Universidade Federal do Rio Grande do Sul
Instituto de Biociências
Programa de Pós-Graduação em Ecologia

Bivalves Límnicos na América do Sul: Subsídios para Conservação de Espécies Nativas e para o Controle do Bivalve Invasor *Limnoperna fortunei* (Dunker, 1857).

Daniel Pereira

Porto Alegre, fevereiro de 2014.

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Dedicado aos grandes malacólogos

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Resumo

Os padrões de distribuição de espécies de bivalves em grandes regiões hidrográficas e ecorregiões, os fatores ambientais que influenciam a estrutura das assembleias de bivalves em macro escala, as variáveis que influenciam as flutuações populacionais de espécies invasoras e métodos eficazes para o controle da população de bivalves invasores, sem efeitos tóxicos para os organismos aquáticos, são os temas menos estudados na América do Sul. Com base na revisão da literatura e coleções malacológicas, 168 espécies de bivalves nativos e cinco espécies invasoras foram registrados para 52 regiões hidrográficas da América do Sul. Presença e ausência de espécies foram analisadas por meio de coordenadas principais pela filogenia-ponderada. Testes de Mantel foram usados para correlacionar a distribuição de espécies invasoras e riqueza de espécies de bivalves nativa em regiões hidrográficas. Com o objetivo de avaliar os fatores ambientais que influenciam a estrutura das assembléias de bivalves ecorregiões da América do Sul, um conjunto de 24 ecorregiões localizadas no Brasil e parte dos países vizinhos foi selecionado devido à maior disponibilidade de dados ambientais e maior número de material depositado em coleções científicas. Atributos fisiográficos, tais como declividade, altitude, área dos polígonos, precipitação, temperatura do ar, bem como indicadores de química da água, especialmente pH e conteúdo catiônico, foram avaliados por meio de vários métodos estatísticos, uni e multivariados. Índice de raridade espécie foi calculado para cada região, a fim de quantificar a endemicidade das áreas. No que diz respeito à avaliação populacional do mexilhão-dourado, a fim de avaliar a influência de variáveis imunológicas em recrutamento, entre outubro de 2006 e setembro de 2007 substratos artificiais foram expostos em duas estações de amostragem, localizadas em um delta interior no Sul do Brasil. As amostras de água para análise de variáveis limnológicas foram coletadas nos mesmos locais. A análise de variância e multivariada das variáveis limnológicas e dos descritores populacionais mostrou sazonalidade definida. Com o objetivo de selecionar agentes microbianos para o controle do mexilhão-dourado, duas linhagens e três formulações comerciais disponíveis no mercado e registrados para o controle de dípteros foram avaliados por meio de bioensaios. Os ensaios ecotoxicológicos foram realizados para avaliar a toxicidade sobre organismos não alvo da formulação comercial mais eficiente para o controle do mexilhão-dourado. A riqueza de espécies mais elevada foi detectada no Atlântico Sul, Uruguai, Paraguai e Amazonas, regiões hidrográficas brasileiras. A linhagem Veneroida foi mais representativa em regiões hidrográficas, que são mais pobres em

espécies e localizados a oeste da América do Sul. As linhagens Mycetopodidae e Hyriidae foram predominantes em regiões que são mais ricas em espécies em direção ao leste do continente. A distribuição da espécie invasora *Limnoperna fortunei* não está relacionado com a riqueza de espécies em diferentes regiões hidrográficas. As regiões hidrográficas apresentaram distinta composição filogenética, independentemente do nível de riqueza. Em relação às assembléias de bivalves em ecorregiões, observou-se a riqueza de espécies de bivalves é maior em grandes áreas de menor declive e alta riqueza de peixes. A elevada riqueza de unionídeos com estágio larval parasita também foi relacionada para a área do polígono e alta riqueza de peixes. A maioria dos fatores ambientais que explicam a estrutura das assembleias bivalves foram atributos fisiográficos e da riqueza de espécies de peixes. Quanto ao mexilhão-dourado, a liberação de larvas e recrutamento começou na primavera. A variação dos descritores populacionais foi associada com a temperatura da água, condutividade, alcalinidade total, e os sulfatos. A sobrevivência do mexilhão dourado na faixa de pH 4-11, após 120 horas de exposição pode permitir a sobrevivência de populações em condições adversas e intermitentes no ambiente aquático. Quanto aos agentes microbianos, *Bacillus thuringiensis* sv . *kurstaski* HD-1 mostrou um elevado potencial para o controle do mexilhão-dourado, com potencial para o desenvolvimento de uma nova formulação comercial . VECTOBAC Solution ® aquoso (AS) foi a formulação comercial mais eficiente para o controle do mexilhão dourado. No entanto, a concentração letal de VECTOBAC para o controle de mexilhão é muito mais elevada do que a concentração eficaz para matar dípteros, e pode ser tóxico para os organismos não alvo. As seguintes conclusões são destacadas. Não só deve a riqueza ser considerado um critério para priorizar áreas para conservação, mas também a diversidade filogenética das comunidades que prestam serviços e aspectos funcionais relevantes a manutenção do ecossistema. Atributos fisiográficos e a riqueza de espécies de peixes explicaram a estrutura das assembleias de bivalves nas ecorregiões aquáticas. Eventos geológicos do passado, que moldaram as paisagens da América do Sul contribuíram para a atual distribuição e composição de espécies de bivalves nas ecorregiões avaliadas. É interessante salientar o potencial do mexilhão dourado para a colonização de águas ácidas da Amazônia. Novas estirpes poderão ser isoladas a partir de mexilhão-dourado e avaliadas em novos bioensaios a fim de encontrar agentes microbianos mais eficazes para o controlo desta espécie invasora.

