1837) and *Ceratophyllum demersum* (Linné 1753) were collected. Zooplankton were sampled by using depth-integrated (to 2 meters) water sampler, comprising a pool of 320L taken in all seasons in littoral and pelagic areas, filtered with a 65 µm net. The fish species *Odontesthes humensis* de Buen, 1953; *Odontesthes aff. perugiae* Evermann & Kendall, 1906; *Astyanax jacuhiensis* (Cope, 1894); *Astyanax eigenmanniorum* (Cope, 1894); *Astyanax* sp.; *Hyphessobrycon luetkenii* (Boulenger, 1887); *Bryconamericus* *iheringii* (Boulenger, 1887); *Oligosarcus jenynsii* (Günther, 1864) and *Cyphocharax voga* (Hensel, 1870) were sampled by using multiple-mesh gill nets. Each specimen was weighed (to nearest 0.1 grams), measured (to 1.0 mm) and frozen. Up to 50 specimens of each species were analyzed in each sample to quantify the stomach content as frequency of occurrence of identifiable items.

Biological samples (muscle for fish and invertebrates) was dried at 60 ºC (>48 h) and stored in a desiccator prior to isotopic analysis. Dry samples were ground to a fine powder (weighed to 10^{-6} g) and disposed into Ultra-Pure tin capsules (Costech, Valencia, CA). Samples were sent to the *UC Davis Stable Isotope Facility*, *Department of Plant Sciences at the University of California*, for determination of stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$). Results are reported as parts per thousand (‰) differences from a corresponding standard: $\delta X = [(R\text{sample}/R\text{standard}) - 1] \times 10^3$, where R = $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Standards were carbon in the PeeDee Belemnite and nitrogen in air. Typical standard deviations of $\delta^{13}C$ and $\delta^{15}N$ replicate analyses are 0.14‰ and 0.13‰, respectively.

Trophic level of fish were estimated assuming an increase in $\delta^{15}N$ values of 2.98‰ between successive trophic levels, following Vanderklift and Ponsard (2003) proposals for freshwater organisms. The choose of a baseline organism follows Post (2002), who propose the use of snails and bivalves (trophic level 2) to estimate the littoral and pelagic bases of a food web. Trophic level (TL_f) were estimated according to the following formula:

$$TL_f = [(\delta^{15}N_f - \delta^{15}N_{ref}) / 2.98] + 2$$

Where $\delta^{15}N_f$ and $\delta^{15}N_{ref}$ are respectively the nitrogen isotopic signature of a fish and a baseline reference organism; 2.98 is the $\delta^{15}N$ expected isotopic fractionation per trophic level; 2 is the trophic level of the baseline organism (primary consumer).

Plots of $\delta^{13}C$ and $\delta^{15}N$ values of plants, invertebrates and fish were used to evaluate the isotopic patterns. The food web structure was graphically represented by plotting $\delta^{15}N$ against $\delta^{13}C$ for all organisms. Frequency of occurrence of stomach content was also applied to infer the community trophic structure. Cluster analysis (Euclidian distance, within group linkage) were applied to $\delta^{13}C$ and $\delta^{15}N$ values, stomach content and joined rescaled data (0-1 by species) with SPSS 11.5 software.

RESULTS

Plotting $\delta^{15}N$ values against $\delta^{13}C$ values provides a visual characterization of the food web structure of Mangueira Lake (Fig. 2). Macrophytes showed higher intra-group variation both in $\delta^{15}N$ and $\delta^{13}C$ signatures. Emergent macrophytes (*Zizaniopsis bonariensis*, *Scirpus californicus* and *Sagittaria montevidensis*) were more enriched in $\delta^{13}C$ and $\delta^{15}N$ than submerged macrophytes (*Egeria densa*, *Cabomba* sp. and *Ceratophyllum* sp.) (Tab. 1).

The periphyton presented the same $\delta^{15}N$ values than emergent macrophytes but higher $\delta^{13}C$ concentration. The zooplankton and *Pomacea* sp. had similar $\delta^{15}N$ values, as primary consumers, but contrasting $\delta^{13}C$ signatures, confirming different carbon source (Tab. 1). Fish had $\delta^{13}C$ values ranging from -22.00 ‰ to -27.00 ‰, whereas $\delta^{15}N$ values ranged from 7.7 ‰ to 12.7 ‰. The lower trophic level for fish species were identified for *Cyphocharax voga* and the *Astyanax* species. *Odontesthes humensis*, *O. aff. perugiae* e *Oligosarcus jenynsii* showed the higher identified trophic position (Tab. 2; Fig. 3).

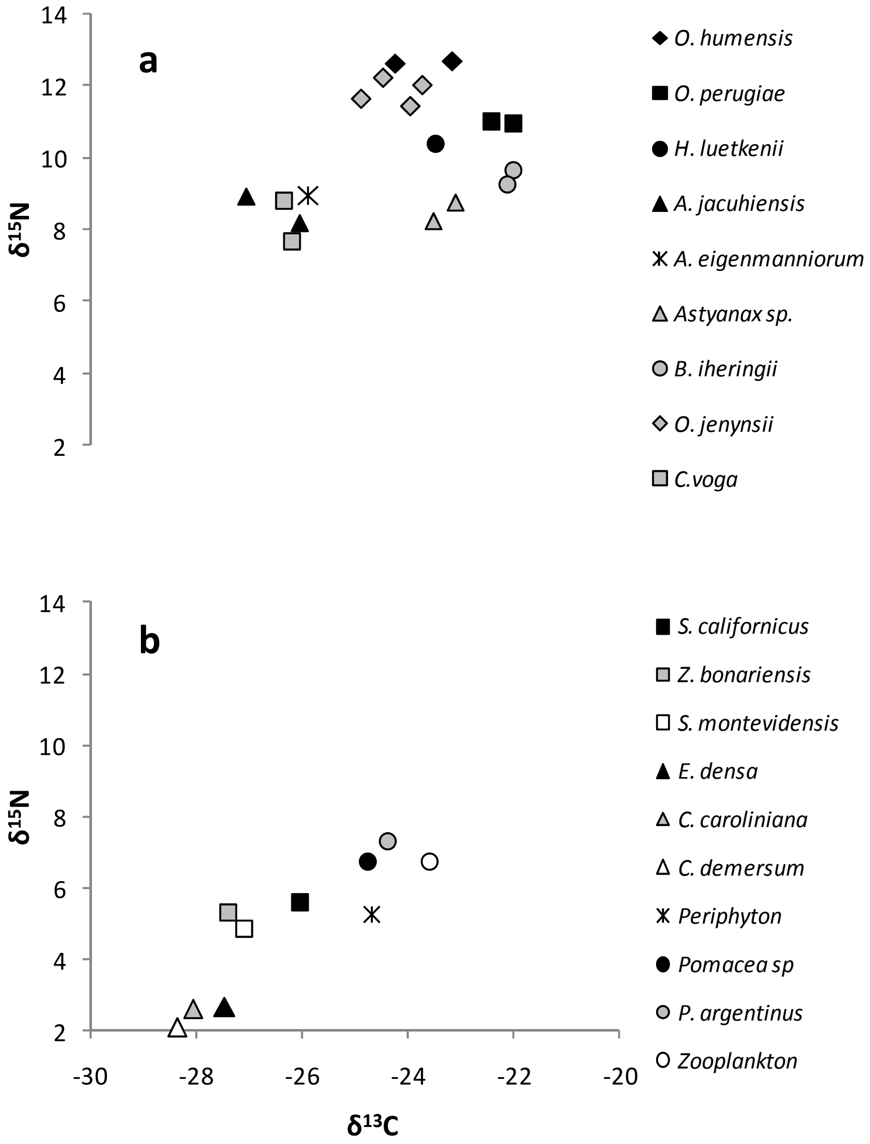

Figure 2. Plot of $\delta^{15}N$ and $\delta^{13}C$ values for fishes (a), and primary producers and primary consumers (b) at Mangueira Lake. Sources of carbon assimilated by consumers are indicated by the relative positions of taxa on the x-axis; trophic level is indicated by relative position on the y-axis.

Analysis of nitrogen isotope ratios yielded to identify two consumer trophic levels in Mangueira Lake (Fig. 2 and 3). *Cyphocharax voga* and Tetragonopterinae (According Géry, J. 1977; Weitzman & Malabarba, 1998) (*Astyanax* species and *Bryconamericus iheringii*), except by *Hyphessobrycon luetkenii* were all in the second trophic level, although with ample variation in nitrogen content. The Characids *Hyphessobrycon luetkenii* and *Oligosarcus jenynsii* and the silversides *Odontesthes aff. perugiae* and *O. humensis* were in the third trophic level.

Table 1. δ^{13}C and δ^{15}N values of primary producers and primary consumers of Mangueira lake.

