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**Variações na estrutura das assembléias de  
peixes ao longo de um amplo gradiente  
estuarino-límnico do complexo Lagunar  
Patos-Mirim**

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## RESUMO

A presente dissertação é composta de um capítulo (em Português) sintetizando os principais resultados obtidos, os quais são apresentados na forma de um manuscrito (em inglês) no apêndice. O principal objetivo foi analisar o padrão de distribuição das assembleias de peixes e a influência de algumas variáveis ambientais na abundância relativa das espécies dominantes ao longo de um amplo eixo espacial (~300 km), englobando o estuário da Lagoa dos Patos, canal São Gonçalo e Lagoa Mirim. No total, sete locais foram amostrados mensalmente entre 03/2004 e 02/2005 com uma rede de arrasto em zonas rasas (< 2 m). Foram capturadas 63 espécies e 45.929 indivíduos. As análises de escalonamento multidimensional (MDS) evidenciaram a presença de dois grupos principais espacialmente distintos: um formado pelas amostras do estuário e outro formado pelo Canal São Gonçalo e Lagoa Mirim. Os peixes foram agrupados em guildas ecológicas e, através da análise de composição e abundância relativa, verificou-se uma marcada substituição dessas guildas entre a zona estuarina (estuário e norte do canal) e zona límnic (sul do canal e Lagoa Mirim). Essa substituição foi mais pronunciada em termos de abundância do que em termos de frequência de ocorrência, sendo que a segregação entre as guildas foi intensificada pela presença de uma barragem-eclusa, posicionada na porção mediana do gradiente. Variáveis físico-químicas (e.g., salinidade e transparência da água) e outras relacionadas às características estruturais dos habitats (e.g., declividade e percentual de silte e argila no sedimento) foram os principais fatores, dentre os investigados, que melhor explicaram a variabilidade na abundância e distribuição da ictiofauna ao longo do gradiente.

**Palavras-chave:** Ecótono, gradiente de salinidade, assembleias de peixes, estuário da Lagoa dos Patos, canal São Gonçalo, Lagoa Mirim.

## **ABSTRACT**

This dissertation is comprised of a chapter (in Portuguese) summarizing our main findings, which are shown in a manuscript (in English) in the annex. Our main goal was to analyze the distribution pattern of fish assemblages and the influence of some environmental variables on the relative abundance of dominant species along a broad spatial axes (~300 km), including the Patos Lagoon estuary, São Gonçalo channel and Mirim Lake. A total of seven sites were sampled monthly between 03/2004 and 02/2005 with a beach seine in shallow areas (<2 m). A total of 63 fish species and 45.929 individuals were caught. The multidimensional scaling (MDS) analyses revealed two main groups spatially distinct: one formed by the estuarine samples and other by freshwater samples from the channel and the Mirim. Fish species were grouped into ecological guilds and the analyses of their composition and relative abundance revealed a marked substitution of ecological guilds between the estuarine zone (estuary and northern portion of the channel) and the limnetic zone (southern portion of the channel and Mirim). This substitution was more pronounced in terms of abundance than in terms of frequency of occurrence. Guilds segregation was intensified by the presence of a dam lock positioned in the middle portion of the gradient. Physico-chemical variables (e.g., salinity and water transparency) and others related to the structural characteristics of habitats (e.g., slope and percentage of silt and clay in the sediment) were the main factors, among those investigated, that better explained the variability in the distribution and abundance of fish fauna along the gradient.

**Keywords:** ecotone, salinity gradient, fish assemblages, Patos Lagoon estuary, São Gonçalo channel, Mirim Lake.

## I. INTRODUÇÃO

Os estuários são zonas de transição entre ecossistemas marinhos e de água doce, representando talvez o mais óbvio ecótono na ecologia aquática. As áreas transicionais (ecótonos), são regiões de grande dinamismo e de uma heterogeneidade constante (Attrill & Rundle, 2002). Nas últimas décadas vários estudos vêm investigando o padrão de distribuição longitudinal das assembléias de peixes ao longo dessas áreas transicionais (Winemiller & Leslie, 1992; Araújo, 1996; Martino & Able, 2003; Akin et al., 2005; Sanchez-Botero et al., 2008; Castro et al., 2009; García et al., 2010; Macedo-Soares et al., 2010; Câmara, 2010). Em larga escala (km) o padrão de distribuição de peixes parece resultar primariamente de respostas ao ambiente físico. Provavelmente variáveis abióticas agem como um filtro fisiológico, desempenhando um papel vital na estruturação da comunidade (Remmert, 1983; Martino & Able, 2003). Consequentemente, o gradiente ambiental em estuários é muito forte, com algumas espécies restritas a uma área particular, resultando em um marcado padrão de zonação (Raffaelli et al., 1991). De fato, as espécies de peixes dessas regiões podem ser consideradas como indicadores de heterogeneidade ao longo do gradiente ambiental (Kremen, 1992; Mônaco et al., 1992; Bulger et al., 1993).

Na porção sul da planície costeira do Rio Grande do Sul, que se estende até o norte do Uruguai, encontra-se o complexo Lagunar Patos – Mirim formado pela confluência do estuário da Lagoa dos Patos e Lagoa Mirim. Esses dois sistemas são interligados por um canal natural, denominado de São Gonçalo. A ictiofauna desse complexo lagunar possui elevada diversidade de espécies com ciclos de vida variados, que, muitas vezes, inclui o deslocamento entre o ambiente marinho, estuarino e límnic (Chao et al., 1985; Malabarba, 1989). Algumas espécies são limitadas a um determinado ambiente por apresentar estreita tolerância fisiológica à salinidade, enquanto outras com ampla tolerância podem estar restritas a certos locais por outros fatores físicos (e.g. profundidade) ou bióticos (e.g.,

predação). A distribuição da salinidade ao longo do complexo lagunar Patos-Mirim depende principalmente das relações entre descarga fluvial e ação dos ventos (Möller & Fernandes, 2010). Em condições de vazante e predomínio de ventos do quadrante Norte, o estuário da Lagoa dos Patos recebe o aporte de água doce dos rios da parte Norte da planície costeira do Rio Grande do Sul e dos rios afluentes da Lagoa Mirim. Assim representa um escoadouro natural da bacia hidrográfica para o oceano através dos molhes da barra de Rio Grande. Já em condições de estiagem e predomínio de ventos do quadrante Sul, a cunha salina pode se estender dezenas de quilômetros à montante das duas lagoas.

Em 1977, com o intuito de prevenir a salinização das extensas lavouras de arroz nas margens da Lagoa Mirim, foi construída uma barragem-eclusa no canal São Gonçalo. Assim, a cunha salina ficou impedida de penetrar na parte sul do Canal São Gonçalo e na Lagoa Mirim, tornando esta região um ambiente límnic permanente e mais estável devido a ausência da intrusão da água do mar. Burns et al. (2006) apresentaram as primeiras evidências sugerindo que a barragem-eclusa acarretou uma descontinuidade na distribuição de juvenis de peixes marinhos e estuarinos entre a porção norte, que possui conexão livre com o estuário, e a porção sul do Canal, restrito à água doce. Uma análise mais aprofundada dessa questão (Burns, 2010) demonstrou que a barragem-eclusa provocou a perda de habitat para as espécies marinhas e estuarinas, e o concomitante aumento de habitat para as espécies de água doce na porção sul do canal e na região da Lagoa Mirim.

No complexo lagunar Patos-Mirim, Raseira (2003) investigou os padrões de distribuição dos peixes ao longo de uma ampla escala espacial (km) englobando o gradiente marinho-estuarino-límnic. Analisando a assembléia de peixes desde o mar até a zona límnic da Lagoa dos Patos, o autor descreve uma mudança gradual na ocorrência das principais espécies, com uma substituição gradativa das espécies marinhas por espécies de água doce à medida que se avança em direção ao norte da Lagoa dos Patos. Também foi

observado um aumento gradativo no comprimento total (mm) dos indivíduos desde o mar até a zona pré-límnica. Dos fatores abióticos analisados por Raseira (2003), a salinidade foi a que melhor explicou e influenciou a estruturação das assembléias de peixes ao longo do eixo longitudinal. Outros fatores, como por exemplo, tipo de habitat, granulometria do sedimento, temperatura, declividade e abundância de alimento também exerceram influência, o que levou o autor a sugerir que o efeito sinérgico desses fatores, aliados à bioecologia das espécies, determinam a distribuição dos peixes nessa região. Porém, a análise de Raseira (2003) foi restrita à Lagoa dos Patos. Até o presente momento, não há informações sobre os fatores que controlam a distribuição dos peixes ao longo do gradiente estuarino-límnico formado pelo estuário da Lagoa dos Patos e a Lagoa Mirim.

Nesse contexto, o presente trabalho investiga os padrões e os fatores abióticos que regulam a distribuição dos peixes de zonas rasas ( $< 2$  m) ao longo de um amplo gradiente estuarino-límnico ( $\sim 300$  km) formado pela confluência de duas importantes lagunas: a Lagoa dos Patos, considerada a maior lagoa costeira do tipo “estrangulada” do mundo (*sensu* Kjerfve, 1986), e a Lagoa Mirim, a segunda maior lagoa do Brasil. As principais questões abordadas são (1) Quais as mudanças na estrutura das assembléias de peixes em termos de composição específica, abundância relativa, estrutura de tamanho e diversidade ao longo do gradiente estuarino-límnico? (2) Qual a importância relativa dos fatores ambientais (e.g., salinidade) e das características estruturais do habitat (e.g., granulometria do sedimento) na estruturação dos atributos das assembléias de peixes ao longo do gradiente? (3) De que modo as guildas de espécies (e.g. estuarino residentes, marinhas, dulcícolas) se distribuem ao longo do gradiente e que fatores abióticos controlam sua distribuição? Além de preencher uma lacuna de conhecimento sobre a distribuição da ictiofauna em um dos maiores complexos lagunares do sul da América do Sul, o presente



trabalho contribui para o entendimento da dinâmica e dos fatores que influenciam a diversidade de peixes em áreas de ecótono estuarino-limnico da região Neotropical.

## II. MATERIAL E MÉTODOS

Os dados foram obtidos junto ao banco de dados do laboratório de Ictiologia do sítio 8 (estuário da Lagoa dos Patos) do Programa de Pesquisas Ecológicas de Longa Duração (PELD), que realizou amostragens mensais entre março de 2004 a fevereiro de 2005 em sete locais ao longo do estuário da Lagoa dos Patos (E1-E2), Canal São Gonçalo (C1 norte - C2 sul) e a Lagoa Mirim (L1-L2-L3). Essas estações de coleta estão distribuídas num eixo espacial de aproximadamente 326 km ao longo do Complexo Lagunar Patos-Mirim (CLPM) (Fig. 1, apêndice). Em cada localidade os peixes foram coletados através de cinco arrastos com uma rede de arrasto de praia (modelo *trawl* – 9 m de largura e 2,4 m de altura, malha 13 mm nas asas e 5 mm no saco) em zonas marginais de pouca profundidade (< 2 m). Após coletados, os peixes foram fixados em formol 10% e, posteriormente, identificados no nível de espécie, e tiveram seu comprimento total (CT) e peso mensurados.

Concomitante com a amostragem dos peixes, a salinidade, temperatura, transparência da água e a profundidade máxima dos arrastos foi registrada em cada localidade durante as saídas de campo. Visando obter uma caracterização relativa da heterogeneidade e complexidade estrutural do habitat, cada uma das sete localidades de amostragem foi caracterizada em relação à granulometria do substrato (grosseiros e finos), porcentagem de matéria orgânica e a declividade da praia (baixa, média e alta). Essa caracterização foi realizada com periodicidade sazonal entre 2009 e 2010.

A composição de espécies e padrão de dominância foram analisados a partir da frequência de ocorrência (FO%) e da abundância relativa (CPUE%) (Garcia et al., 2004).

As espécies com FO% maior ou igual a média de FO% de todas as espécies foram consideradas como frequentes, sendo pouco frequentes aquelas com FO% menor que o FO% médio. O mesmo procedimento foi empregado para a CPUE%. Finalmente, com base nesses critérios, as espécies foram classificadas em quatro grupos em relação a sua abundância e frequência de ocorrência: 1. abundante e frequente, 2. abundante e pouco frequente, 3. pouco abundante e frequente e 4. pouco abundante e pouco frequente (Garcia et al., 2004). Foram consideradas dominantes as espécies classificadas nas categorias 1, 2 e 3 em pelo menos uma das localidades amostradas.