Abstract

The distribution patterns of bivalve species in large hydrographic regions and ecoregions, the environmental factors that influence the structure of the bivalve assemblies in macroscale, the variables that influence population fluctuations of invasive species and effective methods for population control of invasive bivalves without toxic effects to aquatic biota, are the least investigated subjects in South America. Based on literature review and malacological collections, 168 native freshwater bivalve and five invasive species have been recorded for 52 hydrographic regions in South America. Presence or absence data were analysed by Principal Coordinate for Phylogeny-Weighted. Mantel tests were used to correlate the invasive species distribution and native bivalve species richness in hydrographic regions. Aiming to evaluate the environmental factors that influence the structure of bivalve assemblies of South American ecoregions, a set of 24 ecoregions located in Brazil and part of neighboring countries were selected due to the greater availability of environmental data and greater number of mollusk material deposited in scientific collections. The presence and absence of species in each polygon area of each ecoregion was obtained through literature review and examination the scientific collections of renowned museums. Physiographic attributes, such as slope, elevation, polygons area, precipitation, air temperature, as well as indicators of water chemistry, especially pH and cationic contents, were evaluated through several univariate and multivariate methods. Index of species rarity was calculated for each region in order to quantify the endemicity of the areas. Regarding to golden mussel population assessment, in order to evaluate the influence of limnological variables on recruitment, during the period of 12 months between October 2006 and September 2007 artificial substrates were exposed in two sampling stations located in an inner delta in the South of Brazil. Water samples for analysis of larval and limnological variables were collected at the same locations. The variance and multivariate analyses of monthly [larval (ind.m^{-3}) and recruits density (ind.m^{-2})] and cumulative [recruits and adults density (ind.m^{-2})] population descriptors and limnological variables showed definite seasonality. Aiming to select microbial agents to control the golden mussel, two strains and three commercial formulations available in the market and registered for the control of diptera were evaluated through bioassay. Ecotoxicological assays were conducted to assess the toxicity on non-target organisms of the most efficient commercial formulation for the mussel control. The higher species richness has been detected in the South Atlantic, Uruguay, Paraguay, and Amazon Brazilian hydrographic regions. The lineage Veneroida was more representative in hydrographic regions that are poorer in species and located West of South America. The Mycetopodidae and Hyriidae lineages were predominant in regions that are richest in species toward the East of the continent. The distribution of invasive species *Limnoperna fortunei* is not related to species richness in different hydrographic regions there. The hydrographic regions present distinct phylogenetic and species composition regardless of the level of richness. Regarding the bivalve assemblies from ecoregions, we observed higher bivalve species richness in large areas of lower slope and high fishes richness. The high richness of unionids with parasitic larval stage was also related to polygon area and high richness of fishes. The values of rarity index were related to ecoregion with higher pH levels. Most environmental factors that explained the structure of the bivalve assemblies were physiographic attributes and the fish species richness. The release of larvae and recruitment began in the spring. The variation of the descriptors was associated with water temperature, conductivity, total alkalinity, and sulfates. The survival of the golden mussel in the pH range 4-11 after 120 hours of exposure can enable the survival of populations under adverse and intermittent conditions in the aquatic environment. Regarding microbial agents, *Bacillus thuringiensis* sv. *kurstaski* HD-1 showed high potential for the control of golden mussel and could be assessed for development of new commercial formulation. VECTOBAC® aqueous Solution (AS) was the most efficient commercial formulation for the golden mussel control. However, the lethal concentration of VECTOBAC for the mussel control is very higher than effective concentration to kill diptera, and can be toxic to non-target organisms. The following conclusions are highlighted. Not only should the richness be considered to be a criterion for prioritizing areas for conservation, but also the phylogenetic diversity of communities engaged in services and functional aspects relevant to ecosystem maintenance. Physiographic attributes and the fish species richness explained the structure of the bivalve assemblies in the freshwater ecoregions. Geological events of the past that shaped the South American landscapes contributed to the present distribution and composition of bivalve species in the evaluated ecoregions. It is worth noting the potential of golden mussel for colonization of Amazonian acidic waters. 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Introdução

Introdução

As invasões biológicas e a conservação da biodiversidade são um dos temas mais desafiadores na atualidade na área das ciências naturais. O crescimento exponencial da população humana sobre a litosfera tem exercido pressões ambientais multiescalares que afetam todos os níveis de organização da biosfera.

Em algumas áreas, barreiras naturais são rompidas devido a inúmeras atividades antrópicas que aumentam a conectividade em sistemas naturais isolados por milhares de anos. Por outro lado, alguns sistemas são fragmentados e se tornam os únicos refúgios para uma flora e uma fauna remanescente.

A complexidade da matriz de impactos que o homem imprime sobre a face terrestre é tal, que uma única ótica ou ponto de vista não é suficiente para que sejam encontradas soluções para os problemas ambientais complexos.

Desta forma, se faz necessário estabelecer um *zoom* sobre vários compartimentos ambientais, e níveis de organização biológica desde o nível celular até a atmosfera, para que os fenômenos naturais possam ser compreendidos na ordem de magnitude que se expressam.

A presente tese aborda duas linhas de pesquisa, a ecologia da bioinvasão e a ecologia das assembléias de bivalves límnicos. Contextualizando estas temáticas, percebe-se que a abordagem de vários níveis de organização é necessária para que se possa compreender os fatos, mecanismos, processos e números que descrevem estas entidades biológicas.

A matriz energética do ecossistema, segundo Tundisi & Matsumura-Tundisi (2008) adaptado de Likens (1992), ilustra todos os níveis e compartimentos de um ecossistema, seus fluxos, processos e níveis de organização (Figura 1). A presente tese aborda três níveis de organização, indivíduo, população e comunidade, visando contribuir para a elucidação de fatos referentes à bioinvasão e a ecologia de bivalves de água doce na América do Sul e a conservação de espécies nativas.

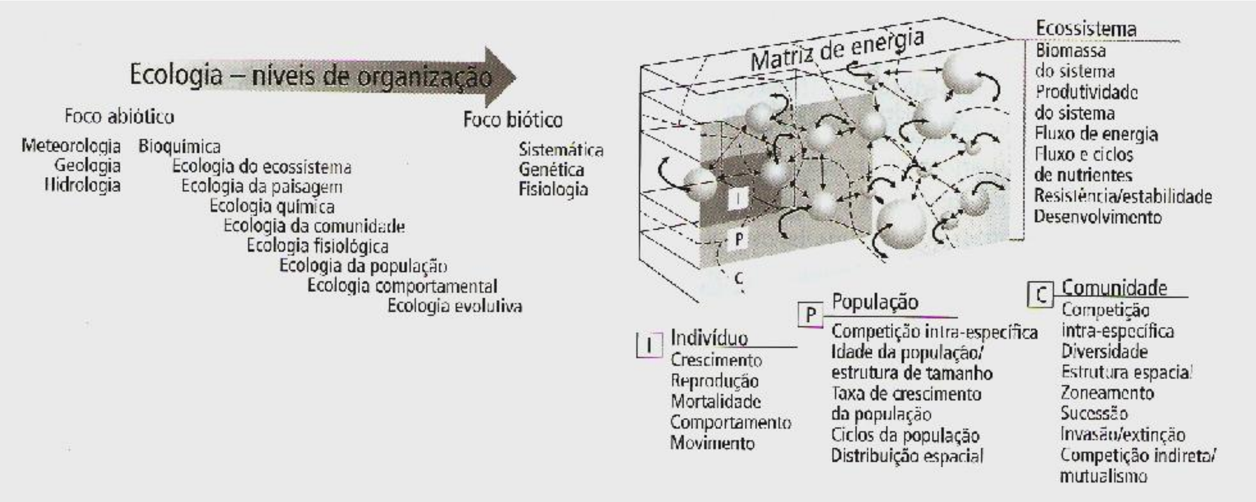


Figura 1. Matriz energética do ecossistema e os níveis de organização e de estudo com base em indivíduos e comunidades. Fonte: extraído de Tundisi e Matsumura-Tundisi (2008), adaptado de Likens (1992).