	Specie	^{13}C	^{15}N
Emergent macrophyte	*Scirpus californicus*	-26.05	5.61
Emergent macrophyte	*Zizaniopsis bonariensis*	-27.41	5.28
Emergent macrophyte	*Sagittaria montevidensis*	-27.10	4.85
Submerged macrophyte	*Egeria densa*	-27.47	2.66
Submerged macrophyte	*Cabomba caroliniana*	-28.06	2.61
Submerged macrophyte	*Ceratophyllum demersum*	-28.36	2.09
	Periphyton	-24.70	5.23
	Zooplankton	-23.60	6.74
Crustacean decapod	*Palaemonetes argentinus*	-24.39	7.31
Mollusk	*Pomacea* sp	-24.74	6.74

Through table 2 are presented also δ^{13}C and δ^{15}N values estimated by Garcia *et al.* (2007) for the Patos Lagoon, a larger lagoon system with common species with Mangueira Lake. A dendrogram applied to joined data (Fig. 4) shows clearly a spatial more than a functional structure. Two major groups were identified, one exclusively with data from the Patos Lagoon, and the second cluster with a mixture of data, but without a clear functional pattern.

Table 2. δ^{13}C and δ^{15}N values (X ± SD) and total length (TL, mm) of fishes sampled in Mangueira Lake and in the upper freshwater portion of the Patos Lagoon (Garcia *et al*. 2007).

			Present work				Garcia et al. 2007			
	Family	Specie	*n*	TL	^{13}C	^{15}N	*n*	TL	^{13}C	^{15}N
Characid	Characidae	*Astyanax* sp.	2	51.0 ± 7.1	-23.3 ± 0.3	8.5 ± 0.4	2	104.9 ± 45.4	-20.3 ± 1.9	11.8 ± 0.3
Characid	Characidae	*Astyanax jacuhiensis*	2	119.1 ± 4.4	-26.5 ±0.7	8.5 ± 0.5	5	74.6 ± 7.6	-21.5	10.5
Characid	Characidae	*Astyanax eigenmanniorum*	1	104.0	-25.9	8.9	2	64.0 ± 9.9	-24.6	10.9
Characid	Characidae	*Astyanax fasciatus*					3	82.7 ± 40.7	-21.9 ± 1.6	11.3 ± 0.9
Characid	Characidae	*Bryconamericus iheringii*	2	76.5 ± 4.9	-22.0 ± 0.1	9.5 ± 0.3				
Characid	Characidae	*Cyanocharax alburnus*					3	45.3 ± 1.5	-20.1	12.8
Characid	Characidae	*Hyphessobrycon luetkenii*	1	94.0	-23.4	10.4				
Characid	Characidae	*Oligosarcus jenynsii*	4	142.75 ± 34.9	-24.2 ± 0.5	11.8 ± 0.4				
Characid	Characidae	*Oligosarcus robustus*					1	96.0	-19.9	14.17
Pike cichlid	Cichlidae	*Crenicichla punctata*					1	128.0	-18.7	12.0
Pearl cichlid	Cichlidae	*Geophagus brasiliensis*					3	105.3 ± 22.7	-20.1 ± 0.3	13.2 ± 0.3
River Plate sprat	Clupeidae	*Platanichthys platana*					3	78.1 ± 3.0	-20.7 ± 0.4	12.6 ± 0.8
	Curimatidae	*Cyphocharax voga*	2	146.5 ± 62.9	-26.2 ± 0.1	8.2 ± 0.8	2	105.3 ± 32.0	-22.0 ± 1.0	9.9 ± 0.6
Freshwater catfish	Pimelodidae	*Parapimelodus nigribarbis*					2	117.1 ± 0.8	-17.8 ± 0.5	11.6 ± 0.0
Freshwater catfish	Pimelodidae	*Pimelodus maculatus*					2	234.8 ± 73.9	-22.6 ± 2.7	13.5 ± 0.3
Freshwater catfish	Heptapteridae	*Pimelodella laticeps australis*					2	75.3 ± 6.1	-20.8 ± 0.5	13.5 ± 0.4
Freshwater catfish	Heptapteridae	*Rhamdia sapo*					1	185.0	-24.7	9.3
Silverside	Atherinopsidae	*Odontesthes humensis*	2	279.15 ± 19.6	-23.6 ± 0.7	12.6 ± 0.1				
Silverside	Atherinopsidae	*Odontesthes perugiae*	2	176.0 ± 11.3	-22.2 ± 0.3	10.9 ± 0.1				
Trahira	Erythrinidae	*Hoplias malabaricus*					2	165.0 ± 45.3	-22.4 ± 0.5	9.6 ± 0.9

When applied to Manguiera Lake data exclusively, cluster analysis presented different results for isotopic signatures and frequency of occurrence of main feeding items grouped by source and relative size (Tab. 3).

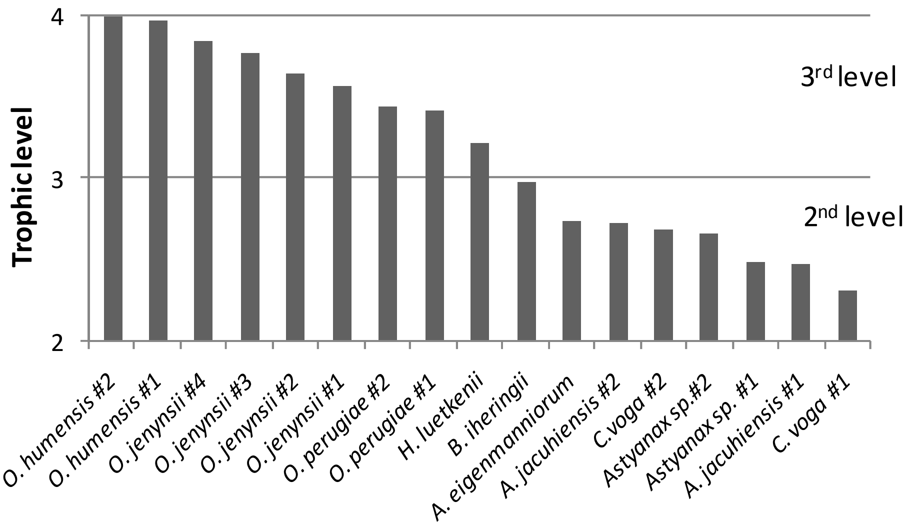

Figure 3. Trophic position estimates of fishes collected in Mangueira Lake, according to the $\delta^{15}N$ signature. # Symbols denotes different individuals of the same species.

By using isotopic signature, three major groups were identified (Fig. 5). The first group clustered the detritivorous *Cyphocharax voga* with *Astyanax jacuhiensis* and *A. eigenmanniorum.* The second group joined two larger predator species, *Odontesthes humensis* and *Oligosacus jeninsii.* The third group joined loosely *Odontesthes aff. perugiae* and Tetragonopterinae species, mainly known as generalist feeders (*Hyphessobrycon luetkenii, Bryconamericus iheringii* and *Astyanax* sp.).

A completely different result was obtained by using stomach content (Fig. 5). The detritivorous C*yphocharax voga* stayed apart from all the other species. Nevertheless, for the remaining species, a phylogenetic structure was identified. The tree *Astyanax* species joined all together, and then with other Tetragonopterinae

(*Hyphessobrycon luetkenii* and *Bryconamericus iheringii*). Next, *Oligosarcus jenynsii* joins the group, forming a monophyletic cladus (Characidae). The Atheriniphorms *Odontesthes humensis* and *O. aff. perugiae* grouped together and apart of the Characidae. However, when all data were used to identify the functional structure, a perfect phylogenetic arrangement was achieved, with *Cyphocharax voga* grouping with the Characids and forming a Characiform cladus (Fig. 5).

Table 3. Frequency of occurrence of main feeding items grouped by source and relative size.

Species	Large-Benthos	Sediment-Detritus	Large-Neritic	Small-Neritic
Astyanax eigenmanniorum	23	52	0	25
Astyanax jacuhiensis	33	48	0	19
Astyanax sp	28	54	0	18
Bryconamericus iheringii	20	44	0	36
Cyphocharax voga	0	100	0	0
Hyphessobrycon luetkenii	32	43	0	25
Odontesthes perugiae	72	3	13	12
Odontesthes humensis	81	3	16	0
Oligosarcus jenynsii	79	5	16	0

DISCUSSION

Stable isotopes have most often been used to provide qualitative summaries and diagrammatic representations of food webs structure (Vander Zanden and Rasmussen 2001). In wetlands and lake littoral zones there are generally three major groups of feeding sources: epiphytic algae (periphyton), macrophytes and suspended particulate matter (SPM; Lamberti & Moore 1984; Frost *et al*. 2002).