A técnica de escalonamento multidimensional (MDS) foi empregada para avaliar a similaridade na composição das espécies entre as estações de coleta tendo como base uma matriz de presença/ausência, e outra matriz com a abundância relativa das espécies dominantes. Em algumas das análises da abundância, as espécies de peixes foram agrupadas nas seguintes guildas ecológicas: (a) estuarino residente; (b) estuarino dependente; (c) visitantes marinhos; (d) água doce secundário; (e) água doce primário. Essas guildas foram baseadas e adaptadas de Garcia et al. (2001) e Garcia et al. (2003b) que propuseram uma versão simplificada das guildas ecológicas da ictiofauna do estuário da Lagoa dos Patos, originalmente propostas por Chao et al. (1985) e Vieira et al. (1998). No entanto, ao contrário dos trabalhos anteriores que tiveram como foco apenas o estuário, o presente trabalho engloba um amplo gradiente estuarino-limnico que contempla populações estuarinas e outras populações de água doce para a mesma espécie. Assim, as espécies *Platanichthys platana* e *Jenynsia multidentata* que possuem populações no ambiente estuarino e limnico foram classificadas na guilda de água doce secundária, e não como estuarino residentes, como apontado por Garcia et al. (2001, 2003b).

A distribuição da abundância e do tamanho (comprimento total, CT, mm) das espécies foi analisada conjuntamente numa única representação gráfica, plotando-se a

Captura por Unidade de Esforço (CPUE, número médio de indivíduos por arrasto) por classes de comprimento (CT, mm) (Garcia et al., 2001; Vieira, 2006). Este procedimento permitiu avaliar quais as unidades de tamanho (por exemplo, juvenis ou adultos) que foram capturadas em maior abundância para cada espécie em diferentes locais e estações do ano, possibilitando assim a inferência dos padrões de recrutamento destas espécies (Vieira, 1991; Geracitano, 1998). O teste de Kolmogorov-Smirnov foi utilizado para comparar a similaridade no formato das distribuições nas classes de tamanho das assembléias do estuário da Lagoa dos Patos, Canal São Gonçalo e Lagoa Mirim (Zar, 1996).

A diversidade foi analisada separadamente em dois componentes: riqueza observada de espécies (S) e equitatividade. A equitatividade, ou seja, a proporção na qual a abundância está distribuída entre as espécies, foi calculada através do índice de Hill (1973) modificado (E5). As possíveis diferenças sazonais entre os sete locais de amostragem na riqueza observada de espécies (S) e na equitatividade (E5) foram examinadas através de ANOVA. As estações do ano foram consideradas a partir do agrupamento dos seguintes meses: Verão (Janeiro, Fevereiro, Março), Outono (Abril, Maio, Junho), Inverno (Julho, Agosto, Setembro) e Primavera (Outubro, Novembro, Dezembro).

Foi utilizada ANOVA de duas vias para testar diferenças significativas entre as variáveis ambientais [ $\log_{10}(\text{Salinidade}+1)$ , temperatura da água e profundidade] por áreas e meses do ano. A transparência da água (disco de *Secchi*) não atendeu os pressupostos da ANOVA, então as comparações foram feitas através do teste não paramétrico de Kruskal-Wallis (Sokal & Rohlf, 1995; Conover, 1999).

A análise de correspondência canônica (ACC) foi utilizada para verificar as relações entre a complexidade estrutural dos habitats (percentual de sedimento fino, percentual de sedimento grosso, matéria orgânica, declividade e profundidade dos arrastos), os fatores abióticos (salinidade, temperatura da água e transparência da água) e a

distribuição e abundância dos peixes dominantes (31 espécies). As variáveis ambientais foram padronizadas e a abundância dos peixes foi expressa como  $\log_{10}(\text{CPUE} + 1)$ . Foi utilizado o procedimento “Forward selection” da ACC para selecionar quais variáveis abióticas tiveram uma contribuição significativa ( $p=0,05$ ) na explicabilidade das variações observadas na matriz de espécies. O teste de permutação de Monte Carlo (com 9999 permutações) foi utilizado para testar a significância ( $p < 0,05$ ) dos eixos da ACC (ter Braak & Verdonschot, 1995).

### III. RESULTADOS

Foram capturadas 63 espécies de peixes compreendidos em 11 ordens e 25 famílias, totalizando 45.929 indivíduos. Do total de 63 espécies, 31 foram consideradas dominantes e 10 espécies representaram 86,61% das capturas em número, sendo elas: *Mugil liza*, *Cyanocharax alburnus*, *Brevoortia pectinata*, *Mugil curema*, *Odontesthes mirinensis*, *Cheirodon ibicuiensis*, *Odontesthes argentinensis*, *Platanichthys platana*, *Astyanax fasciatus* e *Lycengraulis grossidens* (Tabela 1, apêndice).

As análises de escalonamento (MDS) com as matrizes de composição de espécies (presença/ausência) e abundância (CPUE%) das espécies dominantes resultaram em padrões semelhantes. Ambos evidenciaram a presença de dois grupos principais, um formado pelas amostras do estuário (E1 e E2) e o segundo de água doce formado pela região do Canal (C1, C2) e Lagoa Mirim (L1, L2, L3) (Fig. 3, apêndice). De acordo com a análise de similaridade de porcentagens (SIMPER) da contribuição das espécies, o grupo formado pelas amostras do estuário apresentou similaridade média de 28,45%, sendo que as espécies com maior contribuição para esse grupo foram *M. liza*, *M. curema*, *B. pectinata* e *O. argentinensis*. Já o grupo de água doce apresentou similaridade média de 19,57% com

*C. alburnus*, *O. mirinensis*, *A. fasciatus*, *P. platana*, *C. ibicuihensis* e *Bryconamericus iheringii* tendo a maior contribuição na similaridade desse grupo.

Em relação à composição e abundância das guildas, foi possível observar que a maioria das espécies (N=28) foi oriunda da guilda de água doce primário. Já o número de espécies de visitantes marinhos, água doce secundário, estuarinos dependentes e estuarinos residentes foram de 12, 11, 7 e 5 espécies, respectivamente (Tabela 1, apêndice).

Ocorreu uma marcada substituição das guildas ecológicas entre a zona estuarina (estuário e porção norte do canal) e límnic (porção sul do canal e lagoa Mirim) que coincidiu com a diminuição da salinidade ao longo do gradiente. Essa substituição foi mais pronunciada em termos de abundância do que em termos de frequência de ocorrência (Fig. 4, apêndice). A guilda visitante marinho ficou restrita à zona estuarina, que possui conexão livre com o estuário. Em termos de abundância percentual, os estuarinos dependentes dominaram com média de 85% a região do estuário, água doce primário dominou 80% da região do canal, e água doce primário juntamente com água doce secundário, dominaram a ictiofauna da lagoa de água doce com 51% e 45%, respectivamente.

A composição de tamanho no estuário foi diferente daquela observada no canal (K-S teste;  $D = 0,425$ ;  $p < 0,0002$ ) e na lagoa Mirim (K-S teste;  $D = 0,319$ ;  $p < 0,012$ ), porém, não houve diferença na distribuição de tamanho entre canal e lagoa Mirim (K-S teste;  $D = 0,234$ ;  $p > 0,130$ ). No estuário, a distribuição foi unimodal (moda na classe de 25-30 mm de comprimento total), com amplitude de distribuição entre 5 e 130 mm CT. Já no canal e na lagoa Mirim, a distribuição foi bimodal (30-40 e 95-105 mm CT) e ocorreu maior amplitude na distribuição, especialmente no canal (10 a 235 mm) (Fig. 5, apêndice).

Na região estuarina as tainhas (*M. liza* e *M. curema*) foram as mais abundantes em quase todas as classes de tamanho amostradas, sendo especialmente abundantes entre 25 e 105 mm CT. O peixe-rei (*O. argentinensis*) apresentou maior amplitude de tamanhos

variando de 15 até 130 mm CT, enquanto a corvina (*M. furnieri*) foi mais abundante nas classes maiores (CT > 110 mm). Já na região do canal os lambaris foram numericamente dominantes, com *C. alburnus* dominando as classes de tamanho de 10 a 65 mm CT e *A. fasciatus* entre as classes 70 até 110 mm CT. Indivíduos de maior tamanho (entre 150 e 235 mm), como *C. punctata*, *C. voga* e *G. brasiliensis*, ocorreram em baixa abundância (Fig. 5, apêndice).

Na região da lagoa Mirim, os tamanhos menores foram dominados por *P. platana* e *J. multidentata*, enquanto as classes de maior tamanho (90-185 mm CT) foram dominadas por *A. fasciatus* e *C. voga*. O peixe-rei *O. mirinenses* foi a espécie com maior amplitude de tamanho nas capturas nessa região, ocorrendo desde 20 a 180 mm CT, com moda nas classes 70 e 75 mm CT (Fig. 5, apêndice).

Os resultados da ANOVA foram distintos em relação à variabilidade na riqueza de espécies e na equitatividade entre os locais de amostragem e as estações do ano (Tabela 2, apêndice). Para a riqueza houve interação entre as localidades do estudo e sazonalidade ( $p < 0,01$ ). De uma maneira geral, as localidades do canal (C1 e C2) apresentaram médias significativamente superiores às demais localidades do estudo ( $p < 0,000$ ) e o inverno apresentou médias significativamente inferiores ao verão e primavera ( $p < 0,032$ ) (Fig. 6, apêndice). Já a equitatividade apresentou diferenças significativas apenas em relação aos locais de coleta. A localidade C1 apresentou menor equitatividade em relação a E2 e L3, mas não diferindo significativamente em relação as demais localidades (teste de Tukey;  $p > 0,05$ ).

O primeiro eixo da ACC apresentou autovalor de 0,661, sendo responsável por 59,3% da variância total. Em combinação com o segundo eixo, que apresentou autovalor de 0,251, ambos modelaram 81,8% da variância explicada pela ACC. A inércia total dos dados foi de 2,995, sendo que 37% (1,115) pode ser explicada pela análise (Tabela 3,

apêndice). A relação entre as espécies dominantes e as variáveis ambientais representadas por esses dois eixos foi estatisticamente significativa ( $p < 0,05$ ) de acordo com o teste de permutação de Monte Carlo. A profundidade e o percentual de sedimento grosseiro (areia fina, média e grossa) não tiveram uma contribuição significativa na modelagem dos dados (FS teste;  $p > 0,05$ ) e, portanto, foram excluídos da análise.

De modo geral, a salinidade e a declividade foram as variáveis que mais influenciaram a distribuição das espécies nesse estudo, seguidas por transparência da água e percentual de sedimento fino (Fig. 7a, apêndice). As amostras da região estuarina foram associadas com maiores valores de transparência da água e salinidade, enquanto que a região do canal apresentou valores intermediários para essas variáveis e uma menor associação com salinidade. Por outro lado, as amostras obtidas no canal foram correlacionadas com maior declividade e maior contribuição percentual de sedimento fino e matéria orgânica no sedimento. Já a região da lagoa Mirim esteve associada à baixa declividade e uma menor contribuição percentual dos finos e matéria orgânica no sedimento.

As espécies das guildas estuarinos dependentes e estuarinos residentes, que foram abundantes no estuário, estiveram relacionadas aos maiores valores de salinidade no gradiente, enquanto as espécies de água doce primária e secundária ficaram posicionadas no extremo oposto desse gradiente. O peixe-rei, *O. argentinenses*, foi a espécie que apresentou maior correlação com águas transparentes. *Geophagus brasiliensis* e *Crenicichla punctata* tiveram forte relação com a declividade, enquanto *Loricariichthys anus*, *Oligosarcus jenynsii*, *Charax stenopterus*, *Cheirodon ibicuiensis* e *Hyphessobrycon luetkenii* com os grãos finos do sedimento (Fig. 7b, apêndice).