Os bivalves são moluscos bivalves filtradores, geralmente suspensívoros, que representam normalmente o maior percentual de biomassa da comunidade bentônica. Auxiliam na remoção de detritos, exercendo também a limpeza dos corpos d’água, removendo grande quantidade de material particulado em suspensão, depositando-os no fundo (Mcmahon, 1991). Desta forma, concentram tanto no corpo como na concha grande quantidade de nutrientes e minerais, principalmente o cálcio, constituindo alimento para muitos peixes, aves e mamíferos. Vivem semienterrados no fundo de córregos, rios, baias e reservatórios pequenos, ou aderidos aos substratos submersos fixos ou flutuantes, sendo geralmente confundidos com o fundo, por apresentar coloração similar (Mansur et al., 1997). A concentração de metais-traços poluentes também é muito expressiva, o que os torna adequados ao biomonitoramento, sendo considerados indicadores ambientais (Mcmahon, 1991).

Na atualidade, muitas espécies estão sofrendo declínio populacional devido às alterações ambientais causadas pelo homem. Além disso, as invasões biológicas tem sido alvo de preocupação na América do Sul. A presença de espécies invasoras de bivalves de água doce tem causado grandes impactos ambientais e econômicos aos ambientes naturais e construídos (Mansur et al., 2012).

Invasões biológicas

> “A invasão biológica consiste em espécies que adquirem uma vantagem competitiva, seguida do desaparecimento de obstáculos naturais à sua proliferação, o que permite que ela se disperse rapidamente e conquiste novas áreas, nas quais se torna uma população dominante” (Valéry et al., 2008a).

Os inúmeros conceitos de espécies invasoras difundidos pela comunidade científica têm gerado controvérsia e dificultam a compreensão do tema bioinvasão por parte de leigos e tomadores de decisão. Espécies não indígenas, alienígenas, não nativas, estrangeiras, exóticas, transplantadas e alóctones são uma pequena parte dos termos sinônimos que são encontrados na literatura para definir esta questão (Espinola & Ferreira Junior, 2007), mas cada uma destas definições tem suas particularidades e limitações teóricas.

No entanto, espécies introduzidas ou exóticas são geralmente definidas como aquelas espécies que atualmente encontram-se distribuídas além de sua faixa de distribuição original, atingindo novos ecossistemas, muitas vezes em outro continente ou país. O principal problema é como verificar se a espécie esta fora de sua área de distribuição “natural” ou “original”. Para tanto é necessário o monitoramento constante das áreas invadidas e não invadidas próximas, ou seja, os clássicos levantamentos de espécies de uma dada região constituem a base de dados primordial para fornecer subsídios para o reconhecimento do status de uma espécie. Quando dados publicados não são conhecidos, pode-se recorrer aos museus. Estes são os maiores repositórios da biodiversidade e algumas vezes dispõem de uma base de dados completa, com dados georreferenciados que permitem a visualização dos padrões de distribuição em mapas.

A grande capacidade de invasão e colonização de novos ambientes que algumas espécies apresentam é atribuída às características genéticas, bem como às adaptações ecofisiológicas e tolerância a uma ampla faixa de condições ambientais (Machado & Oliveira, 2009, Darrigran e Damborenea, 2009).

A primeira base legal que abordou o assunto no Brasil foi a Portaria do Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) Nº 145-N, de 29 de outubro de 1998, No entanto, a referida portaria não foi revisada e apresenta diversos termos desatualizados no que se refere à bioinvasão. As múltiplas abordagens conceituais dificultam o estabelecimento de estratégias de manejo, o que torna necessário a elaboração de legislações com base em conceitos claros e objetivos (Espinola & Ferreira Junior, 2007).

Um grande avanço realizado recentemente surgiu por meio do livro editado e publicado pelo Ministério do Meio Ambiente intitulado “Informe sobre espécies exóticas invasoras Marinhas no Brasil”. Nesta obra, Lopes & Villac (2009) uniformizam alguns conceitos com o objetivo de orientar ações do Ministério e seus órgãos afiliados. Os autores definem três categorias genéricas de espécies exóticas e quatro específicas. As genéricas compreendem a definição de espécie nativa como aquela que vive em sua região de origem, espécie exótica são consideradas aquelas registradas fora de sua área de distribuição original, e por último, espécies de origem biogeográfica desconhecida ou incerta são denominadas criptogênicas.

As quatro categorias específicas são assim definidas (Figura 1):

Contida: quando a presença de uma espécie exótica foi detectada apenas em ambiente artificial controlado, isolados total ou parcialmente do ambiente natural, como por exemplo, aquário comercial, cultivo para fins científicos, tanque de água de lastro de navios etc.

Detectada: quando a presença de uma espécie exótica foi detectada em ambiente natural, mas não foi observado aumento posterior de sua abundância e/ou de sua dispersão ou sem informações subsequentes sobre a situação populacional da espécie (registro isolado).

Estabelecida: quando a espécie exótica foi detectada de forma recorrente, com ciclo de vida completo na natureza e indícios de aumento populacional ao longo do tempo em uma região restrita ou ampla, porém sem apresentar impactos ecológicos ou socioeconômicos aparentes.

Invasora: quando a espécie estabelecida possui abundância ou ampla dispersão geográfica que interferem na capacidade de sobrevivência de outras espécies ou quando a espécie estabelecida causa impactos mensuráveis em atividades socioeconômicas ou na saúde humana.

Outro conceito interessante não contemplado na obra de Lopes & Villac (2009) é o conceito de espécies engenheiras do ecossistema, estabelecido por Jones et al. (1994). O autor define como engenheiros de ecossistema os organismos que direta ou indiretamente modificam a disponibilidade de recursos para outras espécies, causando alterações bióticas e abióticas.

O ambiente alvo da bioinvasão também tem suas características próprias, como o isolamento histórico e geográfico, baixa diversidade de espécies nativas, alto nível de distúrbio por atividades humanas, bem como ausência de competidores, doenças, predadores e parasitas (Wolfe, 2002; Bohn et al. 2004)

Diversidade de bivalves límnicos na América do Sul

Os mapas da distribuição de bivalves nativos das famílias Mycetopodidae e Hyriidae na América do Sul produzidos por Parodiz & Bonetto (1963) (Figura 2), constituiu o único estudo de larga escala realizado sobre a distribuição e composição de espécies no continente. Posteriormente, Bonetto (1965) elaborou um mapa de distribuição das espécies do gênero *Castalia* no continente, quando revisou o gênero (Figura 3).

Graf & Cummings (2007) realizaram um levantamento global da diversidade de bivalves límnicos (Unionoida) e constataram 172 espécies para a região Neotropical. Estes autores registram 12 espécies na região transandina, 42 espécies no sistema Amazonas-Orinoco, 18 espécies no sistema São Francisco-Atlântico e 41 no Paraná-Paraguai.