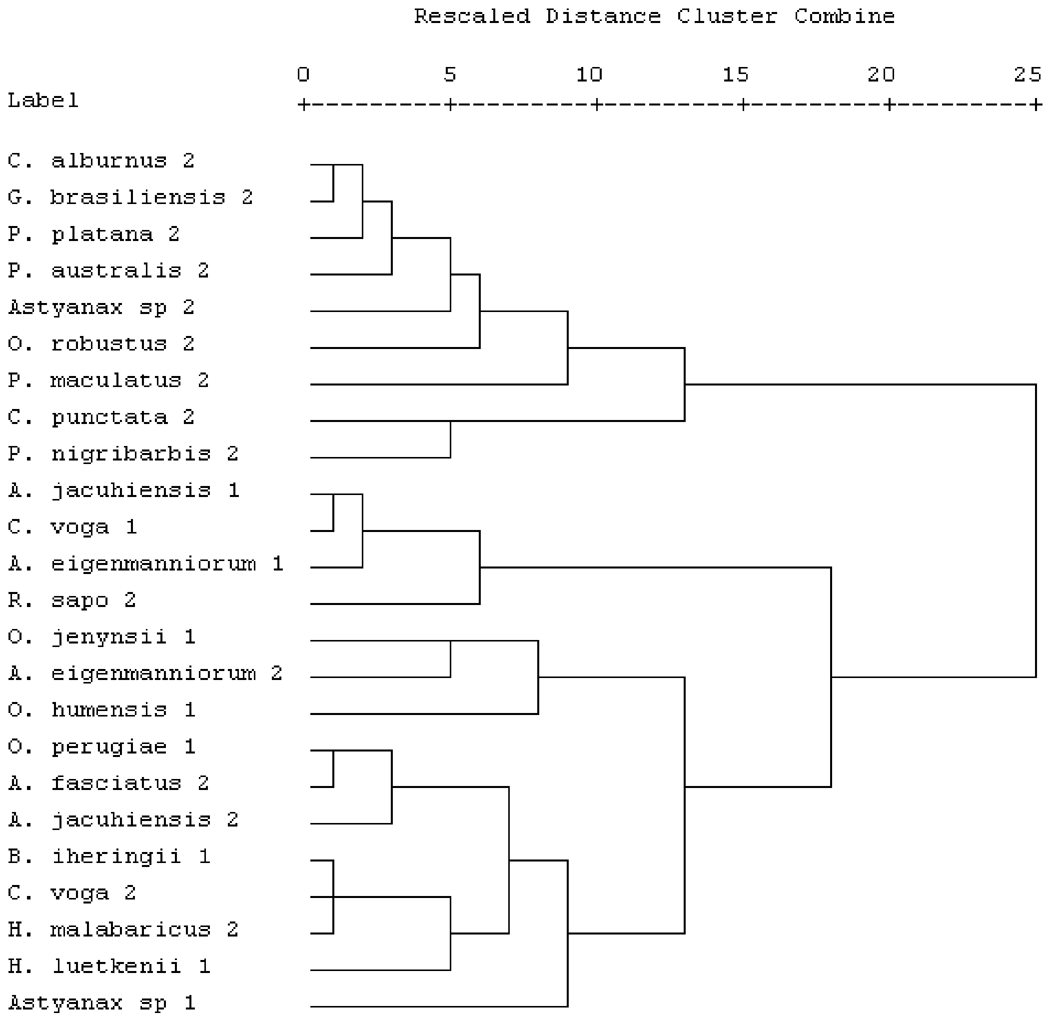

Figure 4. Dendrogram of similarity (Euclidian distance, within group linkage) applied to fish species using $\delta^{13}C$ and $\delta^{15}N$ signature values. Data from the Mangueira Lake (present work; 1) and for the Patos Lagoon (Garcia *et al.*,2007; 2).

Mangueira Lake macrophytes revealed a $\delta^{13}C$ range in accordance with reported values for terrestrial plants using the C_3 photosynthetic pathway (-27 to -29‰, Deegan & Garritt, 1997; -25 to -27‰, Garcia *et al.* 2006). Garcia *et al.* (2006) for the Taim Hydrological System and Manetta *et al.* (2003) for the Paraná River floodplain, found a high linkage between $\delta^{13}C$ values of macrophytes and consumers, suggesting them as a important carbon source supporting aquatic food webs.

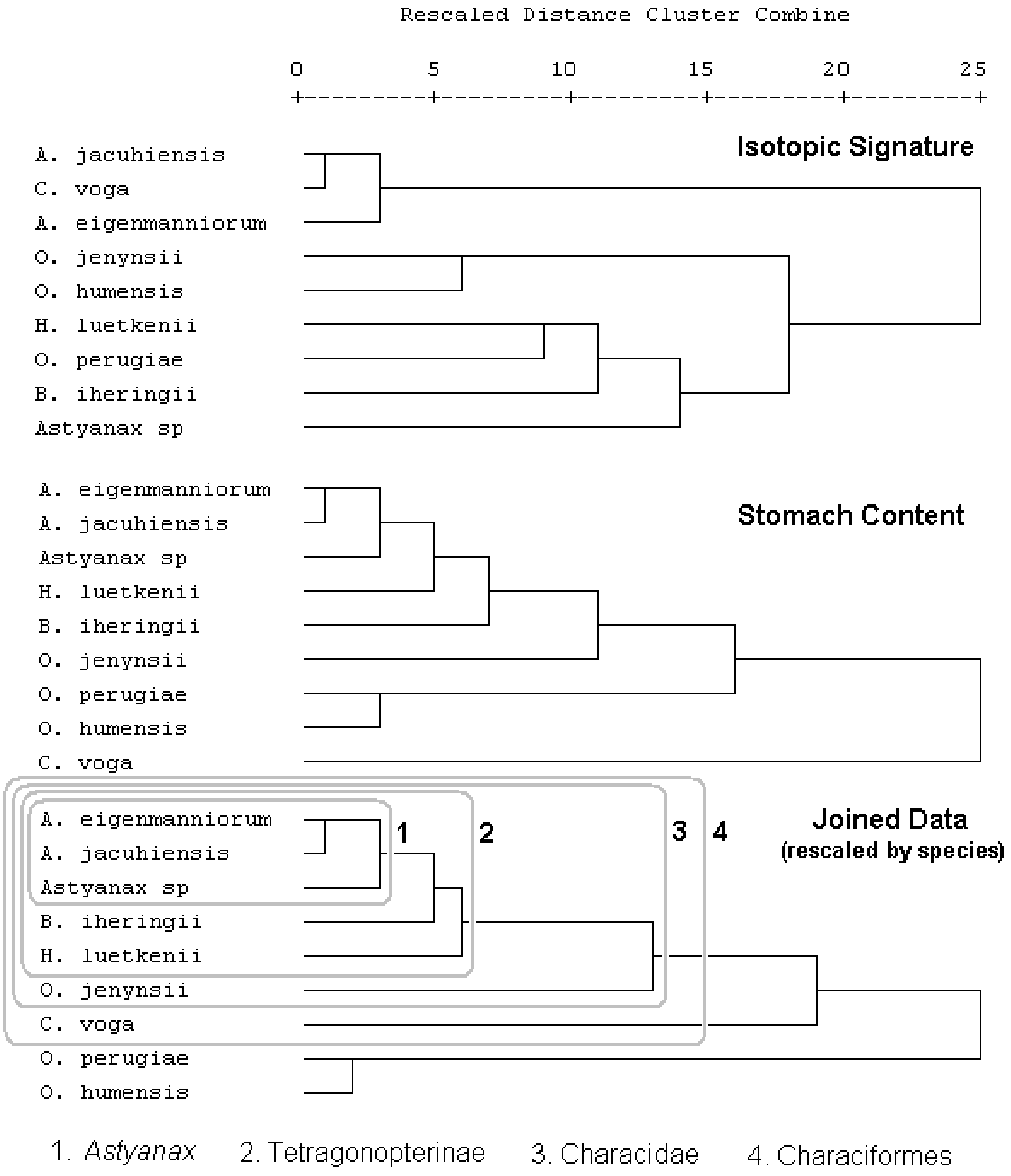

Figure 5. Dendrogram of similarity (Euclidian distance, within group linkage) applied to fish species of the Mangueira Lake by using $\delta^{13}C$ and $\delta^{15}N$ signature values (upper); stomach content (middle) and joined data (lower).

Another carbon source, the periphyton, which covers a wide range of submerged surfaces, can also be a key factor. Periphyton plays a fundamental role in nutrient cycling and storage (Azim *et al*. 2006), and can be used for freshwater fish as food source either in direct or indirect pathways (Petr 2000). The periphyton isotopic signature value reported in this study was inside the range already described for other freshwater environments ($\delta^{13}C$ signature range from -12 ‰ to -30 ‰, Boutton 1991; -15‰ to -27‰, France 1999; -17‰ and -28‰, Trudeau & Rasmussen 2003; and $\delta^{15}N$ signature range of 1.5‰ to 7‰, MacLeod and Barton 1998; 2.3‰ to 7.2‰, Trudeau & Rasmussen 2003).