#### IV. CONSIDERAÇÕES FINAIS

Nossos resultados apontaram uma marcada zonação das assembléias de peixes ao longo do complexo lagunar Patos-Mirim, a qual pode ser observada em diferentes níveis de organização (i.e., espécies e guildas). Uma porção significativa (37%) da variabilidade espaço-temporal da ictiofauna ao longo dessa zonação pode ser explicada por fatores ambientais com marcada variabilidade temporal (e.g., salinidade, transparência) e outros de caráter mais conservativo, associados a estrutura do habitat (e.g., granulometria do substrato e declividade). Fatores antrópicos, como a presença de uma barragem-eclusa, contribui para tornar a segregação e zonação da ictiofauna mais abrupta na porção mediana do gradiente estuarino-límnico. A região de maior abundância e riqueza de espécies ao longo do gradiente ocorreu no canal natural (São Gonçalo) que conecta a zona mixohalina da Lagoa dos Patos com as águas doces da Lagoa Mirim. Esse padrão parece ter sido o resultado de fatores atuando concomitantemente no eixo longitudinal e batimétrico do gradiente, os quais promoveram a confluência das guildas de espécies de origem estuarina e água doce, bem como aquelas oriundas da zona litorânea e limnética. É importante destacar que os padrões revelados no presente trabalho poderão sofrer profundas modificações no futuro, já que alterações nas forçantes físicas (e.g., anomalias de chuva e da descarga continental associados às fases do fenômeno El Nino Oscilação Sul), que controlam as trocas de água ao longo do gradiente estudado (Grimm et al., 1998) são esperadas num cenário de aquecimento global (Schroeder & Castello, 2010). Como já demonstrado em trabalhos anteriores (Garcia et al., 2001; Garcia et al., 2003a; Garcia et al., 2004), a abundância e a diversidade da ictiofauna dessa região é bastante sensível à variabilidade e intensidade dessas forçantes físicas e, portanto, o padrão de zonação descrito no presente trabalho poderá ter sua configuração substancialmente alterada no futuro próximo.



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**VI. APÊNDICE: MANUSCRITO: submetido para o periódico *Estuarine, Coastal and Shelf Science***

**FISH ASSEMBLAGE STRUCTURE ACROSS A LARGE SUBTROPICAL ESTUARINE/FRESHWATER GRADIENT**

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## ABSTRACT

There is a growing interest in understand which ecological processes controls the distribution of fish species across aquatic ecotones. Estuaries represent an excellent opportunity for such studies because they harbor a diverse fish fauna originating from the marine and freshwater environments. The present study investigates the distributional patterns of shallow-water fish and the abiotic factors that influence these distributions along a broad salinity gradient (~300 km) in the Neotropics. This gradient is formed by the confluence of two important bodies of water: Patos Lagoon, the largest "choked" coastal lagoon in the world, and Mirim Lake, the second largest lake in Brazil. Fishes were sampled monthly during 1-yr with a beach seine net in seven sampling sites along the gradient. Specimens were identified and had their size (total length, mm) and weight (g) measured. Physicochemical parameters and habitat features were also recorded at each site. A total of 63 species and 45,929 individuals were caught and, subsequently, classified in estuarine dependent, estuarine resident, primary- and secondary-freshwater guilds. There was a strong longitudinal zonation of the fish assemblages along the estuarine-limnic gradient, which was revealed at distinct levels of organization (i.e., species and guilds). Approximately 37% of the spatiotemporal variability of the ichthyofauna along the gradient was explained by environmental factors with strong temporal variability (e.g., salinity and transparency) and other factors associated with habitat structure (e.g., substrate granulometry and slope). Anthropogenic influences, such as the presence of a dam lock, also contribute to the segregation and fish zonation. The highest abundance and species richness along the gradient occurred in the natural channel linking both aquatic systems. This pattern could be explained by abiotic factors acting along the longitudinal and bathymetric axes of the gradient, promoting the confluence of guilds of estuarine and freshwater species as well as guilds of species from the littoral and limnetic zones.

## 1. INTRODUCTION

Estuaries represent an excellent opportunity for studies about ecological frontiers in aquatic systems because they are regions where marine and freshwater meet and exchange physical properties and biological components. These transitional communities containing freshwater and estuarine taxa provide an opportunity to study immigration and emigration patterns and processes, and are dominated by species with extreme physiological tolerances (Rundle et al., 1998). Several factors may influence the distribution of fish species in these environments, including biotic (e.g., competition and predation) and abiotic factors (e.g., salinity, temperature, turbidity, dissolved oxygen, and depth) (Day et al., 1989), which in some cases, can have synergic effects (Rowe and Dunson, 1995). In estuarine environments, variation in salinity is recognized as the primary environmental factor influencing species' distributional patterns (Vega-Cendejas and Santillana, 2004).

Abiotic factors may define community structure, whereas biotic interactions may refine species' distributional patterns within that structure (Sanders, 1968; Menge and Olson, 1990). Abiotic variables probably act as physiological filters, playing a vital role in the structuring of the community (Remmert, 1983; Martino and Able, 2003). Consequently, the environmental gradient in an estuary is very strong, with some species restricted to particular areas, resulting in a marked zonation pattern (Rafaelli et al., 1991). Certain fish species from these areas may be considered as indicators of heterogeneity along the environmental gradient (Kremen, 1992; Mònaco et al., 1992; Bulger et al., 1993).

The relative proportions of freshwater and marine fish species that use coastal and estuarine zones may differ among zoogeographic regions (Blaber, 2000; Barletta et al., 2003, 2005), influencing the diversity of fish assemblages along the salinity gradient. However, little is known about the distribution of freshwater and marine estuarine fish in the estuarine-limnic ecotone or about the factors that govern its dynamics (Winemiller and



Leslie, 1992; Araújo, 1996; García et al., 2010; Macedo-Soares et al., 2010). For example, studies along the salinity gradient in North Temperate coastal zones have found that marine species contribute more to the total species diversity along the gradient than freshwater species (Martino and Able, 2003; Jung and Houde, 2003; Akin et al., 2005). The inverse pattern would be expected in the Neotropical region, whose rivers, streams, and ponds are home to the largest freshwater fish fauna in the world (Buckup et al. 2007; Helfman et al., 2009). Therefore, it is reasonable to suppose that the composition and diversity of estuarine fish communities in the Neotropics would be more strongly influenced by freshwater fish than those in the North Temperate zone.

The present study investigates the distributional patterns of shallow-water fish and the abiotic factors that influence these distributions along a broad estuarine-limnic gradient (~300 km) in the Neotropics. This gradient is formed by the confluence of two important bodies of water: Patos Lagoon, which is considered the largest "choked" coastal lagoon (*sensu* Kjerfve, 1986) in the world, and Mirim Lake, the second largest lake in Brazil. The primary questions addressed in this study are (1) how does the structure of the fish assemblage change in terms of specific composition, relative abundance, size, and diversity along the gradient? (2) What is the relative importance of various environmental factors (e.g., salinity, temperature, and water transparency) and structural characteristics of the habitat (substrate granulometry and organic matter content, slope, and depth) in structuring fish assemblages along the gradient? (3) How are the species guilds (e.g., estuarine resident, marine, and freshwater) distributed along the gradient, and which of them influence diversity most strongly? In addition to filling a knowledge gap about the distribution of the ichthyofauna in one of the largest lagoon complexes in South America, the present study contributes to our understanding of the abiotic factors that influence fish diversity in estuarine-limnic ecotones in the Neotropical region.

## 2. MATERIAL AND METHODS

### 2.1. Study and sampling area

Situated in extreme southern Brazil, the Patos-Mirim lagoon complex (PMLC) is formed by the confluence of two large aquatic systems: the Patos Lagoon (10,360 km<sup>2</sup>) and Mirim Lake (3,750 km<sup>2</sup>), with a drainage basin of 263,876 km<sup>2</sup> (Seeliger et al., 1997). They are connected by a natural channel called São Gonçalo, which is 76 km long. In 1977, a dam lock was built in this channel to avoid the inflow of salt water during the dry period into part of the channel and Mirim Lake. This structure ensures a freshwater reserve for human consumption and for farm irrigation (CLM, 1970). Our study area encompasses the shallow-water regions (< 2 m) along the PMLC, with sampling stations in the estuarine zone of Patos Lagoon (E1-E2), São Gonçalo Channel (C1-C2), and Mirim Lake (L1-L2-L3). These study regions are hereafter referred as estuary, channel and freshwater lake, respectively. In total, there were seven sampling sites along a spatial axis of approximately 326 km (Fig. 1).

Every month between March 2004 and February 2005, fish were collected using a beach seine net (9 m wide by 2.4 m high; 13-mm mesh) with a pocket of 5-mm mesh in its rear portion (Fig. 1C). In each of the seven sampling sites, five samples were obtained. Following collection, the fish were fixed in 10% formaldehyde and subsequently identified at the species level and measured for total length (TL) in millimeters (mm) and weight in grams (g). If the number of a given species was greater than 50, only the first 50 were counted and individually measured; the rest were simply counted and added to the total. Finally, the total number of individuals in each sample was weighed (g). Species were identified according to Figueiredo and Menezes (1978, 1980), Menezes and Figueiredo (1980), Reis et al. (2003), Benvenuti and Moresco (2005), and Buckup et al. (2007). At the same time as the fish were collected, salinity and temperature were measured using a

YSI multiparameter probe, the water transparency was measured (in cm) using a Secchi disk, and the maximum depth (cm) was recorded at each site.

To characterize the structural heterogeneity and complexity of the habitat, we measured the substrate granulometry and beach slope of each of the seven sampling sites. This characterization was conducted seasonally between 2009 and 2010. For the granulometry analysis, 60 g sediment samples were collected using a 50-mm diameter PVC pipe at each site. The sediment samples were transported in coolers on ice and preserved in a freezer in the laboratory. The organic matter content of the sediment was determined by burning 5 g of the material in a muffle furnace at 550°C for 8 h. The amount of organic matter present in each sample was estimated as the difference between the initial mass and final mass.

For the granulometry analysis, the samples were dried in an oven at 60°C and then quartered and weighed. A total of 50 g from each sample was sifted using the Wentworth method (1/2 phi) to separate the coarse sediments (fine, medium and coarse sand) from the finer sediment fractions (silt and clay, which were separated from each other). Based on the simple percentages (%) from each sieve, the coarse fraction of the sediment was considered as the total percentage of fine, medium and coarse sand, and the fine fraction was considered as the sum of the percentages of silt and clay. Together, the two classifications added up to 100% in each sample.

The slope at each site was obtained from a topographic profile measured using a centimeter-scale ruler. Depth measurements were taken every 5 m from the swash zone to the maximum depth of collection at each site. Slopes were classified as low (0), medium (1), or high (2).

## **2.2 Data analysis**

### **2.2.1. Species composition, abundance, and dominance patterns**

The species composition and patterns of dominance were analyzed based on the frequency of occurrence (%F) and relative abundance (catch per unit effort; %CPUE) of each species (Garcia et al., 2004). Species with %F values equal to or greater than the average value of all species were considered frequent. Species with %F values smaller than the average value were considered to be infrequent. The same procedure was employed for the %CPUE values, resulting in abundant ( $\%CPUE \geq \text{average } \%CPUE$ ) and non-abundant species ( $\%CPUE < \text{average } \%CPUE$ ). Finally, based on these criteria, the species were placed into four groups: 1. abundant and frequent, 2. abundant and infrequent, 3. non-abundant and frequent and 4. non-abundant and infrequent (Garcia et al., 2004). This classification was used to identify the dominant species. Thus, we considered as dominant those species that were classified in categories 1, 2, and 3 in at least one of the sites (see Table 1). These criteria resulted in the identification of 31 dominant species, which were used in subsequent analysis (see below).

The MDS (non-metric multidimensional scaling) ordination technique was used to evaluate the similarity in species composition from a presence/absence matrix including all of the species and another matrix including the relative abundance of the dominant species. The relative-abundance data were square-root transformed, and the similarity matrix was calculated using the Bray-Curtis algorithm in the PRIMER statistical software package version 6.1.9 (Clarke and Gorley, 2006).

In some of the abundance analyses, the fish species were grouped into the following ecological guilds: (a) estuarine resident, fish that occur throughout the year and reproduce in the estuary; (b) estuarine dependent, marine- or freshwater-spawning fish that occur in large numbers in the estuary at certain times of the year; (c) marine vagrant, fish coming from the marine environment that rarely occur in the estuary; (d) secondary freshwater, fish that are restricted to freshwater and occasionally occur in the estuary; and (e) primary

freshwater, inhabitants of the limnic and fluvial environments that rarely occur in the estuary. These guilds were adapted from Garcia et al. (2001, 2003b), who have proposed a simplified version of the classification originally proposed by Chao et al. (1985) and Vieira et al. (1998) for the fish guilds of the Patos Lagoon estuary. However, while these previous studies (Garcia et al., 2001; Garcia et al., 2003b) have focused only on the estuarine environment, the present study sampled a broad estuarine-limnic gradient that encompassed both estuarine populations and other freshwater populations of the same species. Therefore, the species *Platanichthys platana* and *Jenynsia multidentata*, which have populations in both the estuarine and the limnic environment, were classified in the secondary-freshwater guild and not as estuarine residents, as previously classified by Garcia et al. (2001, 2003b).