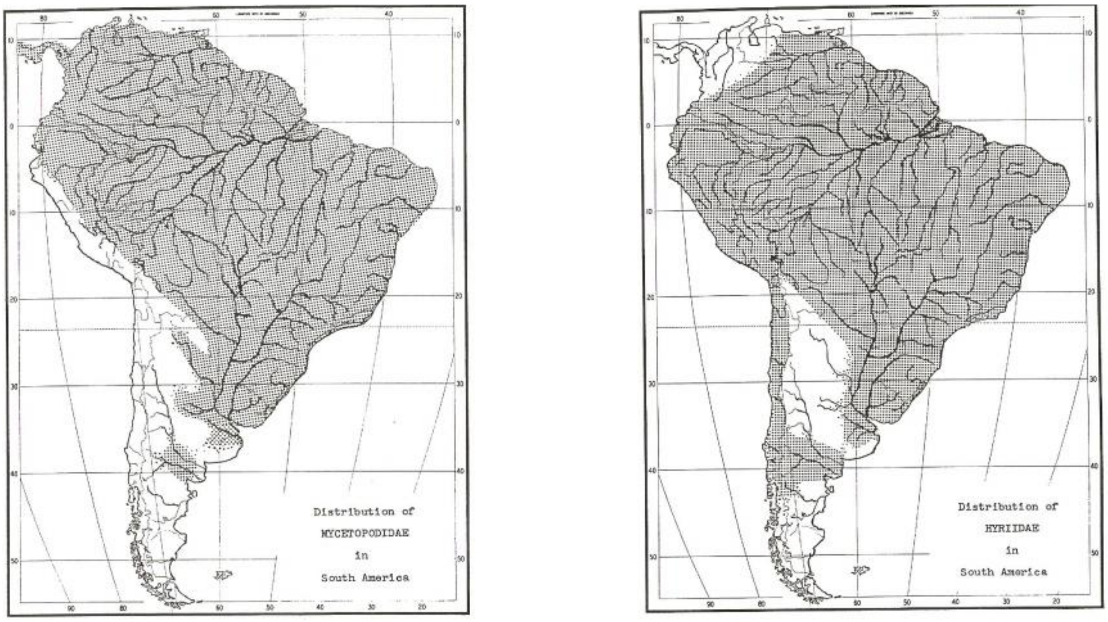


Figura 2. Distribuição de Mycetopodidae (esquerda) e Hyriidae (direita) na América do Sul. Fonte: extraído de Parodiz e Bonetto (1963). Àrea de ocorrência em cinza.

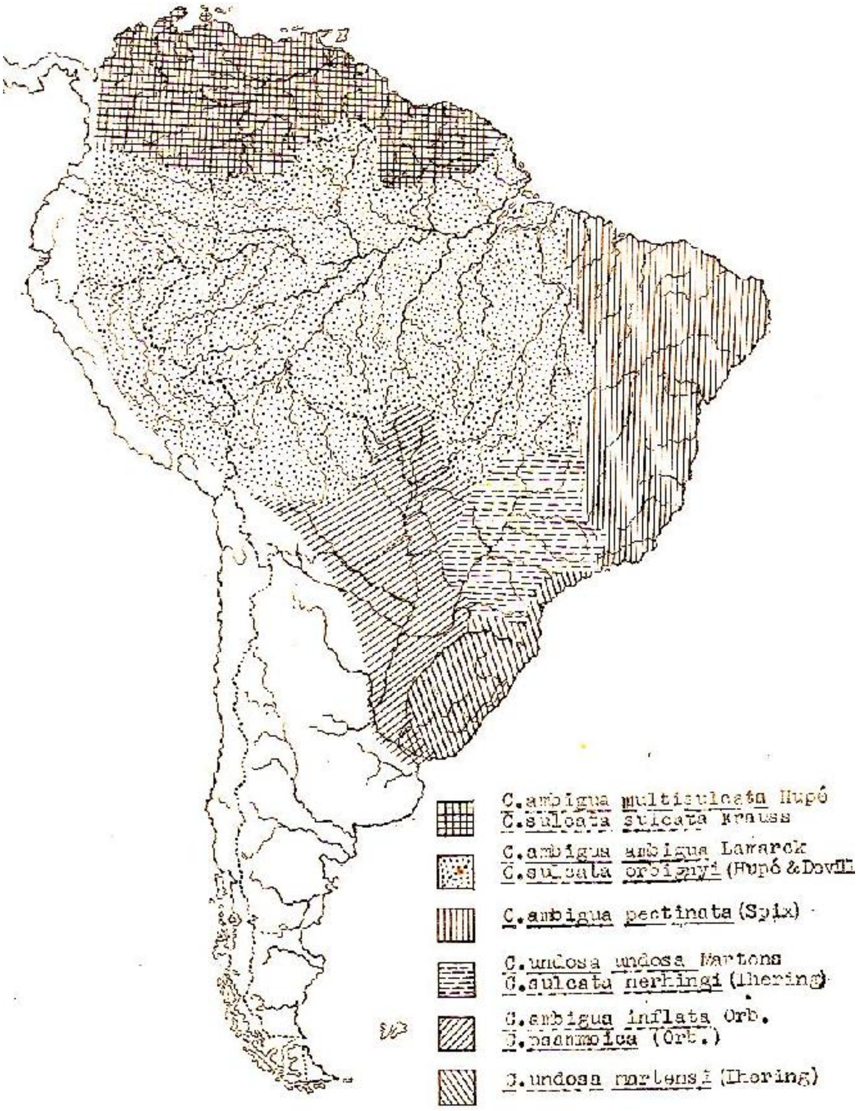


Figura 3. Distribuição das espécies do gênero *Castalia* na América do Sul. Fonte: extraído de Parodiz e Bonetto (1963).

As espécies de bivalves límnicos do Brasil foram recentemente listadas por Pereira et al. (2012) por meio de um levantamento bibliográfico preliminar. Os principais números apresentados pelos autores são relatados a seguir:

- São conhecidos 22 gêneros de bivalves límnicos para o Brasil, sendo que dois destes estão representados apenas por espécies invasoras: *Limnoperna* (Mytilidae) e *Corbicula* (Corbiculidae).

- As famílias mais representativas em número de espécies no Brasil são Hyriidae (52 espécies; 45% das espécies de bivalves límnicos), Mycetopodidae (32; 28%) e Sphaeriidae (20; 17%), sendo estas espécies nativas.

- Dentre os gêneros mais representativos em número de espécies pode-se citar *Diplodon* (37 espécies; 32% das espécies de bivalves límnicos), *Anodontites* (14; 12%), *Castalia* (11; 10%), *Eupera* e *Pisidium* (9; 8%), e *Monocondylaea* (7; 6%), sendo espécies nativas.

- O Brasil apresenta oito grandes bacias hidrográficas ou regiões hidrográficas: 1, Amazonas; 2, Tocantins/Araguaia; 3, do Atlântico Norte/Nordeste; 4, São Francisco; 5, do Atlântico Leste; 6, Paraná/Paraguai; 7, Uruguai; e 8, bacia do Atlântico Sul/Sudeste (Figura 3). O maior número de espécies foi verificado nas bacias: Paraná/Paraguai (51 espécies; 22% das espécies de bivalves límnicos citados para o Brasil), Atlântico Sul/ Sudeste (43; 18%), Uruguai (42; 18%) e Amazonas (40; 17%). No entanto, esses números podem não representar a diversidade real destas bacias, já que as bacias Amazonas, Atlântico Norte/Nordeste, Atlântico Leste, Tocantins/Araguaia e São Francisco carecem de coletas e inventários malacofaunísticos.