Nevertheless, important differences were identified among primary producers. Submerged macrophytes (*Egeria densa*, *Cabomba caroliniana* and *Ceratophyllum demersum*) presented too low values of both $\delta^{13}C$ and $\delta^{15}N$ signatures when compared to the primary consumer *Pomacea* sp. (Gastropod), with a difference ranging from 4.1 to 4.7‰. In the other hand, $\delta^{15}N$ signature of emergent macrophytes (*Zizaniopsis bonariensis*, *Scirpus californicus* and *Sagittaria montevidensis*) were too close, apart only from 1.1 to 2.3‰, suggesting a composition of food sources, although $\delta^{13}C$ values indicate an important role of *Scirpus californicus*.

Peryphyton appear to be an important food source for the prawn *Palaemonetes argentinus*, although other less enriched food sources were necessary to complain with the identified signatures of $\delta^{13}C$ and $\delta^{15}N$.

Analysis of isotopic signatures based on ecological guilds and previous life-history studies within Taim Hydrological System (THS) (Garcia *et al.* 2006) and Patos Lagoon (Garcia *et al.* 2007) provide evidence corroborating the general hypothesis that primary consumers reflects autochthonous organic matter production.

Cyphocharax voga was considered as a 2nd trophic level species by Garcia *et al.* (2007). In this study differences in isotopic signature of *C. voga* related to size were observed. Two values were obtained, whereas both were included in 2nd trophic level. Larger *C. voga* feeds a mix of detritus and invertebrates (including mollusks, cladocerans, copepods, ostracods, nematods and others; Corrêa & Piedras 2008), while smaller *C. voga* feed almost exclusively detritus and algae (Neiff *et al*. 2009).

Because the fractionation value of nitrogen used by Garcia *et al.* (2007), 2.54 per trophic level, these authors estimated a higher trophic position for *C. voga* than in the present study. The same was identified for *A. eigenmanniorum* and *A. fasciatus,* both considered in the 3rd trophic level by Garcia *et al.* (2007), whereas here enclosed in the 2nd trophic level.

Astyanax jacuhienisis and *A. eigenmanniorum* presented comparable isotopic signatures to *C. voga* in this study, although *Astyanax* species are usually reported as omnivorous fish (Teixeira 1989; Esteves & Galetti Jr. 1995; Esteves 1996; Hartz *et al*. 1996; Vilella *et al*. 2002; Rodrigues *et al*. unpublished data). It should be emphasized that detritus/sediment is commonly found in gastric contents of *Astyanax* species. However, it use to appear in small volumes, being predominantly associated to aquatic invertebrates or plant structures accumulated in the bottom, indicating the accidental ingestion during food intake (Abelha *et al*. 2006). These newly described invertebrate intake by large *C. voga* and the already know detritus consumption by several *Astyanax* species may explain the unexpected similarity of isotopic signatures of *C. voga*, *A. jacuhienisis* and *A. eigenmanniorum*.

Bryconamericus iheringhi was the more enriched species both in δ^{13}C and δ^{15}N still classified inside the 2nd trophic level. Studies of trophic niches of several fish species in an Argentinean lake (Grosman *et al*. 1996), classified *B. iheringhi* as phytoplankton-periphytophagous species, whereas Oricolli and Bennemann (2006) found the use of detritus as the main food for *B. iheringhi*, what do not comply with our results. *Bryconamericus iheringhi* presented similar δ^{13}C signature than *Odontesthes perugiae*, which feeds mainly on large benthos and is more δ^{15}N enriched. Nevertheless, it should be remembered that Tetragonopterinae constitute a large and diverse group in need of species revision, especially large distributed ones, which may represent distinct taxa inside the same specific name.

The characids *H. luetkenii* and *O. jenynsii* and the silversides *O. perugiae* and *O. humensis* were classified inside the 3rd trophic level in this study.

Hyphessobricon luetkenii was classified just above the threshold between the second and third trophic level. Some studies considered that *H. luetkenii* feeds mainly algae and detritus (Soneira *et al.* 2006), others, as omnivorous specie (Sánchez-Botero *et al.* 2008) or as omnivore–benthi–planktivorous (Teixeira de Mello *et al.* 2009). Rodrigues *et al.* (unpublished data) classified *H. luetkenii* in the omnivorous guild, feeding mainly on insects, but also finding algae and fish eggs in the stomach content. The consuming of insects and fish eggs could explain the enhanced δ^{15}N signature of the species in relation to other Tetragonopterinae.

A seasonal and ontogenetic change in the isotopic signature of *O. jenynsii* was already identified (Rodrigues *et al.*, unpublished data). The δ^{15}N signature was constant for the all period, whereas variations in δ^{13}C were observed. Animals around 170 mm (total length) were less δ^{13}C enriched than 110 mm specimens, suggesting distinct carbon sources, although this it was not verified in the present work.

The observed differences in isotopic signature of analyzed species could be related to carbon source, suggesting efficient resource partitioning within the community, although seasonal changes in resource availability and ontogenetic diet shifts can also affect both predator-prey and competitive interactions among size-structured fish populations (Winemiller, 1989).

Studies concerning feeding dynamics include basic knowledge related the biology of species and quantitative knowledge about the mechanisms of interaction among species, such as predation and competition (Esteves & Aranha, 1999). In this context, ecomorphology is the branch of ecology that investigates the relationships between the morphological and ecological aspects of individuals, populations, guilds and communities (Nunes & Hartz, 2006). Ecomorphological studies also constitute an important tool to draw inferences concerning the resource partitioning, defined as any substantial difference in resource exploitation among species, which may be related to diet, spatial and temporal differences in the use of habitat (Ross, 1986).

Species with great ecomorphological similarities may coexist through mechanisms as resource partitioning. Evolutionary pressures for resource partitioning are more evident in close related species.

Although convergent evolution pressures may approximate phylogenetically diverse species, it was not identified in the present work. When food items were classified inside larger groups by relative size and source, the combined analysis of isotopic signature and feeding preferences revealed a perfect phylogenetically structured arrangement. Despite initially unexpected, this result reflects that major feeding niches are shared by taxonomically related species. These findings, of course, are biased by the small number of analyzed species and arrangement of feeding items as large groups.

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5. Feeding dynamics of *Oligosarcus jenynsii* (Gunther, 1864) in a subtropical lake using gut content analysis and stable isotope

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ABSTRACT

The trophic niche of a species can be depicted by the identification and quantification of the diet components found in its digestive tract. The present study aimed to identify the seasonal feeding dynamics of *Oligosarcus jenynsii* by using analyses of stomach contents and the stable isotopes signature. Sampling was carried out seasonally, from winter 2006 to autumn 2007 in the northern part of Mangueira Lake, southern Brazil. Fish were caught overnight (15 h) by using multiple-mesh gill nets. *Palaemonetes argentinus* (Crustacea, Decapoda, Palaemonidae) was the dominant prey in all seasons, with the exception of summer for *O. jenynsii* less than 14 cm long (TL). Insects were dominant in the winter and summer, and *Aegla* sp. (Crustacea, Decapoda, Aeglidae) dominated in spring for animals larger than 14 cm (TL). Analysis of the trophic changes during ontogeny showed that the ingestion of shrimps (*P. argentinus*) decreased with an increase of body size in *O. jenynsii*, while the ingestion of *Aegla* sp. and Insecta increased. Isotope analysis showed that *O. jenynsii* contained constant concentrations of $\delta^{15}N$, although the $\delta^{13}C$ signature varied. Animals 17 cm long showed lower values of $\delta^{13}C$ than individuals 11 cm long, suggesting that the larger individuals obtained carbon from insects and macrophytes, while the high values of $\delta^{13}C$ in the smaller individuals would be associated with periphyton and *P. argentinus*. During the study, the seasonal differences in the diet composition of *O. jenynsii* showed that this species is opportunistic, changing its diet according to food availability. This high trophic plasticity may be one of the factors responsible for the broad distribution of the species.

Key-words: Diet, isotopic analysis, stomach content, Taim Hydrological System.

INTRODUCTION

The trophic niche of a species can be depicted by the identification and quantification of the diet components found in its digestive tract (Grosman *et al*., 1996). Fish diets are usually studied by describing the food items found, calculating the frequency of each item or the volume occupied, etc. (Hyslop, 1980; Bowen, 1984).