### **2.2.2. Size and diversity structure**

The abundance and size (TL) distribution of species were analyzed jointly in a single graphical representation, plotting the catch per unit effort [(individuals per haul; data transformed by  $\text{Log}_{10}(\text{CPUE} + 1)$ ] versus the total length classes (CPUE-CC) (Garcia et al., 2001, Vieira, 2006). This procedure enabled us to evaluate which size classes (for example, juvenile or adult) were caught in greater abundance for each species at different sites and under different conditions and thus to infer the recruitment patterns of each species (Vieira, 1991; Geracitano, 1998). The Kolmogorov-Smirnov test was used to compare the shapes of the size-class distributions for the estuary, channel, and freshwater lake assemblages (Zar, 1996).

Two components of diversity were analyzed separately: observed species richness (S) and evenness. The evenness (i.e., the distribution of the total abundance among the species) was calculated by the modified (E5) Hill index (1973):

$$E = \frac{\left( \frac{1}{D_s} - 1 \right)}{e^{H'} - 1},$$

where D is the Simpson Index and H' is the Shannon Index. This index assumes its maximum value when all the species in a sample are equally abundant and decreases toward zero as the difference in relative abundance between the species increases (Ludwig and Reynolds, 1988).

The possible differences in the observed species richness (S) and evenness (E5) between seasons and sampling sites were examined using a two-way ANOVA. The assumptions of homogeneity of the variance and normality were evaluated using Cochran's test and the Kolmogorov-Smirnov test, respectively (Sokal and Rohlf, 1995). The post-hoc Tukey test was employed to determine which averages were significantly different from each other. The seasons of the year were defined as follows: summer (January, February, and March), autumn (April, May, and June), winter (July, August, and September) and spring (October, November, and December).

### **2.2.3. Relationships between species and abiotic factors**

A two-way ANOVA was used to test for significant differences in environmental variables [ $\log_{10}(\text{Salinity}+1)$ ], water temperature, and depth) between months and sampling sites. The water transparency (Secchi disk) data did not meet the ANOVA assumptions, so comparisons were made using the Kruskal-Wallis non-parametric test (Sokal and Rohlf, 1995; Conover, 1999).

Canonical correspondence analysis (CCA) was used to evaluate the relationships among the structural complexity of the habitats (percentage of fine sediment, percentage of coarse sediment, organic matter, slope, and depth of the haul), the abiotic factors (salinity, water temperature, and water transparency) and the distribution and abundance of the dominant fish species (31 species).

In the CCA module, the unimodal method was used with biplot scaling, focusing on the inter-specific distance scale. The environmental variables were standardized, and fish abundance was expressed as  $\log_{10}(\text{CPUE} + 1)$ . The forward selection procedure was used to select which abiotic variables contributed significantly ( $\alpha = 0.05$ ) to explaining the observed variation in the species matrix. For the variables that were significantly correlated with each axis, a series of permutations were performed to determine which variables best explained the variation in the fish assemblage. The Monte Carlo permutation test (with 9999 permutations) was used to test the significance ( $p < 0.05$ ) of the contribution of each variable to each of the CCA axes (ter Braak and Verdonschot, 1995).

### **3. RESULTS**

#### **3.1. Environmental Variation**

The salinity varied from zero to 28.8. Values above zero occurred only in the estuary (E1 and E2) and in the northern portion of the channel (C1), which is downstream of the São Gonçalo's dam lock and has a free connection with the estuarine region of Patos Lagoon. With respect to seasonal variation, salinity was higher during the summer months (January and February) than during October ( $p < 0.0079$ ) (Fig. 2a). The water temperature varied from 10°C (July) to 31.2°C (January) and differed significantly among the months of the year ( $p < 0.0001$ ), with high values in the summer and low values in the winter. There were no significant differences among sites ( $p > 0.07$ ) (Fig. 2b). The water transparency (Secchi disk) ranged between 8 and 100 cm. There were no significant differences among months ( $p < 0.6643$ ); however, the estuary (E1 = 62.45) and the channel (C1 = 27 and C2 = 27.5) differed significantly ( $p < 0.005$ ) in average water transparency (Fig. 2c). The depth at the sampling sites varied from 10 to 130 cm, with no significant differences among months ( $p < 0.082$ ). The average depth values were significantly higher

( $p < 0.0001$ ) at the channel sites (~99 cm) than at the other collection sites (~50 cm) (Fig. 2d).

### 3.2. Species composition and abundance

A total of 63 fish species, representing 11 orders and 25 families, and 45,929 individuals were collected, excluding those identified only to the level of the family Clupeidae and the genus *Odontesthes* spp.. Of these 63 species, 31 were considered dominant (Table 1), and 10 species represented 86.61% of the total number of individuals: *Mugil liza*, *Cyanocharax alburnus*, *Brevoortia pectinata*, *Mugil curema*, *Odontesthes mirinensis*, *Cheirodon ibicuihensis*, *Odontesthes argentinensis*, *Platanichthys platana*, *Astyanax fasciatus*, and *Lycengraulis grossidens*.

The non-metric multidimensional analyses (MDS) based on the species composition (presence/absence) and abundance (%CPUE) of dominant species matrices resulted in similar patterns. Both supported two main groups, one formed by the estuary samples (E1 and E2) and one formed by freshwater sites from the channel region (C1 and C2) and freshwater lake (L1, L2,L3) (Fig. 3). The only exception was the occurrence of a single channel sample (C1) in the estuary group; this sample came from the sampling site at the northern end of the channel, which is located downstream the São Gonçalo's dam lock and has a free connection with the estuarine region of Patos Lagoon. This sample was collected in February and showed a typically estuarine ichthyofauna due to the inflow of saline water into the channel during January and February 2005. Aside this only exception within the freshwater group, the samples formed two subgroups, one consisting of the channel samples and the other consisting of the freshwater lake samples (Fig. 3).

According to the percentage similarity analysis (SIMPER), the group of estuary samples presented an average similarity of 28.45% in species composition, and the species that contributed most to this group were *M. liza*, *M. curema*, *B. pectinata*, and *O.*



*argentinensis*. The freshwater group formed by the channel and freshwater lake regions showed an average similarity of 19.57%, with *C. alburnus*, *O. mirinensis*, *A. fasciatus*, *P. platana*, *C. ibicuhiensis*, and *Bryconamericus iheringii* contributing most to the species similarity among samples.

With respect to the composition and abundance of guilds, we observed that most of the species (N = 28) belonged to the primary-freshwater guild. The numbers of marine vagrant, secondary freshwater, estuarine dependent, and estuarine resident species were 12, 11, 7, and 5 species, respectively (Table 1).

A strong substitution of ecological guilds occurred between the estuarine zone (estuary and northern portion of the channel) and the limnetic zone (southern portion of the channel and freshwater lake) (Fig. 4), coinciding with the decrease in salinity along the gradient (Fig. 2a). This substitution was more pronounced in terms of abundance (Fig. 4b) than in terms of frequency of occurrence (Fig. 4a). The marine vagrant guild was restricted to the estuarine zone, which has a free connection with the estuary. In terms of abundance percentage, the estuarine dependent guild was dominant in the estuary region (with an average of 85%), the primary freshwater guild was dominant in the channel region (80%), and the primary- and secondary-freshwater guilds were dominant in the freshwater lake region (51% and 45%, respectively).

### **3.3. Size and diversity structure**

The size distribution observed in the estuary differed from those observed in the channel (K-S test;  $D = 0.425$ ;  $p < 0.0002$ ) and in the freshwater lake (K-S test;  $D = 0.319$ ;  $p < 0.012$ ). However, the size distribution did not differ between the channel and the freshwater lake (K-S test;  $D = 0.234$ ;  $p > 0.130$ ). In the estuary, the distribution was unimodal (with the mode in the 25-30 mm total length class), with a distributional amplitude between 5 and 130 mm TL. In the channel and in the freshwater lake, the

distribution was bimodal (30-40 and 95-105 mm TL) and had a larger amplitude, especially in the channel (10-235 mm) (Fig. 5).

In the estuarine region, two mullet species (*M. liza* and *M. curema*) were the most abundant in almost all of the sampled size classes, especially between 25 and 105 mm TL. *Odonthestes argentinensis* showed the largest amplitude of sizes, varying from 15 to 130 mm TL, while *M. furnieri* was more abundant in the larger classes (TL > 110 mm). In the channel region, *O. argentinensis* were numerically dominant, with *C. alburnus* dominating the 10 to 65 mm TL size classes and *A. fasciatus* dominating the 70 to 110 mm TL classes. Larger individuals (between 150 and 235 mm), such as *Crenicichla punctata*, *C. voga*, and *G. brasiliensis*, occurred in low abundance.

In the freshwater lake region, the smaller size classes were dominated by *P. platana* and *J. multidentata*, whereas the larger size classes (90-185 mm TL) were dominated by *A. fasciatus* and *C. voga*. *Odonthestes mirinensis* exhibited the largest size amplitude among the species from that region, ranging from 20 to 180 mm TL with the mode in the 70 and 75 mm TL classes.

Table 2 shows the ANOVA results concerning the variation in observed species richness and evenness among collection sites and seasons of the year. For species richness, there was a significant interaction between the study sites and seasonal conditions ( $p < 0.01$ ) (Table 2). In general, species richness was significantly higher on average at the channel sites (C1 and C2) than at the other sites ( $p < 0.00001$ ) and significantly lower on average during the winter than during the summer and spring ( $p < 0.0318$ ) (Fig. 6). Evenness differed significantly only among collection sites. The site C1 exhibited lower evenness compared to E2 and L3 but did not differ significantly from the other sites (Tukey test;  $p > 0.05$ ).

#### **3.4. Relationships among species and abiotic factors**

The results of the canonical correspondence analysis (CCA) are shown in Table 3. The first CCA axis had an eigenvalue of 0.661 and was responsible for 59.3% of the total variance. The second axis had an eigenvalue of 0.251, and the first and second axes combined accounted for 81.8% of the variance explained by the CCA. The total inertia of data was 2.995, of which 37% (1.115) could be explained by the analysis. The relationships between the dominant species and the environmental variables represented by these two axes were statistically significant ( $p < 0.05$ ) according to the Monte Carlo permutation test. The depth and the percentage of coarse sediment did not contribute significantly to the model (FS test;  $p > 0.05$ ) and were therefore excluded from the analysis.

In general, salinity and slope had the strongest influence on species' distributions, followed by water transparency and fine sediment percentage. The samples from the estuarine region exhibited higher water transparency and salinity values, whereas those from the channel region had intermediate values of those variables and a weaker association with salinity. On the other hand, the samples from the channel were associated with higher slopes and larger percentages of fine sediment and organic matter. The freshwater lake region was associated with lower slopes and smaller percentages of fine sediment and organic matter in the sediment (Fig. 7).

Species belonging to the estuarine dependent and estuarine resident guilds, which were abundant in the estuary, were associated with higher values along the salinity gradient, whereas primary- and secondary-freshwater species were found at the opposite far end of this gradient. *Odonthestes argentinensis* exhibited the strongest correlation with water transparency. The distributions of *G. brasiliensis* and *C. punctata* were closely related to slope, and those of *Loricariichthys anus*, *Oligosarcus jenynsii*, *Charax*

*stenopterus*, *Cheirodon ibicuihensis*, and *Hyphessobrycon luetkenii* were closely related to fine-grained sediment.

## **4. DISCUSSION**

### **4.1. Spatial distribution and zonation of species**

Fish assemblages along a ~326 km estuarine-limnic gradient in the Patos-Mirim Lagoon Complex show a marked longitudinal zonation pattern, forming two main groups: one dominated by estuarine and marine species and the other dominated by freshwater species. Most species that occur in the Patos Lagoon estuary are of marine origin and they use the estuarine habitats in similar manner to marine-related fishes found in most estuaries worldwide (Day et al., 1989; Vieira and Musick, 1993, 1994). Its ichthyofauna is dominated by small juvenile individuals, which find an abundance of shelter and food in its shallow waters (< 2m) (Chao et al., 1985). In spite of the fact that few species can withstand the variable salinity of the estuarine environment (Day et al., 1989), Patos Lagoon estuary contains a diverse (~167 species) and abundant fish fauna associated with its high primary and secondary productivity (Seeliger et al., 1997; Vieira et al., 2010). Some marine species, such as mullets (genus *Mugil*) and the whitemouth croaker (*M. furnieri*), use the estuary as a growth area for juveniles. Other species use the estuary more sporadically, when the adults enter the region with saline inflows, probably in search of food (Vieira and Castello, 1997).