- Das 114 espécies citadas para o Brasil, 45 carecem de revisão taxonômica (35% das espécies citadas). As maiores dificuldades são verificadas quanto à identidade taxonômica das espécies do gênero *Diplodon* que apresentam ampla variação morfológica. A falta de conhecimento da real identidade taxonômica das espécies é um agravante no que diz respeito à conservação, sendo que algumas espécies constam em listas vermelhas. Apenas 1% das espécies citadas para o Brasil está enquadrada na categoria Criticamente Em Perigo (CEP) na lista vermelha brasileira de espécies ameaçadas; 11%, na categoria Em Perigo (EP) e 9% em Vulnerável (VU) (Figura 4). As demais espécies não constam em listas, mas isso não significa que não estejam ameaçadas, pois as listas não foram revisadas desde suas publicações. Além disso, muitas destas espécies têm sofrido ameaças consideráveis, destacando-se a construção de novas barragens, assoreamento, desmatamento, destruição de habitats, poluição e a ampliação da dispersão das espécies de bivalves invasoras. Desta forma, 46 espécies (40,3% das espécies de bivalves límnicos citadas para o Brasil) são sugeridas como candidatas à avaliação criteriosa em nova revisão da lista de espécies ameaçadas da fauna brasileira. As demais espécies carecem de dados e, assim como as espécies candidatas, deverão ser alvo de pesquisas quanto aos seus níveis populacionais, preferências ambientais e distribuição geográfica atual no país.

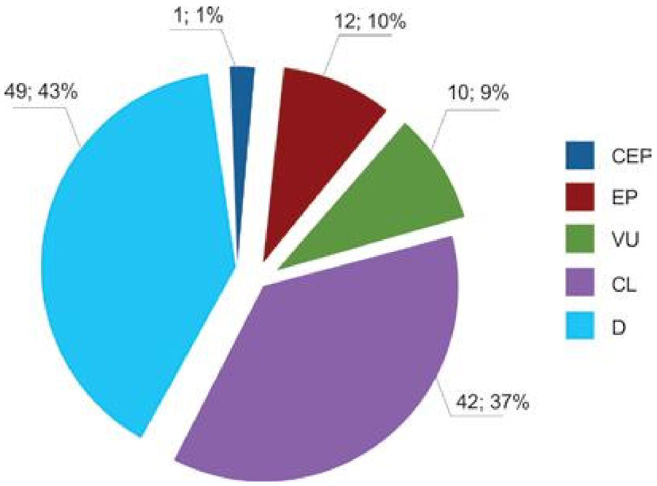


Figura 4. Bivalves límnicos (Número de Espécies – N, percentual - %) enquadrados em categorias de ameaça em listas vermelhas de espécies ameaçadas de extinção no Brasil, e espécies candidatas à inclusão nas listas: criticamente em perigo (CEP), em perigo (EP), vulnerável (VU). Espécies candidatas à lista de espécies ameaçadas de extinção do Brasil (CL) que deverão ser avaliadas por meio de critérios apropriados; espécies desconhecidas (D) quanto a quaisquer aspectos da sua conservação. Fonte: extraído de Pereira et al. (2012).

A distribuição das espécies invasoras é bem conhecida e a dispersão das mesmas tem sido acompanhada por meio de vários projetos de pesquisa realizados no Brasil, Argentina e Uruguai. Santos et al. (2012) apresentou mapas da distribuição atual de *L. fortunei* (Figuras 5) e as espécies de *Corbicula* (Figuras 6). Cenários futuros de ocorrência de *L. fortunei* nas bacias hidrográficas no Brasil foram previstos por Oliveira et al. (2010) (Figuras 5).