Stable isotope ratios, particularly carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), have been used since the 1970s to provide information on the flow of energy through aquatic ecosystems (West *et al*., 2006). The ratios of stable carbon isotopes (C13:C12) within the body tissues of the producers and the consumers give an indication of food sources (Fry & Sherr, 1984; Froneman, 2001). The isotope signatures of consumers are closely related to that of their diet, and if food sources are isotopically distinct, one can clearly identify a particular food source of a consumer (France & Peters, 1997).

Differences in fish dietary patterns are generally due to distinct feeding physiology, predator-prey behavior, and environmental constraints (Persson & Crowder, 1997; Abelha *et al*., 2001). Fish not only control prey populations, but they can also alter both the diversity and demographic structure of prey populations (Jacobsen *et al*., 1997; Moss, 1998).

Plant diversity and abundance may have differential impacts on how lakes function. Structurally complex habitats generally support a higher diversity of organisms because they provide refuge from predators and substrate to support food resources (Burks *et al*., 2006). Aquatic plants exert a multiple effect on the structure and functioning of shallow lakes by affecting the communities that live permanently or temporarily in the littoral zone. The structure of the fish community in the lake, however, strongly regulates the effects of the plants (Jeppesen *et al*., 1997). Fish, because of their mobility and flexible feeding behavior, link the littoral, benthic, and pelagic habitats in a much more significant manner than was historically considered (Schindler & Scheuerell, 2002; Vander Zanden & Vadeboncoeur, 2002), and thus affect the nutrient transport and predator-prey interactions in both the littoral and pelagic zones.

Fishes of the genus *Oligosarcus* (Characidae) have a large buccal aperture, allowing the ingestion of whole prey in a single bite (Casatti *et al*., 2001). Most species of this genus feed mainly on insects, crustaceans, and small fish (Lowe-McConnell, 1987). *Oligosarcus jenynsii* (Günther, 1864) occurs in the state of Rio Grande do Sul in Brazil, and in Uruguay and northern Argentina. Some studies have recorded a preferentially piscivorous feeding habit for the species (Hartz *et al*., 1996; Hermes-Silva *et al*., 2004; Nunes & Hartz, 2006). Other studies have described it as a generalist carnivore, with shrimp and terrestrial insects as the main items in its diet (Haro & Gutiérrez, 1985; Barros, 2004).

The goal of this study was to describe the seasonal feeding dynamics of *O. jenynsii* in a subtropical Brazilian lake, using analysis of the stomach contents and stable isotopes.

METHODS

Study site

Mangueira Lake, part of the Taim Hydrological System, was formed after the last ocean regression during the Pleistocene, around 5,000 years ago. It is a large shallow lake (33º31’22”S 53º07’48”W), with a mean depth of 3 m, 90 km in length and covering about 820 km^2 (Fig. 1). The lake runs northeast to southwest, parallel to the Atlantic Ocean coastline, in the same direction as the prevailing winds. In its northern end, the lake interfaces with wetlands and contains large macrophyte stands.

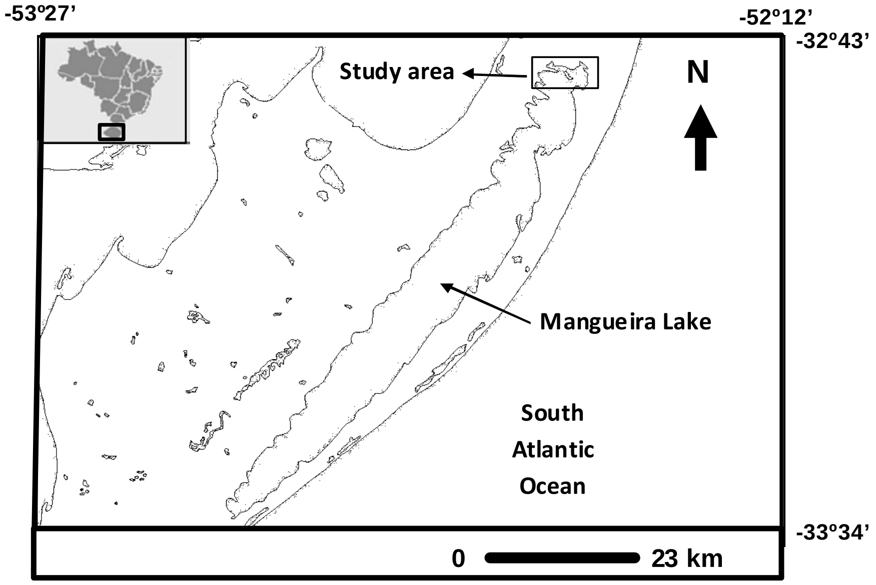

Figure 1. Mangueira Lake, coastal large lake in Rio Grande do Sul state, Southern Brazil.

Fish sampling and data analysis

Sampling was carried out seasonally, from winter 2006 to autumn 2007, in northern Mangueira Lake. Fish were caught overnight (15 h) by using multiple-mesh gill nets (5, 6.25, 8, 10, 12.5, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65, and 70 mm mesh size, modified EU Standard). Each sample unit was sampled in triplicate. All captured fish were preserved in 4% formalin, except samples for isotopic analysis, which were frozen. In the laboratory, fish were identified, counted, weighed (to the nearest 0.1 g), measured (to 1.0 mm), and dissected for digestive-tract analysis.

Food items were examined using a stereomicroscope, and analyzed for frequency of occurrence (Hyslop, 1980) according to size (<14< cm total length) and season of the year. The items were also classified through the Dajoz constancy index (Dajoz, 1973). The constancy index is the percentage ratio between the number of samples in which an item is present and the total number of samples. It is defined as: constant items, present in more than 50% of the samples; accessory items, present between 25% and 50% of the samples; and accidental items, present in less than 25% of the samples.

Sample processing and data analysis for isotope analysis

Primary producers (the emergent macrophytes *Zizaniopsis bonariensis* and *Sagittaria montevidensis*, and periphyton removed from the macrophytes), the decapod crustacean (*Palaemonetes argentinus*), and the fish (*Oligosarcus jenynsii*) were collected and immediately placed on ice for transport to the laboratory, where they were frozen (-18ºC). All samples were dried in an oven at 60 ºC to constant weight (minimum of 48 h). Dry samples were ground to a fine powder with a mortar and pestle and stored in glass vials. Subsamples were weighed to 10^{-6} g, placed in Ultra-Pure tin capsules (Costech, Valencia, CA), and sent to the UC Davis Stable Isotope Facility, Department of Plant Sciences at the University of California Davis, for determination of stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$).

Results are reported as parts per thousand (‰) differences from a corresponding standard: $\delta X = [(R\text{sample}/R\text{standard}) - 1] \times 10^3$, where $R = {}^{15}N/{}^{14}N$ or ${}^{13}C/{}^{12}C$. Standards were carbon in the PeeDee Belemnite and nitrogen in air. Standard deviations of $\delta^{13}C$ and $\delta^{15}N$ replicate analyses were 0.14‰ and 0.13‰, respectively.

Plots of $\delta^{13}C$ and $\delta^{15}N$ values of *O. jenynsii* were used to evaluate patterns of isotopic variation across seasons. Sources of organic carbon assimilated by consumers are indicated by the relative positions of taxa on the x-axis ($\delta^{13}C$ values), and trophic level is indicated by the relative position on the y-axis ($\delta^{15}N$) (Peterson & Fry, 1987).

RESULTS

A total of 365 specimens of *Oligosarcus jenynsii* were captured. The weights of the specimens ranged between 4.8 and 120 g, and the lengths between 7.8 and 22.5 cm. The stomach contents of 337 individuals were analyzed. *Oligosarcus jenynsii* showed a high trophic plasticity (Fig. 2). Considering the variety of animal items that composed its diet, the species was classified as a generalist carnivore, but preferred crustacean decapods such as *Palaemonetes argentinus* and *Aegla* sp.

Seasonal changes in the diet of *O. jenynsii* were mainly related to individual size (Fig. 2). In the winter, animals longer than 14 cm (92%) dominated (Fig. 3). For fish in this size class, the item Insects was the most frequent, occurring in 22% of the stomachs that contained food. Fish, *Aegla* sp., and tanaidaceans (Crustacea) were also observed, but only in animals longer than 14 cm. The main diet item in specimens smaller than 14 cm was the decapod crustacean *P. argentinus*, found in 50% of the stomachs (Fig. 2).

During the spring, specimens larger than 14 cm fed mainly on *Aegla* sp. (50%), while individuals smaller than 14 cm consumed preferentially *P. argentinus* (32%).

Fish, insects, and macrophyte fragments were also identified, but only for animals longer than 14 cm.

In the summer of 2007, *Aegla* sp. made an important contribution to the diet of *O. jenynsii*, occurring in 83% of the stomachs of fish smaller than 14 cm. For individuals longer than 14 cm, this item was present in 21% of the stomachs. Insects were a main part of the diets in fish of this size class, occurring in 26% of the stomachs. Fish were present in low frequency in this season (13%).