In contrast with the unimodal size class distribution and the dominance of juveniles (mode: 25-30mm) found in the fish assemblage of the estuary, the freshwater species that are abundant in the channel and freshwater lake regions show larger size amplitudes. This difference in general size amplitude among the estuary and freshwater assemblages might be explained by the fact that both juvenile and adult forms of most of the studied fish species complete their entire life cycles in the limnic regions upstream the dam lock. In

contrast, there is a numerical prevalence of immature, juvenile forms in the estuarine area of Patos Lagoon, because adults of several species from the estuarine dependent and marine vagrant guilds did not occur in the estuary year round. For instance, adult individuals of estuarine dependent species (e.g., *M. liza*, *M. furnieri*, *O. argentinensis*) leave the estuary during their reproductive migration towards the sea, whereas marine vagrant species (e.g., *Eucinostomus melanopterus*, *Anchoa mitchilli*) only occur in the estuary eventually during prolonged salinity intrusions (Chao et al., 1985, Vieira et al., 2010).

As preliminary pointed out by Burns et al. (2006), the dam lock in the São Gonçalo channel makes it difficult for fish to move between the estuary and the freshwater lake, creating an abrupt separation in the species composition between the two systems. Our analysis shows that species guild substitution along the gradient is gradual in terms of frequency of occurrence, but becomes abrupt if considered in terms of abundance data, especially among the sampling sites downstream and upstream the dam lock.

It seems reasonable to hypothesize that in the absence of a dam lock, the abundance of the ecological guilds would shift gradually along the estuarine-limnic ecotone, like we observed for the frequency of occurrence analysis. This gradual shift would result from differential species-level responses to physicochemical parameters (e.g., salinity, pH, dissolved oxygen), habitat selection (e.g., type of substrate, bathymetry) and to biotic constraints (e.g., predation, competition) along the gradient. Other studies of species' distributions across broad estuarine-limnic gradients that are not interrupted by dams seem to corroborate the hypothesis that fish abundance shifts gradually. For example, when analyzing fish assemblages across a gradient from the adjacent marine area to the limnetic zone of Patos Lagoon, Raseira (2003) observed that marine species are gradually replaced by freshwater species. Likewise, García et al. (2010) have studied the La Plata River along

a broad environmental gradient extending from a limnic region to the continental slope and observed that marine species gradually replace the freshwater ichthyofauna along the gradient, with no conspicuous transitional area (ecotone). Therefore, comparing the results of the present study to those performed in regions without dam locks (e.g., Raseira, 2003; García et al., 2010) suggests that the São Gonçalo channel dam lock creates an abrupt transition in the distribution of fish abundance along the estuarine-limnic ecotone between the Patos Lagoon estuary and Mirim Lake.

#### **4.2. Diversity variation along the gradient**

The highest species richness occurred in the channel region, especially at the northern sampling site, which has a free connection with the estuarine area of Patos Lagoon. This site is subject to the sporadic inflow of saltwater during some seasons of the year, usually in warmer months. Hence, the northern reaches of the natural channel can harbor both freshwater and marine fish species during favorable brackish conditions, resulting in higher species richness in this transitional region of the studied gradient. Prior works in other systems also suggest that transitional zones (ecotones) stand out within aquatic gradients because they shelter greater number of species. For example, Sosa-López et al. (2007) have studied species' distributions along a salinity gradient in Terminos Lagoon (Mexico) and have observed higher species richness in low salinity areas (5-10‰). In an ocean-estuarine transition zone in New Jersey (USA), Martino and Able (2003) have also found higher diversity in the ocean/bay interfaces and between the intermediate salinity areas in the Mullica River. Similarly, Akin et al. (2005) have found higher fish abundance in the transitional region between freshwater and saltwater in the Koycegiz Lagoon estuary (Turkey).

Another factor that may have contributed to higher species richness in the natural channel area (São Gonçalo) is the local slope. Whereas the natural channel region shows a

pronounced depth profile, the estuary and freshwater lake sampling sites are characterized by vast shallow areas (< 2 m) (Seeliger et al. 1997). Therefore, unlike the estuary and the freshwater lake, the natural channel region has a very narrow shoreline (< 2m) that is close connect to the deeper zones (> 3 m) of the channel. Usually, fish faunas of littoral and limnetic zones show distinct species compositions (Lowe-McConnell, 1999; Garcia et al., 2006; Souza et al., 2008). For example, in lakes adjacent to the present study area, Garcia et al. (2006) have observed that smaller species (e.g., *Cyanocharax alburnus*, *Jenynsia multidentata*, *Bryconamericus iheringii*) predominate in the littoral zone and larger species (e.g., *Cyphocharax voga*, *Astyanax fasciatus*, *Oligosarcus jenynsii*, *Odontesthes mirinensis*) predominate in the limnetic zone. Thus, the closer proximity between these zones in the natural channel probably favored the collection of species from both regions. Therefore, the higher abundance and species richness in the natural channel seemed to be result of a combination of factors related to longitudinal zonation (i.e., the confluence of guilds with different degrees of salinity tolerance originated from marine/estuarine and limnic environments) and bathymetry (i.e., the confluence of littoral and limnetic taxocenoses due to a steeper slope).

#### **4.3. Relationships between species and abiotic factors**

According to the direct gradient analysis (CCA), 37% of the spatial and temporal variability of the fish assemblages along the gradient can be explained by the biotic variables considered in the present study. This percentage is somewhat higher than those obtained in other studies of marine-freshwater gradients using the same technique (CCA). For example, Martino and Able (2003) have reported that five environmental variables explain 29.9% of the total variation of species in an ocean-estuarine ecotone in New Jersey (USA). Using the same number of variables, Akin et al. (2005) have accounted for 26.6% of the variation of species in the Koycegiz Lagoon estuary in Turkey. As in the present

study, those authors studied the changes in the ichthyofauna along a broad spatial scale and with similar salinity variations [0.1-32 in Martino and Able (2003), 5-40 in Akin et al. (2005) and 0-28 in the present study].

In general, salinity, slope, substrate granulometry (percentage of fine sediment), and water transparency were the factors that best explain the variability in the abundance of dominant fish species in the study area. With a few exceptions, the salinity gradient segregated fish guilds into two groups: the estuarine dependent, estuarine resident and marine vagrant species, which were associated with the brackish estuarine waters, and the primary- and secondary-freshwater species, which were restricted to the limnic region. Previous studies have highlighted the predominant role of salinity in structuring estuarine fish assemblages (Martino and Able, 2003; Akin et al., 2005). However, the marked segregation of guilds along the salinity gradient in the present study is probably strengthened by the presence of the dam lock in the middle portion of the gradient, which partially impairs the free movement of water and fish between the estuary and the limnic region upstream.

In contrast with the role of salinity, which has been systematically incorporated in direct gradient analyses in previous studies (Martino and Able, 2003, Akin et al., 2005), little is known about the role of factors such as sediment granulometry in structuring fish assemblages along marine-freshwater ecotones. Our results show that this factor could play an important role in structuring the fish assemblages in these regions. For example, the abundance of many species from the primary- and secondary-freshwater guilds is strongly connected to the predominance of fine sediment (silt and clay) and to higher percentages of organic matter in the substrate. It seems reasonable to suppose that these substrate characteristics reflect favorable conditions for spawning, counter-shading, and/or foraging, especially for fish with benthonic habits. In fact, the dominant species in those guilds that



exhibit morpho-anatomical characteristics associated with feeding on benthonic prey (e.g., *Loricariichthys anus*, *Geophagus brasiliensis*, *Gymnogeophagus gymnogenys*, *Corydoras paleatus*, and *Rineloricaria longicauda*) are more abundant in the portion of the gradient with higher percentages of fine particles and organic matter in the substrate.

Despite the relatively high percentage of the variation explained in the CCA (37%), much of the temporal and spatial variation in the abundance of species is not explained in the present study. As highlighted by other authors (Martino and Able, 2003; Akin et al., 2005), this unexplained variation might be due to other environmental factors (e.g., dissolved oxygen and pH) or other factors reflecting the structural complexity of the habitat (e.g., the presence of aquatic macrophytes) that were not accounted for in the present study. In addition to physical and chemical factors, it is important to highlight the role of biotic interactions (e.g., competition and predation) in the structuring of fish communities (Menge and Olson, 1990). As suggested by Martino and Able (2003), broad-scale patterns in the structure of estuarine fish assemblages are primarily due to the responses of individual species to the dominant environmental gradient, whereas small-scale patterns seem to result from biotic interactions, such as predator avoidance, competition, and habitat selection.

In summary, our results revealed a strong zonation in fish assemblages of the Patos-Mirim Lagoon complex. This zonation can be observed at different levels of organization (i.e., species and guilds). A large portion (37%) of the spatial and temporal variability of the ichthyofauna along the estuarine-limnic gradient can be explained by environmental factors with strong temporal variability (e.g., salinity and water transparency) and by more stable factors associated with the structure of the habitat (e.g., sediment granulometry and depth profile). Anthropogenic factors, such as the presence of a dam lock, also contribute to the segregation and zonation of the ichthyofauna. The highest abundance and species

richness along the estuarine-limnic gradient occur in the natural channel (São Gonçalo) that connects the mixohaline zone of Patos Lagoon with the freshwater of Mirim Lake. This pattern seems to be the result of factors that act concomitantly along the longitudinal and bathymetric axes of the gradient, promoting the confluence of guilds of estuarine and freshwater species as well as guilds of species that originate in the littoral and limnetic zones. It is important to highlight that the patterns revealed here might be substantially altered in the future due to changes in the physical forcing mechanisms (e.g., rain anomalies and variations in the continental discharge associated with ENSO phases) that can control the water exchange along the studied gradient (Grimm et al., 1998). Such changes are expected under a global warming scenario (Schroeder and Castello, 2010). As shown in previous studies (Garcia et al., 2001, Garcia et al., 2003a, Garcia et al., 2004), the abundance and diversity of the ichthyofauna in this region are highly sensitive to the variability and intensity of these physical forcing mechanisms. Therefore, the zonation pattern described here may be substantially altered in the near future.

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## FIGURES

Figure 1. Patos-Mirim Lagoon Complex (a) showing the location of the sampling stations in estuarine zone of Patos Lagoon (E1-E2), São Gonçalo Channel (C1-C2) and Mirim Lake (L1-L2-L3) (b). Drawing of the beach seine net employed in fish collections (c).

Figure 2. Spatiotemporal variation in salinity (a), water temperature (b), water transparency (c), and depth (d) in the estuarine zone of Patos Lagoon (E1-E2), São Gonçalo Channel (C1-C2) and Mirim Lake (L1-L2-L3).

Figure 3. MDS ordination of fish samples based on abundance of dominant species collected in the estuarine zone of Patos Lagoon (E1, E2), São Gonçalo Channel (C1, C2), and Mirim Lake (L1, L2, L3). Data values were square-root transformed and Bray-Curtis similarity were used. The continuous line indicates the two main groups formed (estuary vs. freshwater samples), whereas the dotted line indicates the two sub-groups (Channel vs. Lake) within the freshwater group.

Figure 4. Frequency of occurrence (%F) and relative abundance (%CPUE) of estuarine resident (ESTRES), estuarine dependent (ESTDEP), marine vagrant (MARVAG) and secondary freshwater (2ndFRESH), and primary freshwater (1stFRESH) in the estuarine zone of Patos Lagoon (E1-E2), São Gonçalo Channel (C1-C2) and Mirim Lake (L1-L2-L3).

Figure 5. Catch per effort unit [ $\text{Log}_{10}(\text{CPUE}+1)$ ] by size classes (total length, TL, mm) for all species (global average), and %CPUE by size classes (TL, mm) for selected species caught in the estuarine zone of Patos Lagoon (E1-E2), São Gonçalo Channel (C1-C2) and Mirim Lake (L1-L2-L3). Referred to table 1 for species and guild codes.