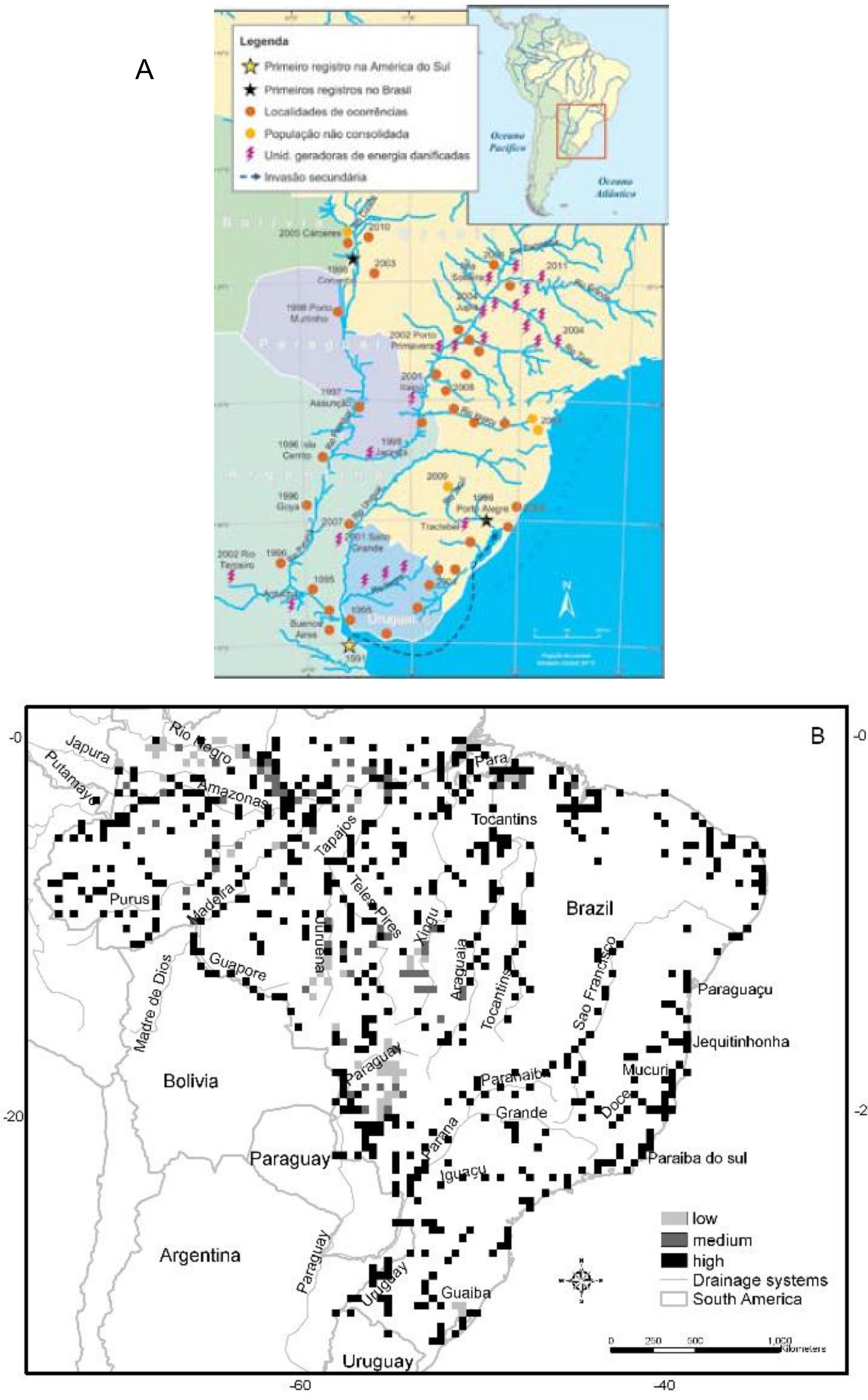


Figura 5. Distribuição atual (A) e potencial de (B) *L. fortunei* nos sistemas fluviais do Brasil com base em limites mais baixos de concentração de cálcio e calcita: pior cenário previsto. Baixo risco de *L. fortunei* ocorrência em rios onde a concentração média de cálcio foi de 0,0 e índice de saturação de cálcio de 1,0 mg L^{-1} e foi e índice de saturação de cálcio de <-4.0, médio risco entre as concentrações de cálcio de 1,0 e 3,0 mg L^{-1} e entre -4,0 e e índice de saturação de cálcio de -3.0, E de alto risco, onde a concentração de cálcio foi> 3,0 mg L^{-1} e índice de saturação de cálcio de foi> -3.0. Fonte: extraído de A, Santos et al. (2012) e B, Oliveira et al. (2010).

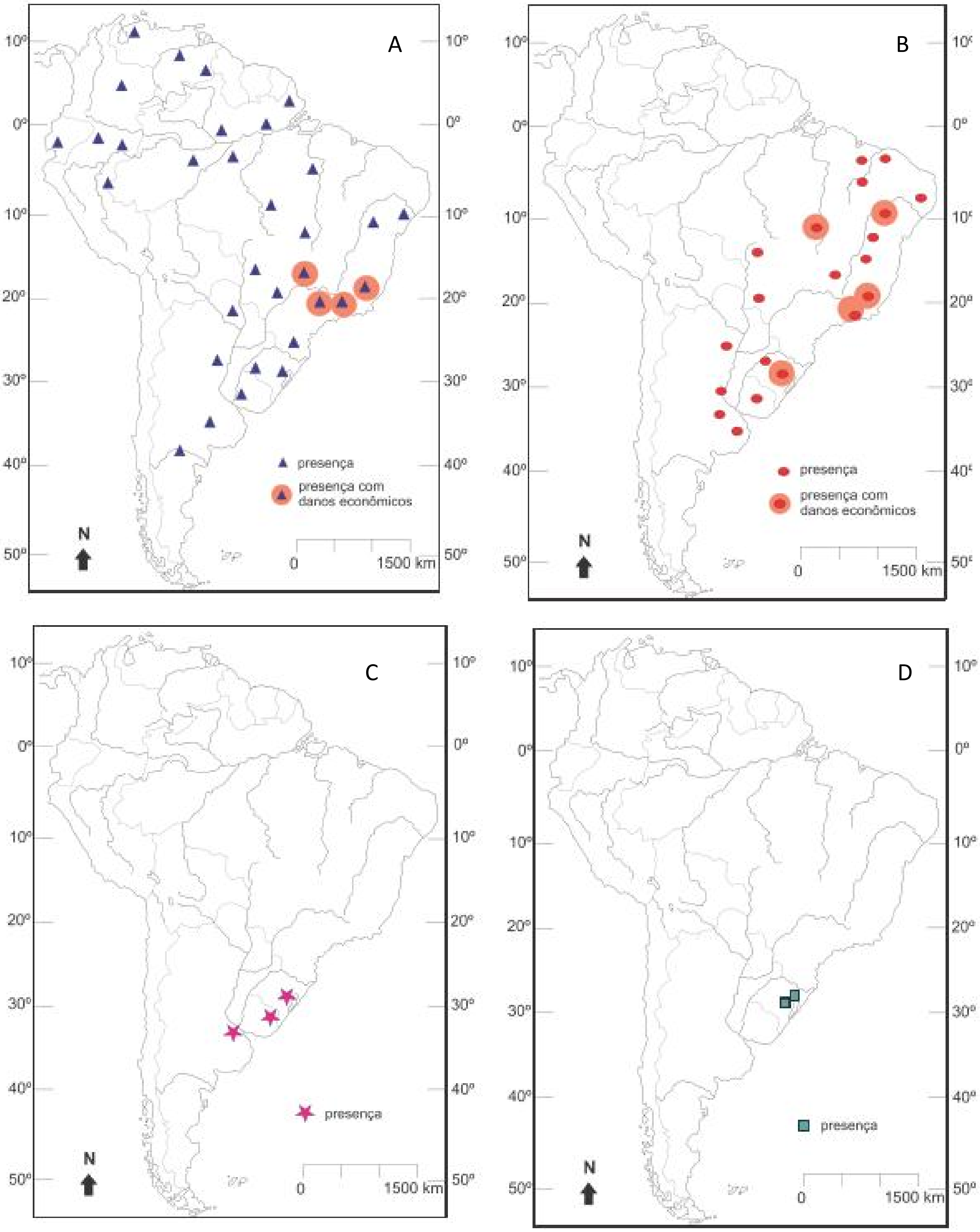


Figura 6. Distribuição atual de *Corbicula fluminea* (A), *Corbicula largillierti* (B), *Corbicula fluminalis* (C) e *Corbicula* sp. (D) nos sistemas fluviais sulamericanos. Fonte: extraído de Santos et al. (2012).

Fatores ambientais e composição de espécies

Quanto a espécies nativas de Unionoida da América do Norte, de acordo como Haag (2012), a distribuição dos bivalves em um determinado gradiente ambiental é influenciada principalmente por fatores climáticos e fisiográficos, bem como quimísmo das bacias (Tabela 1). A maioria das espécies é generalista e não apresentam distribuição específica em micro-habitats aquáticos. A maioria dos bivalves sul-americanos da ordem Unionoida se dispersa fixando suas larvas em peixes hospedeiros, os quais carregam os moluscos rio por vários setores de uma bacia hidrográfica (Mansur, 2012). Por tanto, estes moluscos tem uma relação estreita com a ictiofauna, sendo que os padrões de riqueza de bivalves e peixes muitas vezes estão correlacionados (Haag, 2012)