Palaemonetes argentinus was the preferred item in both size classes during the autumn. Fish and *Aegla* sp. were also ingested by both size classes, whereas insects occurred only in individuals smaller than 14 cm.

According to the Constancy Index, *P. argentinus* was classified as a constant item in the diet of *O. jenynsii* smaller than 14 cm, whereas individuals longer than 14 cm had Insecta and *Aegla* sp. as accessory items, and all other items as accidental (Table I).

With regard to the isotopic analysis of *O. jenynsii*, values of $\delta^{15}N$ remained constant (11.4 to 12.2‰), whereas $\delta^{13}C$ values were size-dependent (Fig. 4). Larger *O. jenynsii* showed a lower $\delta^{13}C$ signature (-24.9‰; -24.4‰), suggesting a carbon source from emergent macrophytes (-26.05 to -26.41‰), perhaps through insects. In contrast, the carbon signature for smaller *O. jenynsii* (-23.9‰; -23.7‰) was closer to *Palaemonetes* (-24.39 ‰) and periphyton (-24.70‰), indicating a different carbon pathway.

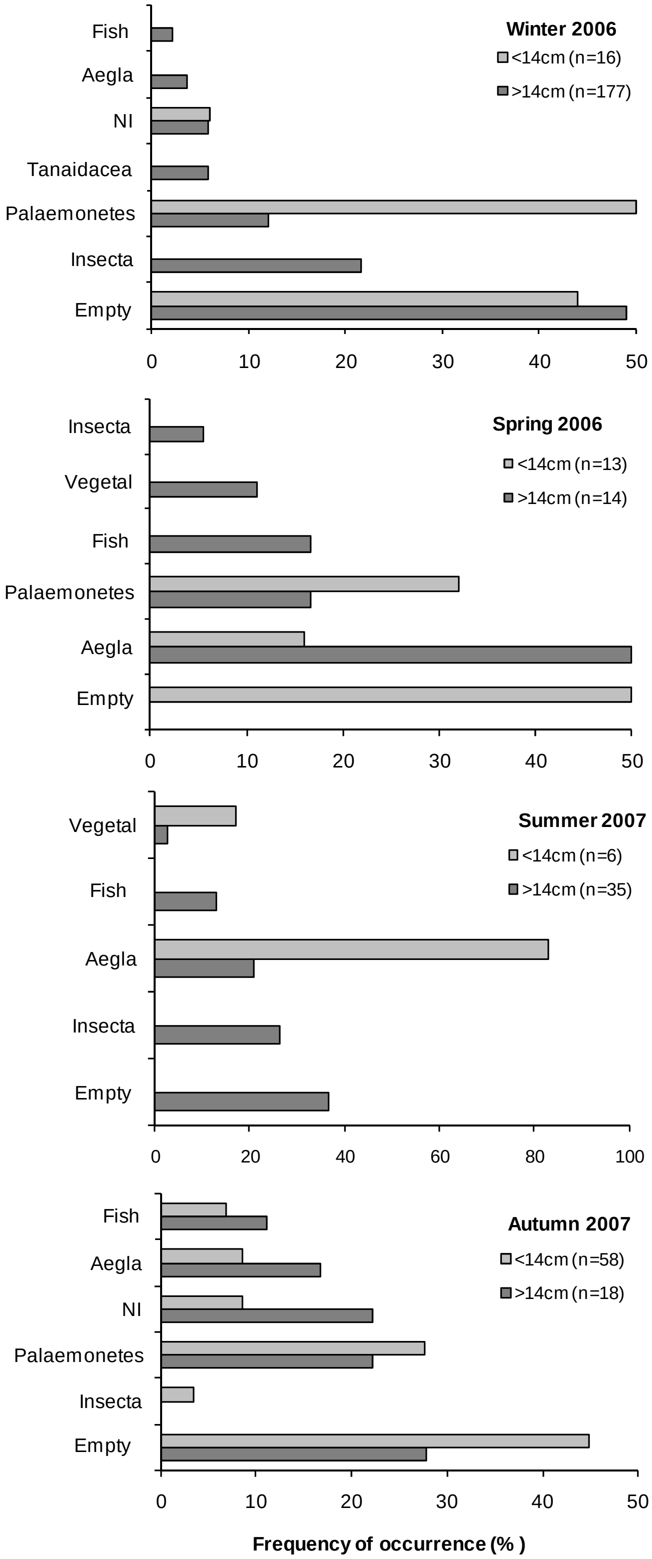

Figure 2. Frequency of occurrence (%) by food item and length classes (cm) of *Oligosarcus jenynsii* in Mangueira Lake.

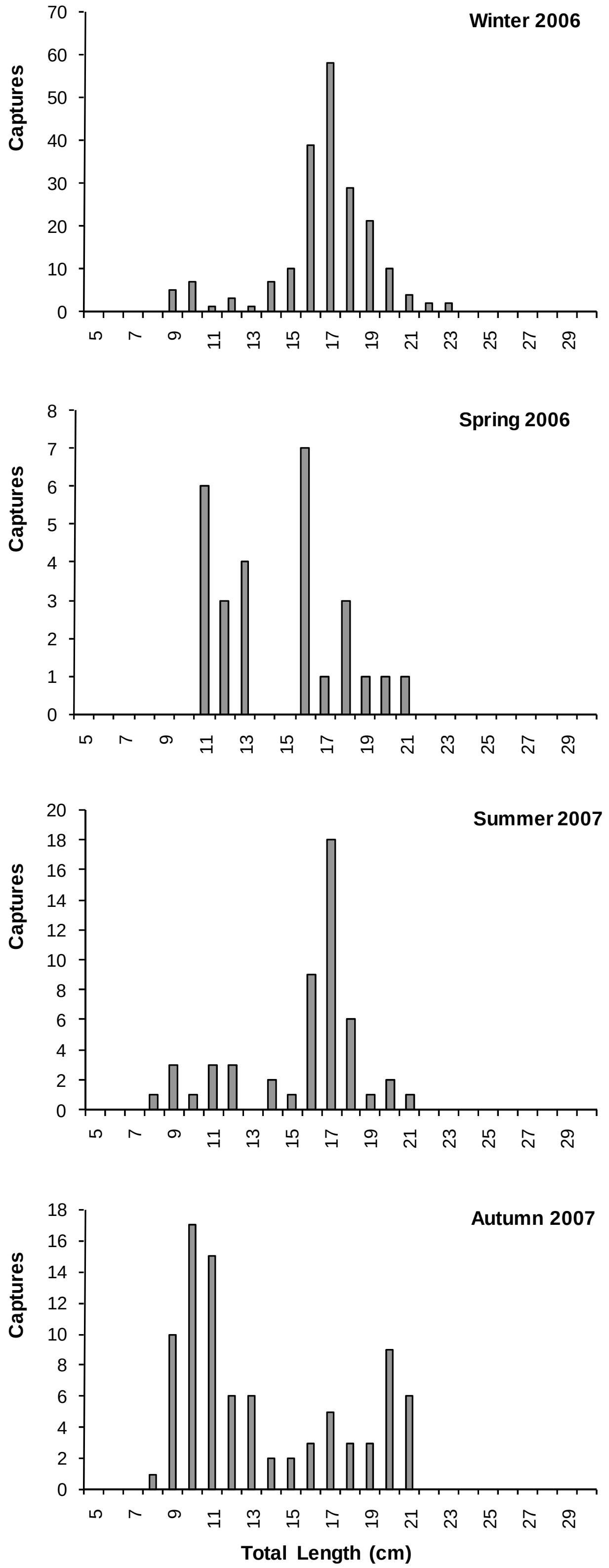

Figure 3. Length classes (cm) of captures of *Oligosarcus jenynsii* in Mangueira Lake.

DISCUSSION

In Mangueira Lake, *Oligosarcus jenynsii* showed a carnivorous food habit, feeding mainly on decapod crustaceans and insects, but changing its diet over the seasons and through its life cycle. Haro & Gutiérrez (1985) and Barros (2004) reported a similar food habit for *O. jenynsii* in Argentina, with juveniles feeding on insects and prawns. Hartz *et al*. (1996) found high prey diversity in *O. jenynsii* guts, with fish, decapod crustaceans, and insects being the major items.

During the study, the seasonal differences in the diet composition of *O. jenynsii* demonstrated an opportunistic character of the species, which changed its diet according to food availability. This high trophic plasticity may be one of the factors responsible for the broad distribution of the species. Wooton (1992) stated that spatial and seasonal changes in the diet of the fish are very common, usually associated with prey reproductive pulses and environmental changes in an ecosystem. Food availability is another important factor dictating these changes in the diet.