Figure 6. Average values (+ standard error) of species richness (S) across sampling stations (E1, E2: estuarine zone of Patos Lagoon; C1, C2: São Gonçalo Channel; L1, L2, L3: Mirim lake) and seasons (▲ summer, ○ autumn, ■ winter, □ spring).

Figure 7. CCA ordination plot. (a) sample sites (● estuarine zone of Patos Lagoon, ● São Gonçalo Channel, ○ Mirim Lake) and environmental variables (% fine granulometry, % organic matter, slope, salinity, water temperature, and water transparency). Each point represents a single sample station and date (five beach seine hauls at the location for a given month). (b) Association of fish species with each axis is represented by its score (plotted) and correlation between environmental variables and axes are represented by the length and angle of arrows. Refereed to table 1 for species and guild codes.

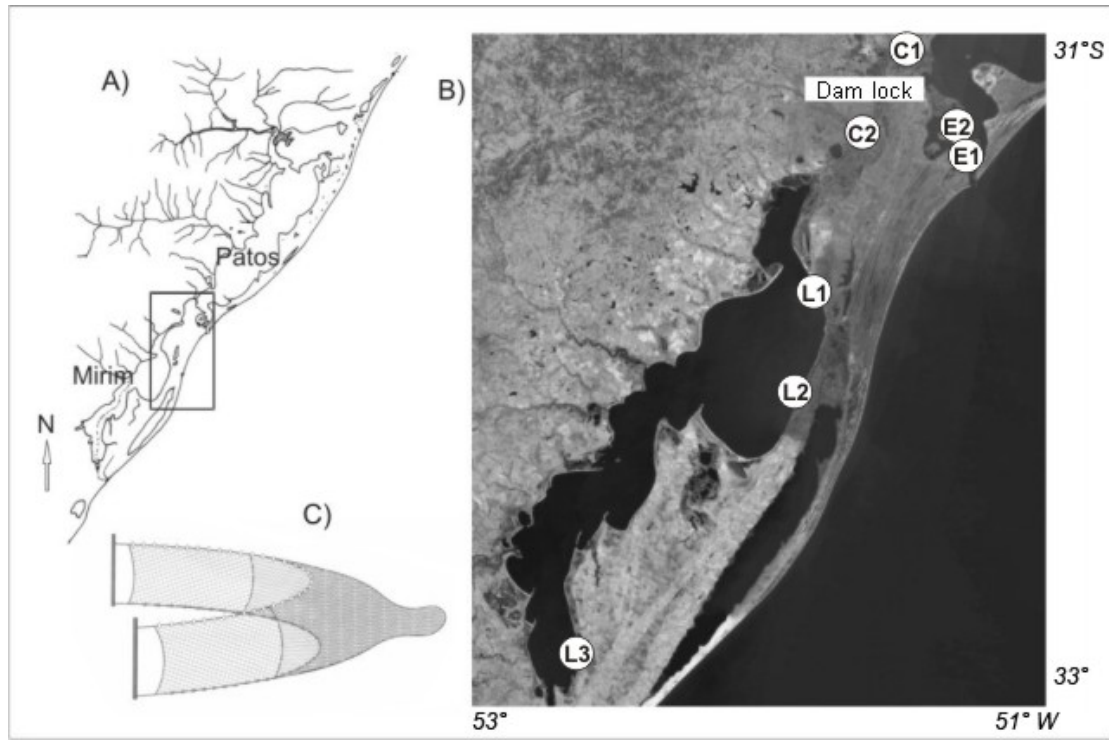