Na América do Sul pouco se conhece sobre os fatores ambientais que influenciam a composição de espécies de bivalves em termos de microhabitat e mesohabitat, muito menos quanto ao macrohabitats. Pereira et al. (2011) avaliou a riqueza e composição de espécies ao longo de um córrego no sul da América do Sul e verificou que a riqueza aumentava em direção a foz mas diminuía junto desta devido ao efeito de salinidade da Laguna dos Patos, onde o arroio desaguava (Figura 7). Os bivalves se concentravam em poças junto a barras laterais como descreveu Haag (2012) para América do Norte. Padrão semelhante foi verificado no arroio Ayui Grande na Argentina (Bonetto & Di Persia, 1975). Muitos outros estudos foram realizados avaliando relações de microhabitat e as assembleias de bivalves (Henry & Simão, 1984 e 1986, Mansur et al. 1994, Duarte & Diefenbach, 1994, Duarte et al., 1996, Suriani et al., 2007, França et al, 2007, Pereira et al., 2012, Colle e Callil 2012). A distribuição de espécies de moluscos, com ênfase em gastrópodes, em gradientes geográficos de macroescala foi avaliado em uma série de trabalhos realizados em áreas úmidas do Estado do Rio Grande do Sul (Brasil) (Lanzer e Shafer, 1985, 1987, 1988, Lanzer, 2001, Maltchick et al., 2010).

Extensa revisão literária sobre a temática dos bivalves de água doce na América do Sul poderá ser verificada no capítulo 1 desta tese.

Até o momento não se obteve informações sobre os fatores que influenciam a distribuição de bivalves nativos de água doce na América do Sul, em macroescala.

Tabela 1. Fatores que influenciam a distribuição de bivalves límnicos nativos (Unionoida), na América do Norte (Haag, 2012).

Fatores	
Macrohabitat	Microhabitat
Clima Temperatura Precipitações Fisiografia Área de drenagem de bacias Área de províncias zoogeográficas ou ecorregiões Efeito de marés Química da água Conteúdo de cátions (principalmente cálcio) pH Oxigênio dissolvido Nutrientes Comunidade Aquática Riqueza de espécies de peixes	Espécies generalistas (maioria) Não apresentam padrões claros quanto à distribuição em níveis distintos de profundidade, velocidade da água e substrato como os demais organismos aquáticos Espécies especialistas (minoria) Estão relacionadas às áreas deposicionais dos rios, em poções e depósitos de lama atrás de barras laterais ou transversais de resultantes da deposição de areia e cascalhos, ou ao longo das margens dos rios. Ao longo das margens de rios e lagos

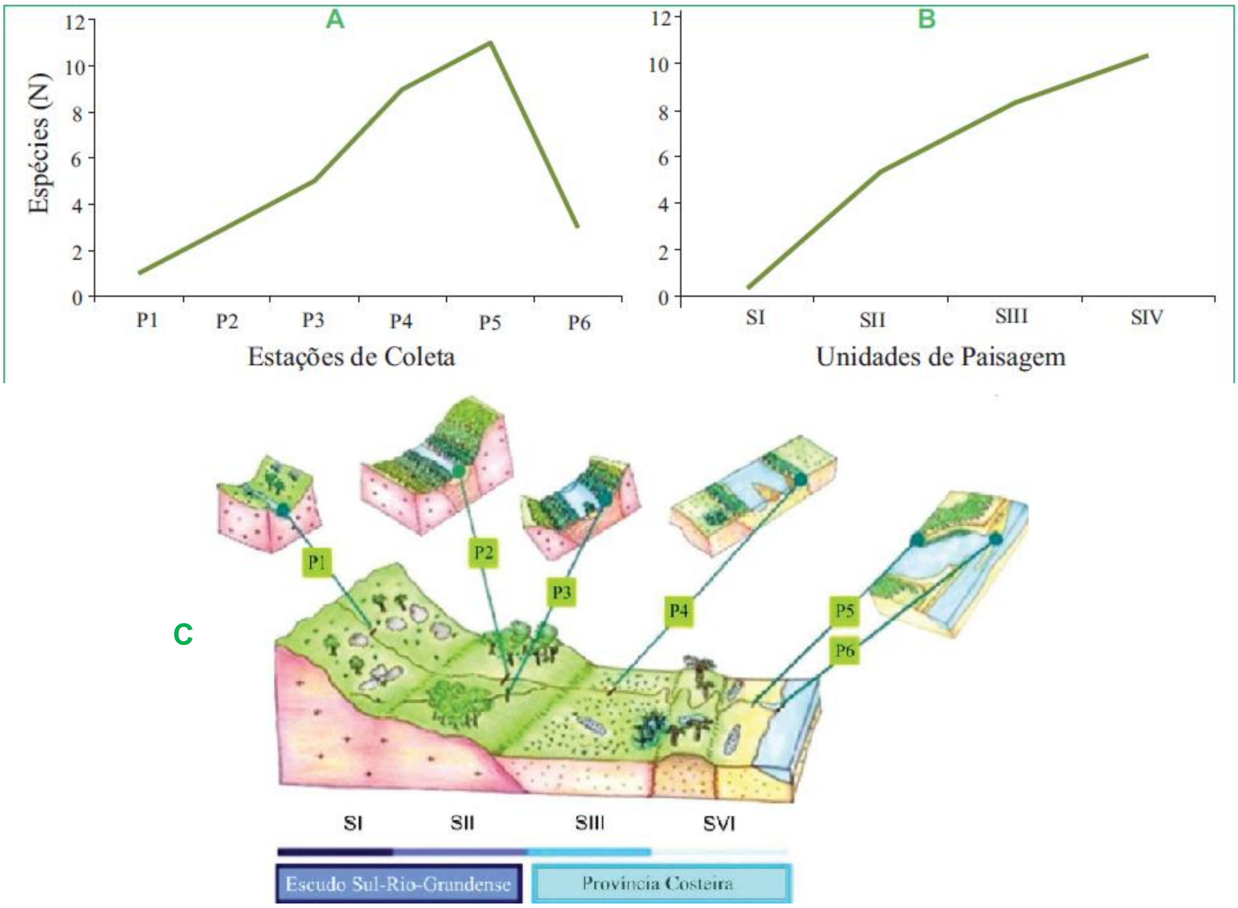


Figura 7. Riqueza de espécies em (A e B) estações de coleta (C) e unidades de paisagem (C) no arroio Velhaco (RS, Brasil). Fonte: extraído de Pereira et al. (2011). SI, Setor das Nascentes; SII, Setor Intermediário Proximal; SIII, Setor Intermediário Proximal e SIV, Setor Final ou da Foz.

Quanto às espécies invasoras, o cenário é um pouco distinto devido ao grande interesse econômico em controlar estas espécies principalmente devido aos impactos na geração de energia, pesca e captação de água.

Os Dreissenidae são amplamente estudados quanto aos fatores limitantes da sua ocorrência em ecossistemas continentais (Tabela 2). Um grande número de informações relativas às variáveis ambientais que determinam a distribuição de moluscos invasores na América do Norte pode ser verificado em Claudi & Mackie (2010) e do América do Sul, em Darrigran e Damborenea, (2009) e Mansur el al. (2012).