Oligosarcus jenynsii changes its diet markedly according to the season and ontogenetic variation. *Palaemonetes argentinus* was the dominant prey in all seasons, with exception of the summer (<14 cm animals). Insects dominated in the winter and summer, while *Aegla* sp. dominated in the spring and autumn (>14 cm animals). Analysis of the trophic changes during ontogeny showed that ingestion of shrimp (*P. argentinus*) decreased with an increase of the body size of *O. jenynsii*, while the ingestion of *Aegla* sp. and Insecta increased. Shrimp were ingested preferentially by individuals smaller than 14 cm (TL). Ontogenetic changes in diet can be related to size, pattern of habitat distribution, and as a tool to avoid intraspecific competition (Wooton, 1992). Although the intraspecific competition hypothesis cannot be neglected, prey distribution is also a key factor for opportunistic species. Beckett *et al.* (1991) proposed a relationship between the surface area covered by macrophyte stands and the abundance of macroinvertebrates. Chilton (1990) also suggested that the close proximity of different macrophyte beds could allow migration of invertebrates between stands. Our data do not allow us to determine whether the identified ontogenetic diet shift is associated with distributional patterns related to prey abundance, predator avoidance by small *O. jenynsii,* or even a mechanism to minimize intraspecific competition, and additional and dedicated sampling designs should be applied.

Another important item in the diet of *O. jenynsii*, the insects, are very abundant in the littoral zone of lakes, because in addition to shelter and support, they find in the macrophytes food in the form of detritus attached to the walls of the plants, acting as herbivores and scrapers (Merritt & Cummins, 1988; Ward, 1992; Trivinho-Strixino & Strixino, 1993). Insects are also found in the bottom of shallow lakes and are available to open-water predators; insects in this group are mostly collectors and predators (Trivinho-Strixino & Strixino, 1993).

Table 1. Classification of the items that composed the diet of O. jenynsii in Mangueira Lake, RS, Brazil, according to the Constancy Index (constant, >50%; accessory between 50 and 25%; accidental, <25%).

Food item	Length classes (cm) <14	 >14
Insecta	accidental	accessory
Palaemonetes argentinus	constant	accidental
Tanaidacea	not occur	accidental
Aegla sp.	accessory	accessory
Fish	accidental	accidental
Plant	accidental	accidental

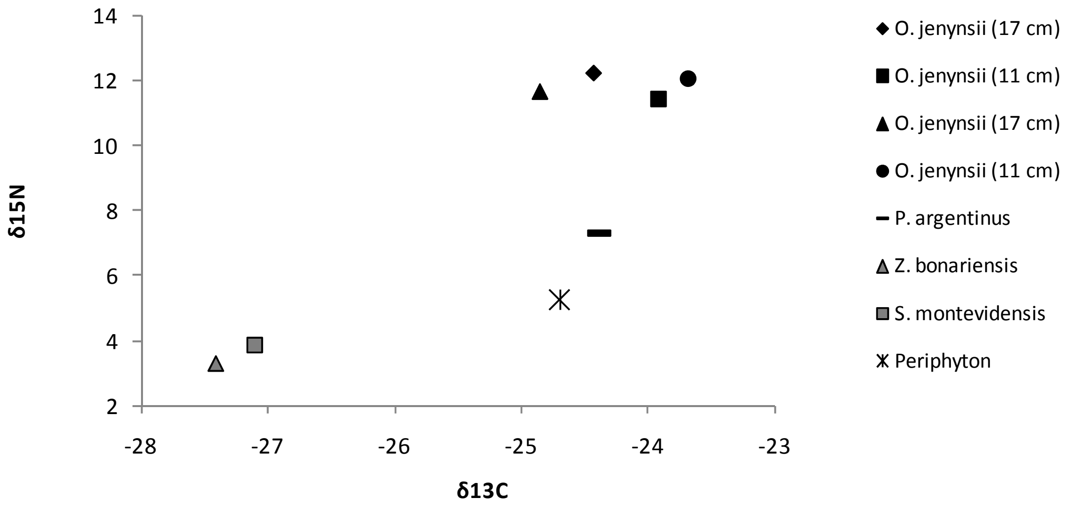

Figure 4. Plot of δ^{15}N and δ^{13}C values for *Oligosarcus jenynsii* at Mangueira Lake, Taim Hydrological System. Sources of carbon assimilated by consumers are indicated by the relative positions of taxa on the x-axis; trophic level is indicated by relative position on the y-axis.

The isotopic analysis (Fig. 4) indicated that *O. jenynsii* contained constant concentrations of δ^{15}N (11.4 to 12.2 ‰), suggesting a constant trophic position throughout its development. However, variations in the concentration of δ^{13}C indicated a shift in the main carbon source. Individuals 11 cm long showed the highest values of δ^{13}C, on the order of 24‰, about 1‰ above the values found for *P. argentinus*, indicating that this is one of the main food items for individuals in this size class. *Palaemonetes argentinus,* on the other hand, showed a concentration of δ^{13}C, just above that observed for periphyton. Although this may not be the only carbon source, our data suggest a direct energy flow from periphyton to *Palaemonetes* and *Oligosarcus*.

Oligosarcus jenynsii 17 cm in length showed concentrations of δ^{13}C equal to or even smaller than those observed for *P. argentinus* or for the periphyton. Considering a predictable increase of about 1‰ in the concentration of δ^{13}C at each trophic level (Fry & Sherr, 1984), the values of δ^{13}C identified for *O. jenynsii* are incompatible with those obtained for *P. argentinus* and periphyton as primary sources of carbon. On the other hand, values of $\delta^{13}C$ for the observed macrophytes (-26.05 to -26.41 ‰) showed differences greater than 1‰ in relation to the values observed for *O. jenynsii*, suggesting that they may contribute as carbon source through a primary consumer. Considering that *O. jenynsii* 17 cm in length fed on insects, a carbon route pathway from macrophytes to phytophagous insects and large *O. jenynsii* is suggested. Unfortunately, there are no data on the isotopic concentration for insects and *Aegla*, so this carbon pathway cannot be proved yet.

Overall, our results indicated a seasonal and ontogenetic change in the feeding biology of *Oligosarcus jenynsii*. The high feeding plasticity, in addition to an opportunistic strategy of this generalist carnivore species, explains why *O. jenynsii* is one of the most abundant species in the ichthyofauna of Mangueira Lake.

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6. DISCUSSÃO GERAL

Os resultados deste trabalho indicaram que os ecossistemas límnicos estudados (banhados temporários e lagoa Mangueira) apresentaram distintas características limnológicas e distintas dinâmicas das comunidades planctônicas e íctica associadas com gradientes espaciais e temporais.

A ocorrência de períodos distintos durante o desenvolvimento dos banhados temporários evidencia o forte gradiente temporal destes ecossistemas. Nestes banhados temporários, as rápidas mudanças químicas e físicas, decorrentes da alternância de seca e alagamento (Fernando, 2005) são certamente decisivas na composição da biota, favorecendo organismos que possuem estratégias de sobrevivência e reprodução adaptadas a essas condições extremas.

O período inicial dos cultivos foi caracterizado pelas maiores concentrações de nutrientes. A disponibilidade de nutrientes e luz nesta fase permitiram as maiores concentrações de chl *a*, refletindo no aumento do zooplâncton. A distribuição do zooplâncton, além de ser influenciada pelas condições abióticas do ambiente, é fortemente regulada pela disponibilidade de alimento e interações bióticas.

Os peixes, por sua vez, na medida em que entram nas quadras de cultivo e encontram alimento em abundância, considerando a alta biomassa de zooplâncton existente no sistema, apresentam um aumento de capturas e biomassa.

Durante o período de estudo, a dinâmica dos nutrientes, decorrente das práticas agrícolas apresentou reflexos na estrutura da comunidade como um todo, e carbono orgânico dissolvido (COD) demonstrou ser um elemento chave na produção primária desses ecossistemas temporários.

Da mesma maneira como nos banhados temporários, notáveis diferenças (temporal e espacial) nas características físicas e químicas da água e entre as comunidades planctônicas e íctica foram observadas na lagoa Mangueira.

Um gradiente temporal governado pela dinâmica dos nutrientes e profundidade foi encontrado. Diferenças sazonais são provavelmente relacionadas com fatores ambientais, como temperatura e disponibilidade de recursos, especialmente nutrientes e luz (Wersal *et al*., 2006). Na lagoa Mangueira as variações sazonais (temporais) nas características químicas, físicas e hidrológicas influenciaram diretamente a dinâmica das comunidades planctônicas.