Figure 1

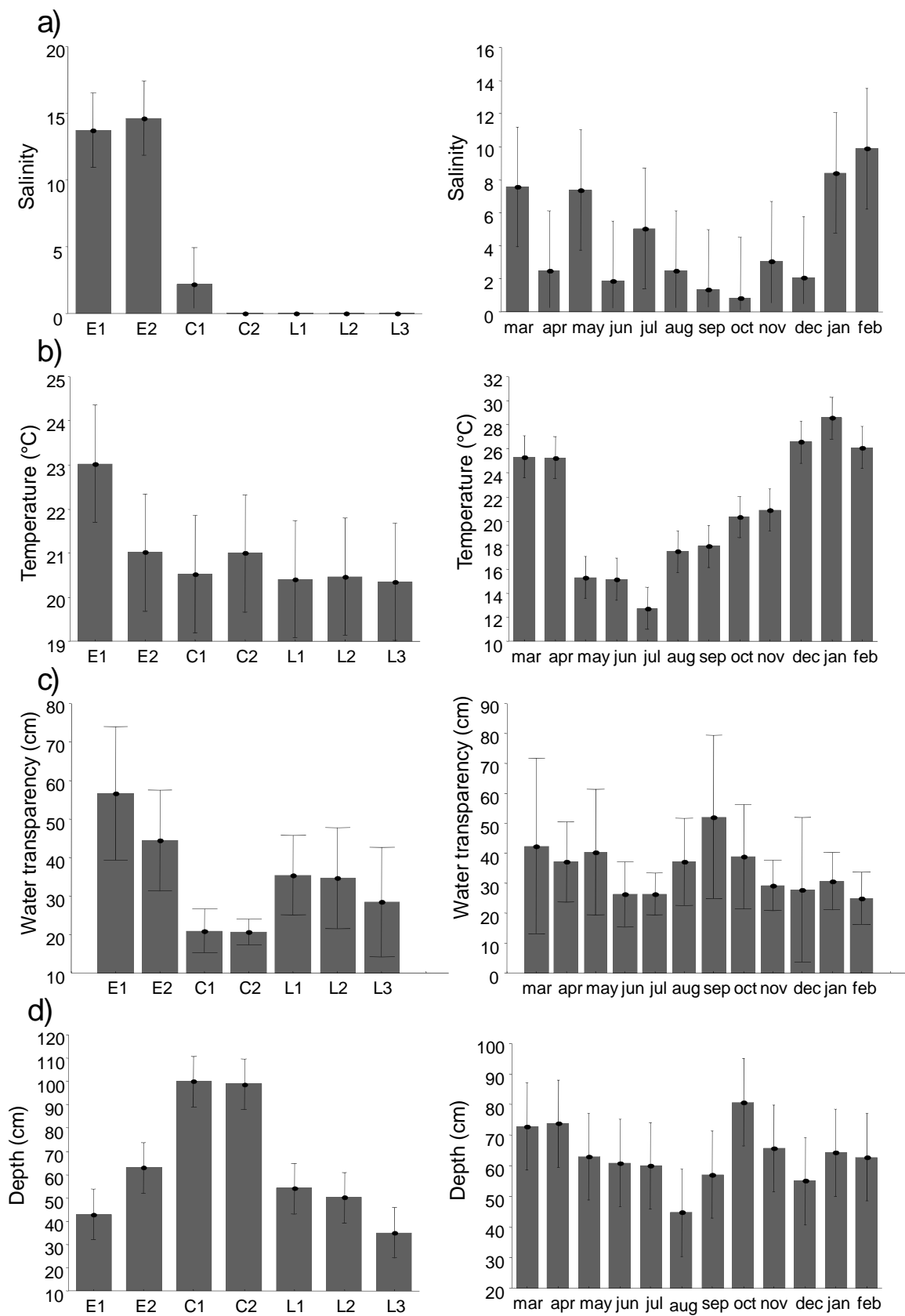


Figure 2

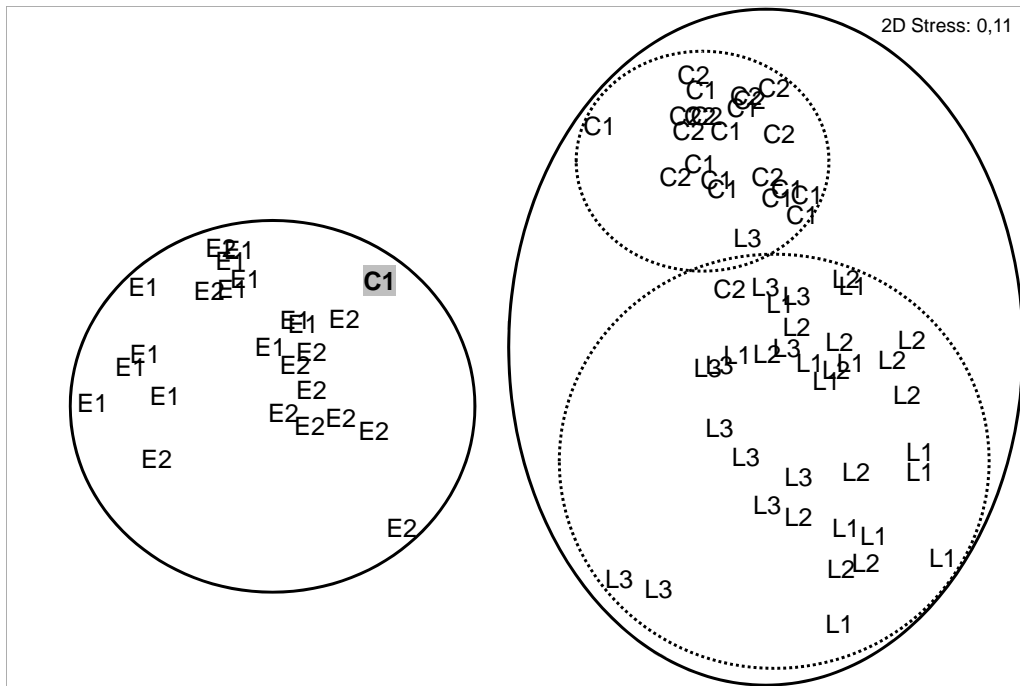


Figure 3

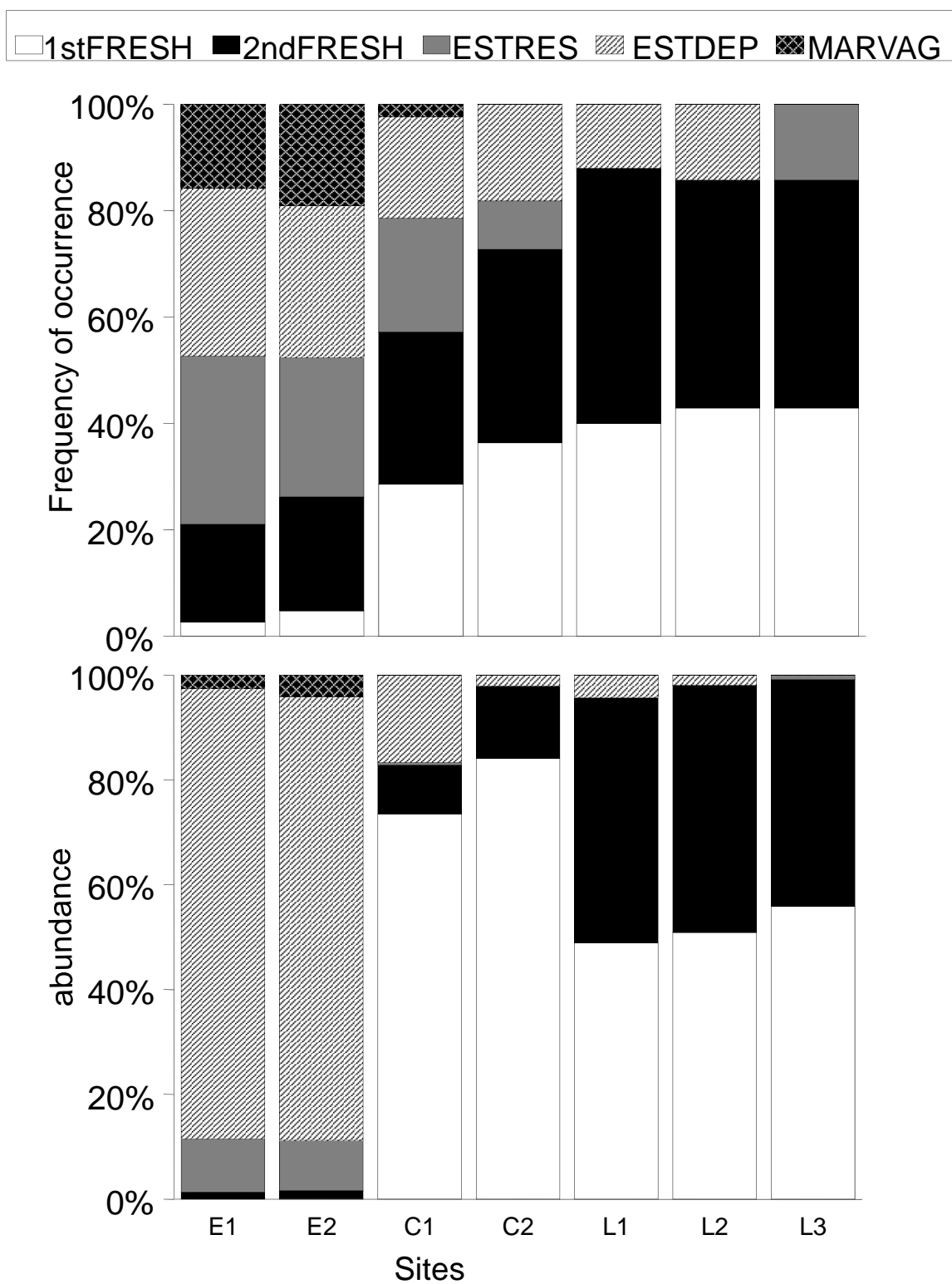


Figure 4

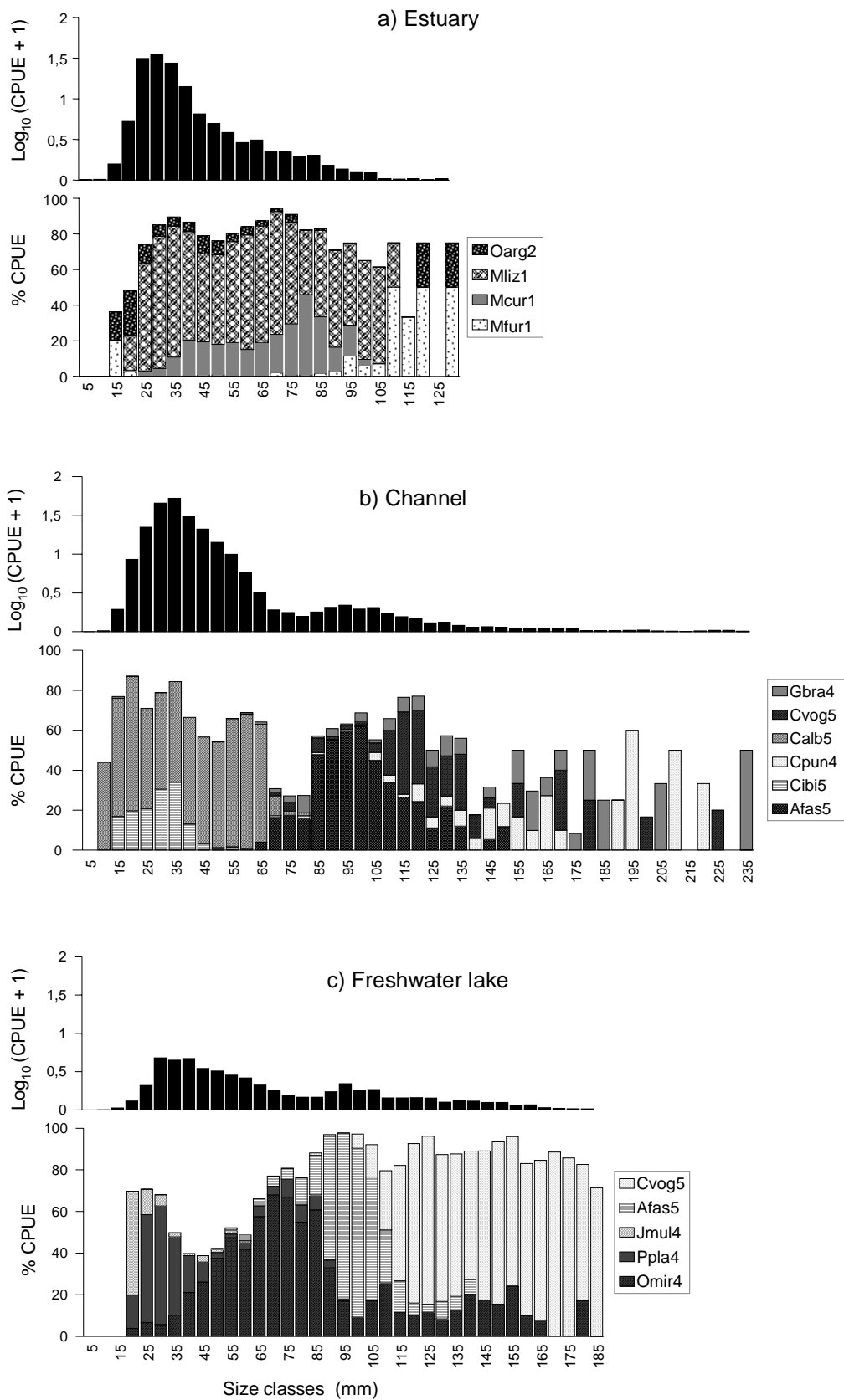


Figure 5



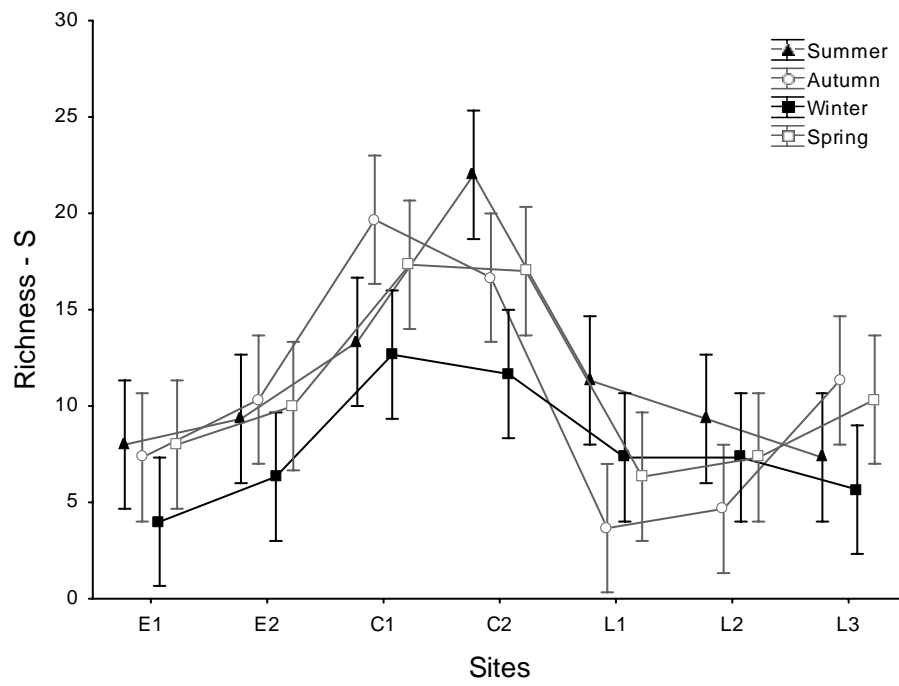


Figure 6

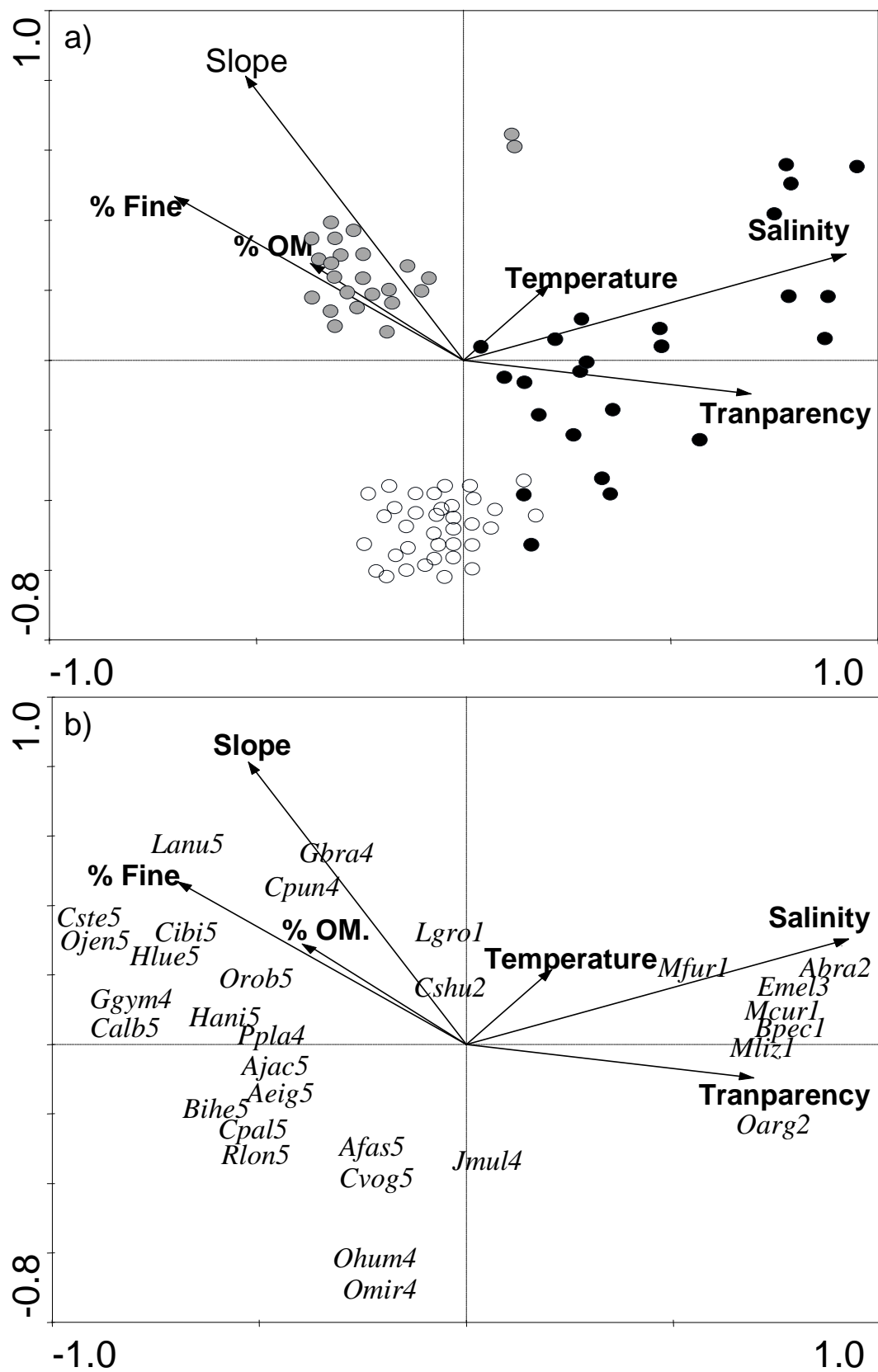


Figure 7

## TABLES

Table 1

Number of individuals and minimum-maximum (min-max), average, and standard deviation (s.d.) of total length (mm) of fish species caught in the three study systems (estuary, channel, freshwater lake) grouped in the following guilds: (1) estuarine dependent, estuarine resident, marine vagrant, secondary freshwater, and primary freshwater. Species codes (Spcode) for each fish were based on the contraction of its scientific name and the number code of its guild (1-4). Dominant species (see M&M) are denoted by an asterisk.

|                                    | Spcode       | Regions |         |                 | Total length (mm) |         |         |      |
|------------------------------------|--------------|---------|---------|-----------------|-------------------|---------|---------|------|
|                                    |              | Estuary | Channel | freshwater lake | Minimum           | Maximum | Average | S.D. |
| <b>Estuarine dependent</b>         |              |         |         |                 |                   |         |         |      |
| <i>Brevoortia pectinata</i> *      | <i>Bpec1</i> | 1501    | 2       | -               | 20                | 105     | 36,4    | 15,7 |
| <i>Lycengraulis grossidens</i> *   | <i>Lgro1</i> | 123     | 1358    | 88              | 17                | 201     | 42,5    | 21,3 |
| <i>Mugil curema</i> *              | <i>Mcur1</i> | 1462    | 327     | -               | 21                | 128     | 46,8    | 15,5 |
| <i>Mugil liza</i> *                | <i>Mliz1</i> | 10067   | 289     | -               | 21                | 336     | 38,4    | 15,6 |
| <i>Mugil gaimardianus</i>          | <i>Mgar1</i> | 20      | -       | -               | 30                | 87      | 61,8    | 15,5 |
| <i>Micropogonias furnieri</i> *    | <i>Mfur1</i> | 82      | 4       | -               | 13                | 174     | 54,3    | 39,9 |
| <i>Paralichthys orbignyanus</i>    | <i>Porb1</i> | 1       | -       | -               | 46                | 46      | 46,0    | -    |
| <b>Estuarine resident</b>          |              |         |         |                 |                   |         |         |      |
| <i>Atherinella brasiliensis</i> *  | <i>Abra2</i> | 286     | -       | -               | 8                 | 131     | 48,1    | 21,3 |
| <i>Odontesthes argentinensis</i> * | <i>Oarg2</i> | 1182    | -       | -               | 17                | 131     | 34,5    | 11,4 |
| <i>Rammogaster arcuata</i>         | <i>Rarc2</i> | 52      | -       | -               | 23                | 54      | 41,3    | 6,2  |
| <i>Syngnathus folletti</i>         | <i>Sfol2</i> | 1       | -       | -               | 75                | 75      | 75,0    | -    |
| <i>Ctenogobius shufeldti</i> *     | <i>Cshu2</i> | 29      | 44      | 16              | 12                | 108     | 41,5    | 17,9 |
| <b>Marine vagrant</b>              |              |         |         |                 |                   |         |         |      |
| <i>Harengula clupeiola</i>         | <i>Hclu3</i> | 8       | -       | -               | 49                | 70      | 58,3    | 7,1  |
| <i>Anchoa maringii</i>             | <i>Amar3</i> | 11      | -       | -               | 52                | 60      | 57,0    | 2,4  |
| <i>Urophycis brasiliensis</i>      | <i>Ubra3</i> | -       | 2       | -               | 68                | 144     | 106,0   | 53,7 |
| <i>Trachinotus falcatus</i>        | <i>Tfal3</i> | 3       | -       | -               | 15                | 68      | 32,7    | 30,6 |
| <i>Trachinotus marginatus</i>      | <i>Tmar3</i> | 1       | -       | -               | 31                | 31      | 31,0    | -    |
| <i>Centropomus undecimalis</i>     | <i>Cund3</i> | 1       | -       | -               | 48                | 48      | 48,0    | -    |
| <i>Eucinostomus argenteus</i>      | <i>Earg3</i> | 23      | -       | -               | 20                | 80      | 34,9    | 14,1 |
| <i>Eucinostomus lefroyi</i>        | <i>Elef3</i> | 5       | -       | -               | 37                | 51      | 42,6    | 5,2  |
| <i>Eucinostomus melanopterus</i> * | <i>Emel3</i> | 396     | -       | -               | 15                | 72      | 32,9    | 11,8 |
| <i>Ctenogobius stigmaticus</i>     | <i>Csti3</i> | 2       | -       | -               | 50                | 57      | 53,5    | 5,0  |
| <i>Citharichthys spilopterus</i>   | <i>Cspi3</i> | 1       | -       | -               | 26                | 26      | 26,0    | -    |
| <i>Gobionellus oceanicus</i>       | <i>Goce3</i> | 4       | -       | -               | 34                | 105     | 78,5    | 31,1 |
| <b>Secondary freshwater</b>        |              |         |         |                 |                   |         |         |      |
| <i>Odontesthes humensis</i> *      | <i>Ohum4</i> | -       | 4       | 68              | 19                | 188     | 80,1    | 36,5 |
| <i>Odontesthes mirinensis</i> *    | <i>Omir4</i> | 1       | 59      | 1400            | 11                | 223     | 68,6    | 26,5 |
| <i>Odontesthes perugiae</i>        | <i>Oper4</i> | -       | -       | 5               | 140               | 287     | 201,2   | 77,5 |
| <i>Odontesthes retropinnis</i>     | <i>Pret4</i> | -       | 2       | 0               | 179               | 228     | 203,5   | 34,6 |
| <i>Platanichthys platana</i> *     | <i>Ppla4</i> | 52      | 2871    | 465             | 17                | 99      | 41,7    | 12,7 |
| <i>Jenynsia multidentata</i> *     | <i>Jmul4</i> | 157     | 47      | 150             | 10                | 67      | 34,1    | 11,3 |
| <i>Cichlasoma portalegrense</i>    | <i>Cpor4</i> | -       | 1       | -               | 125               | 125     | 125,0   | -    |
| <i>Crenicichla punctata</i> *      | <i>Cpun4</i> | -       | 43      | 1               | 115               | 128     | 142,6   | 33,9 |
| <i>Crenicichla lepidota</i>        | <i>Clep4</i> | -       | 10      | -               | 70                | 351     | 144,8   | 50,3 |
| <i>Geophagus brasiliensis</i> *    | <i>Gbra4</i> | 4       | 70      | -               | 17                | 238     | 109,4   | 38,7 |
| <i>Gymnogeophagus gymnogenys</i> * | <i>Ggym4</i> | -       | 20      | 7               | 21                | 167     | 89,6    | 35,0 |
| <b>Primary freshwater</b>          |              |         |         |                 |                   |         |         |      |
| <i>Astyanax eigenmanniorum</i> *   | <i>Aeig5</i> | 1       | 54      | 30              | 26                | 103     | 59,1    | 18,6 |
| <i>Astyanax fasciatus</i> *        | <i>Afas5</i> | -       | 474     | 569             | 39                | 150     | 97,2    | 13,7 |
| <i>Astyanax jacuhiensis</i> *      | <i>Ajac5</i> | -       | 56      | 43              | 31                | 122     | 69,1    | 14,6 |
| <i>Astyanax spp</i>                | <i>Aspp5</i> | -       | 1       | 1               | 24                | 79      | 51,5    | 38,9 |
| <i>Bryconamericus iheringii</i> *  | <i>Bihe5</i> | 1       | 415     | 212             | 20                | 91      | 48,5    | 11,8 |
| <i>Charax stenopterus</i> *        | <i>Cste5</i> | -       | 156     | 1               | 44                | 125     | 88,7    | 14,9 |
| <i>Cheirodon ibicuiensis</i> *     | <i>Cibi5</i> | -       | 5025    | 40              | 16                | 56      | 33,4    | 5,9  |
| <i>Cheirodon interruptus</i>       | <i>Cint5</i> | 4       | 30      | 1               | 22                | 41      | 31,0    | 3,8  |
| <i>Cyanocharax alburnus</i> *      | <i>Calb5</i> | 1       | 12995   | 832             | 12                | 84      | 39,8    | 10,5 |
| <i>Hyphessobrycon anisitsi</i>     | <i>Hani5</i> | 1       | -       | 1               | 44                | 81      | 62,5    | 26,2 |
| <i>Hyphessobrycon luetkenii</i> *  | <i>Hlue5</i> | -       | 776     | 18              | 20                | 75      | 45,9    | 7,4  |
| <i>Macropsobrycon uruguayanae</i>  | <i>Muru5</i> | -       | -       | 4               | 29                | 33      | 30,5    | 1,7  |
| <i>Oligosarcus jenynsii</i> *      | <i>Ojen5</i> | 2       | 193     | 7               | 34                | 246     | 88,0    | 32,4 |
| <i>Oligosarcus robustus</i> *      | <i>Orob5</i> | -       | 69      | 15              | 56                | 252     | 122,6   | 35,0 |
| <i>Pseudocorynopoma doriae</i>     | <i>Pdor5</i> | -       | 11      | -               | 34                | 117     | 69,7    | 21,3 |
| <i>Characidium spp</i>             | <i>Cspp5</i> | -       | 1       | -               | 50                | 50      | 50,0    | -    |
| <i>Cyphocharax voga</i> *          | <i>Cvog5</i> | -       | 131     | 477             | 52                | 230     | 131,0   | 21,9 |
| <i>Hoplias malabaricus</i>         | <i>Hmal5</i> | -       | 29      | -               | 115               | 264     | 211,4   | 30,0 |
| <i>Brachyhypopomus spp</i>         | <i>Bspp5</i> | -       | 1       | -               | 130               | 130     | 130,0   | -    |
| <i>Corydoras paleatus</i> *        | <i>Cpal5</i> | -       | 64      | 102             | 23                | 75      | 56,4    | 9,7  |
| <i>Pimelodella australis</i>       | <i>Paus5</i> | -       | 40      | 3               | 35                | 101     | 57,0    | 13,9 |
| <i>Loricariichthys anus</i> *      | <i>Lanu5</i> | -       | 29      | -               | 23                | 202     | 109,8   | 62,1 |
| <i>Rineloricaria cadeae</i>        | <i>Rcad5</i> | -       | 38      | -               | 65                | 189     | 119,3   | 33,9 |
| <i>Rineloricaria longicauda</i> *  | <i>Rlon5</i> | -       | 18      | 13              | 47                | 161     | 98,2    | 32,1 |
| <i>Parapimelodus nigribarbis</i>   | <i>Pnig5</i> | -       | 1       | 35              | 78                | 128     | 111,4   | 9,0  |
| <i>Pimelodus maculatus</i>         | <i>Pmac5</i> | -       | 4       | 3               | 95                | 180     | 149,3   | 30,9 |
| <i>Microglanis cottooides</i>      | <i>Mcot5</i> | -       | 1       | -               | 50                | 50      | 50,0    | -    |
| <i>Homodiaetus anisitsi</i> *      | <i>Hani5</i> | -       | 58      | 14              | 23                | 42      | 32,7    | 4,1  |
| N° of individual                   |              | 15485   | 25823   | 4621            |                   |         |         |      |

Table 2

ANOVA results of species richness and evenness (E5 ratio method of Hill) parameters in relation to site locations (E1, E2: estuarine zone of Patos Lagoon; C1, C2: São Gonçalo Channel; L1, L2, L3: Mirim lake) and seasons.

| Source               | DF        | SS             | MS            | F            | p           |
|----------------------|-----------|----------------|---------------|--------------|-------------|
| <b>Richness - S</b>  |           |                |               |              |             |
| Sites locations (SL) | <b>6</b>  | <b>1299,98</b> | <b>216,66</b> | <b>26,11</b> | <b>0,00</b> |
| Seasons (S)          | <b>3</b>  | <b>164,70</b>  | <b>54,90</b>  | <b>6,62</b>  | <b>0,00</b> |
| SL*S                 | <b>18</b> | <b>344,21</b>  | <b>19,12</b>  | <b>2,30</b>  | <b>0,01</b> |
| Residual             | 56        | 464,67         | 8,30          |              |             |
| <b>Evenness - E5</b> |           |                |               |              |             |
| Sites locations (SL) | <b>6</b>  | <b>0,32</b>    | <b>0,05</b>   | <b>2,90</b>  | <b>0,02</b> |
| Seasons (S)          | 3         | 0,03           | 0,01          | 0,51         | 0,67        |
| SL*S                 | 18        | 0,13           | 0,01          | 0,38         | 0,99        |
| Residual             | 56        | 1,04           | 0,02          |              |             |

Table 3  
Results of CCA performed on the relative abundance (CPUE) of the dominant fish species in the Patos-Mirim Lagoon Complex.

| Axes  | 1       | 2       | 3       | 4       |
|---|---------|---------|---------|---------|
| <u>Correlation of environmental variables</u> |         |         |         |         |
| Water transparency (Secchi)                   | 0.6100  | -0.0815 | 0.1802  | 0.1333  |
| Temperature                                   | 0.1817  | 0.1825  | -0.5908 | -0.1423 |
| Salinity                                      | 0.8123  | 0.2572  | 0.0000  | -0.0672 |
| Slope   | -0.4628 | 0.6897  | 0.1216  | 0.0828  |
| % fine granulometry                           | -0.6133 | 0.3974  | 0.1708  | -0.0547 |
| % organic matter                              | -0.3244 | 0.2351  | 0.0234  | 0.3630  |
| Eigenvalues                                   | 0.661   | 0.251   | 0.073   | 0.067   |
| Species-environment correlations              | 0.880   | 0.850   | 0.680   | 0.673   |
| Cumulative percentage relation                |         |         |         |         |
| of species data:                              | 22.1    | 30.5    | 32.9    | 35.2    |
| of species-environment relation:              | 59.3    | 81.8    | 88.4    | 94.4    |
| Sum of all eigenvalues                        |         |         |         | 2.995   |
| Sum of all canonical eigenvalues              |         |         |         | 1.115   |