A lagoa Mangueira apresentou grande heterogeneidade espacial e claro gradiente longitudinal dos fatores abióticos, com reflexos na distribuição e abundância de plâncton e peixes. O norte da lagoa apresentou maior turbidez da água, sedimento lamosos, maiores concentrações de chl *a* e grande biomassa de bacterioplâncton, zooplâncton e peixes.

Concentrações de chl *a* foram maiores na zona vegetada tanto no norte quanto no sul da lagoa, provavelmente devido ao fato do perifíton e metafíton estar associado aos estandes de macrófitas. Para o bacterioplâncton não foi observado o gradiente espacial (N/S e relacionado a presença da vegetação) de maneira clara, considerando as variações sazonais ocorridas na biomassa bacterioplanctônica durante o estudo.

Foram encontradas diferenças na biomassa zooplantônica entre os extremos da lagoa e quanto a presença da vegetação. No sul da lagoa as maiores biomassas de zooplâncton foram encontradas nas zonas vegetadas, caracterizando esse microhabitat como um refúgio potencial para o zooplâncton contra predatores, favorecendo sua densidade e diversidade (Meerhoff *et al*., 2003). Já no norte, este padrão não foi observado, provavelmente devido a maior turbidez da água.

Foram identificadas também importantes diferenças na estrutura da comunidade de peixes entre os extremos da lagoa. Abundância, riqueza, número de capturas e biomassa total apresentaram maiores valores no norte da lagoa, provavelmente devido ao aumento da complexidade de hábitat derivado da interface banhado-lagoa e da maior produtividade primária indicada pela concentração de chl *a*.

A heterogeneidade espacial da lagoa também foi identificada através da distribuição de freqüência das diferentes guildas. Freqüências de onívoros no norte e no sul foram similares, enquanto os peixes planctívoros apresentaram baixa biomassa capturada. Peixes que se alimentam de invertebrados foram dominantes nos dois extremos da lagoa. Entretanto, é interessante salientar que a guilda representada pelos peixes que comem invertebrados foi diferente nos extremos da lagoa. No norte, *Oligosarcus jenynsii* foi a espécie mais abundante desta guilda, alimentando-se principalmente de crustáceos (*Aegla* sp. and *Palaemonetes argentinus*). Em contraste, a espécie mais abundante desta guilda no sul da lagoa foi *Odontesthes humensis*, consumindo preferencialmente moluscos (*Heleobia sp.* and *Corbicula sp.*). Também foi observada uma inversão relacionada às freqüências de detritívoros e piscívoros entre os extremos da lagoa. Sedimentos lamosos do norte da lagoa podem explicar a abundância relativa de detritívoros, enquanto que sedimentos arenosos e as águas claras poderiam ser relacionados à maior freqüência de piscívoros no sul, supondo uma detecção mais fácil das presas.

O gradiente longitudinal identificado no sistema pode ser relacionado com dois principais fatores direcionadores. Ventos predominantes de nordeste para sudoeste (Fragoso Jr. *et al.* 2008), seguindo o eixo principal da lagoa, podem mover as águas superficiais em direção ao Sul da lagoa Mangueira, desenvolvendo energia considerável para a ressuspensão de sedimentos finos, resultado de um longo *fetch* que pode alcançar

90 km. Ao mesmo tempo, sedimentos finos e nutrientes associados são transportados para o Norte através de contra-corrente de fundo, resultando em sedimentos arenosos, elevada transparência e baixa concentração de clorofila *a* no sul da lagoa, com conseqüências em toda a cadeia trófica.

A segunda pressão reguladora constitui-se na interface da lagoa Mangueira com o banhado do Taim. Através do fluxo de água do banhado para o corpo da lagoa são transportados tanto material particulado como nutrientes para o norte da lagoa. Ao mesmo tempo, a complexidade estrutural da interface banhado-lagoa contribui para aumentar a riqueza específica em todos os grupos taxonômicos, resultando, conseqüentemente, em uma estrutura mais complexa.

A complexidade espacial do norte da lagoa também foi verificada na estrutura trófica vertical representada por análise de isótopos estáveis. Em banhados e zonas litorâneas de lagos há geralmente três grupos de produtores primários: algas epifíticas (perifíton), macrófitas aquáticas e material particulado em suspensão (Lamberti & Moore 1984; Frost *et al*. 2002).

Macrófitas emergentes e perifíton revelaram-se importantes fontes de carbono assimilado na estrutura trófica da lagoa Mangueira, corroborando a hipótese dos consumidores primários refletirem a produção autóctone do sistema.

Análises de agrupamento de dados de assinatura isotópica comparados com dados de conteúdo estomacal de peixes da lagoa Mangueira evidenciaram diferenças entre as duas abordagens. Embora arranjos funcionais possam, através de evolução convergente, aproximar espécies sem relação filogenética, isto não foi verificado no presente trabalho. Quando os itens alimentares foram classificados em grandes grupos por tamanho e fonte, a análise combinada de assinatura isotópica e conteúdo estomacal revelou um arranjo entre espécies que emulou perfeitamente o arranjo filogenético.

Embora este resultado fosse inicialmente inesperado, fica claro que nichos alimentares, em sentido amplo, são compartilhados por espécies filogeneticamente relacionadas. Entretanto, estes resultados devem ser considerados com cautela, considerando o pequeno número de espécies analisadas, assim como pelo arranjo de itens alimentares em grandes grupos funcionais.

Em especial, para uma espécie de peixe dominante (*Oligosarcus jenynsii*) na lagoa Mangueira foi possível analisar mudanças sazonais e ontogenéticas na dinâmica alimentar através de análises de assinatura isotópica e conteúdo estomacal. *Oligosarcus jenynsii* demonstrou grande plasticidade trófica associada com uma estratégia oportunista, característica de espécies carnívoras generalistas.

Com base nas informações obtidas nos capítulos desta tese, relacionadas principalmente à heterogeneidade espacial da lagoa Mangueira, foi possível alcançar um entedimento sobre a estrutura atual do sistema, bem como os direcionadores da sua dinâmica. A abordagem direcionada neste trabalho sobre o entendimento da estrutura atual de um lago raso subtropical possibilita futuros estudos na área promissora da modelagem ecológica, devido à consistência de dados e forte heterogeneidade espacial do sistema. A dinâmica das comunidades abordadas pode subsidiar a parametrização de um modelo ecológico, com capacidade de estabelecer prognósticos, tendo como contorno, estressores naturais e antrópicos.

Um grande problema relacionado aos modelos ecológicos complexos é o grande número de parâmetros envolvidos. Isto dificulta a calibração e validação destes modelos, e ainda, os parâmetros geralmente são definidos utilizando dados da literatura de lagos europeus. Há, portanto, a necessidade de parametrização dos modelos já existentes para a realidade tropical e subtropical.

Além disso, estes modelos, na prática, são validados e comparados com informação empírica (Rykiel, 1996). Assim, fica evidente a relevância dos resultados obtidos para as futuras aplicações em modelagem ecológica, visando verificar a real possibilidade de ocorrência dos cenários simulados. Somente desta forma, torna-se exeqüível gerar elementos para uma gestão abrangente de usos da água e conservação de lagos, como no caso da Lagoa Mangueira.

7. CONCLUSÕES

- A disponibilidade de nutrientes demonstrou ter papel essencial na dinâmica das comunidades planctônicas e íctica tanto nos banhados temporários (‘*rice fields*’) quanto na lagoa Mangueira;

- Macrófitas aquáticas emergentes desempenharam efeito estruturador na abundância e distribuição espacial das comunidades planctônicas e íctica da lagoa Mangueira;

- A complexidade estrutural da interface banhado do Taim com o norte da lagoa Mangueira promove o contínuo fluxo de água do banhado do Taim para o corpo da lagoa transportando tanto material particulado como nutrientes para o Norte do sistema, contribuindo para o aumento da riqueza específica em todos os grupos taxonômicos;

- A lagoa Mangueira apresentou grande heterogeneidade espacial e claro gradiente longitudinal dos fatores abióticos, com reflexos da distribuição e abundância das comunidades aquáticas;

- Análises de isótopos estáveis de carbono ($\delta^{13}C$) e nitrogênio ($\delta^{15}N$) revelaram que macrófitas emergentes e perifíton são importantes fontes de carbono que sustentam a estrutura trófica da lagoa Mangueira, bem como determinou a posição trófica dos organismos do sistema;

- Dados de assinatura isotópica das espécies de peixes da lagoa Mangueira evidenciaram diferenças quando comparados com dados de análises de conteúdo estomacal, entretanto, a combinação das duas análises revelou um arranjo filogenético entre as espécies;

- Mudanças sazonais e ontogenéticas na dinâmica alimentar de *Oligosarcus jenynsii* através de análises de assinatura isotópica e conteúdo estomacal evidenciaram a grande plasticidade trófica associada com uma estratégia oportunista, característica de espécies carnívoras generalistas.

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