No entanto, as variáveis que influenciam o recrutamento anual do mexilhão dourado e sua sobrevivência são pouco conhecidas.

Tabela 2. Fatores que influenciam a distribuição de bivalves invasores na América do Norte (Claudi & Mackie, 1993) e do Sul (Darrigran e Damborenea, 2009, Mansur el al., 2012).

Fatores
pH
Oxigênio dissolvido
Nutrientes (formas de nitrogênio e fósforo)
Dureza
Alcalinidade
Salinidade
Condutividade

Conservação da fauna de bivalves

Dentre as principais ameaças à conservação dos bivalves límnicos pode-se citar: a presença de espécies invasoras, que competem por espaço e alteram a estrutura das comunidades bentônicas; alterações de habitat, o assoreamento e erosão marginal de rios e lagos, resultantes do desmatamento da mata ciliar de rios; a construção de barragens; alteração do nível hídrico resultante da drenagem de rios até sua intermitência; diminuição da riqueza de peixes hospedeiros; explotação, entre outras (Mansur et al, 2004).

Em junho de 1997, o *The National Native Mussel Conservation Committee*, nos Estados Unidos da América, elaborou um documento chave que estabelece diretrizes para a conservação da fauna de bivalves nativos norte-americana. Neste documento consta uma série de estratégias para a conservação das espécies nativas: a elaboração de protocolos de biomonitoramento, os estudos das populações e suas histórias de vida, descrição dos ciclos reprodutivos, elaboração de catálogos ilustrativos com mapas de distribuição de espécies, estudos biogeográficos e genéticos, avaliação da perda e degradação de habitats, bem como monitoramento das espécies invasoras, avaliação da competição e do impacto das mesmas sobre as espécies nativas e o controle da dispersão das espécies invasoras, entre muitas outras estratégias. O documento ressalta, ainda, o levantamento de dados históricos da distribuição das espécies nativas e fatores ambientais que possam servir para predição dos bivalves, o levantamento da riqueza junto a coleções científicas para subsidiar o mapeamento e categorização de bacias hidrográficas e ecorregiões quanto à riqueza e composição de espécies. Uma das ações de sucesso foi à criação e realocação de bivalves em áreas recuperadas.

Manejo de espécies invasoras

Segundo Darrigran et al. (2012) o manejo das espécies invasoras deve ser realizado logo que são detectadas no novo ambiente após sobreviver ao transporte. Como pode ser verificado no diagrama abaixo descrito por estes autores, quando a espécie atingiu um novo local, já rompeu a barreira da prevenção. Após esta fase, começa a se dispersar por novas áreas. Medidas de erradicação são apenas possíveis durante a fase de lapso quando danos econômicos e ambientais ainda não são notáveis. Mas quando a dispersão é acentuada causando impactos de ordem econômica e ambiental, não é mais possível erradicar e sim apenas restaurar algumas áreas afetadas e ou exercer o controle em sistemas fechados (Figura 8).

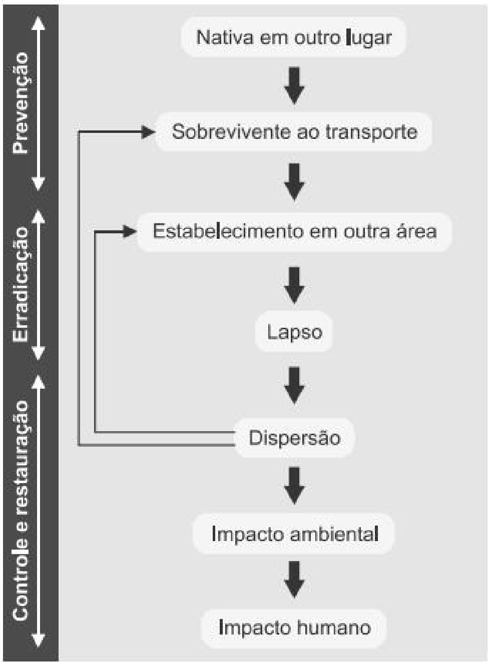


Figura 8. Etapas no processo de invasão de uma espécie exótica. Fonte: extraído de Darrigran et al. (2012) modificado de Lockwood et al. (2007).

Um dos grandes desafios é sensibilizar os diferentes setores da sociedade, principalmente aqueles que atuam na gestão dos recursos naturais e os órgãos de fomento em pesquisa, em induzir e aplicar investimentos em projetos de pesquisa e programas de manejo logo no início da invasão. Segundo Darrigran et al. (2012), se isso ocorrer as chances de obter sucesso no manejo integrado são enormes, mas do contrário, com o passar do tempo as somas em investimentos necessários serão elevadas e com pouco retorno aplicável (Figura 9).

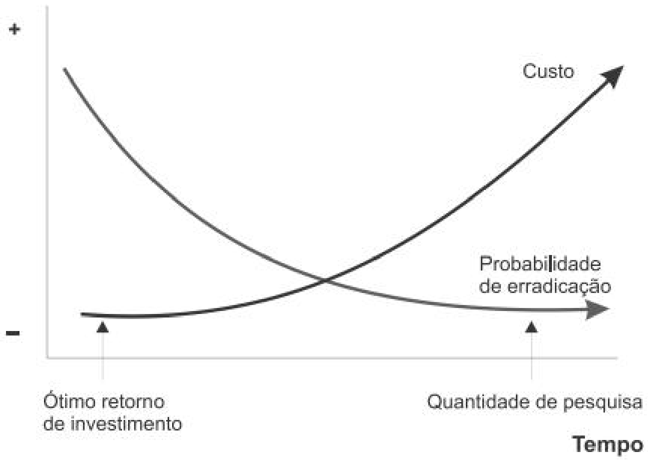


Figura 9. Relação entre o custo da erradicação de uma espécie invasora e a probabilidade de erradicação ao longo do tempo. Fonte: extraído de Darrigran et al. (2012).

A prevenção e o controle dependem da integração de conhecimento de várias áreas das ciências, bem como de ações socioambientais (Figura 10).

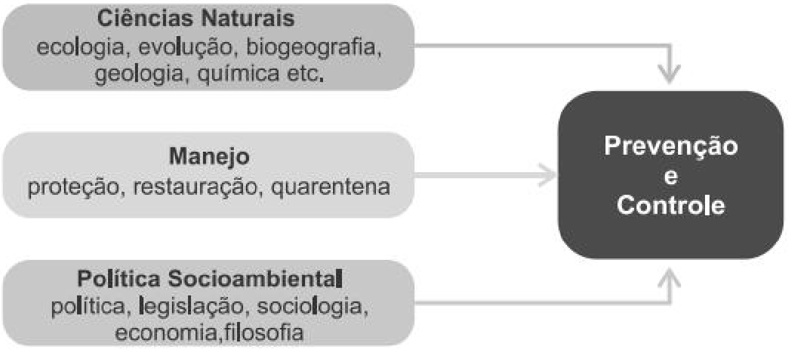


Figura 10. Componentes básicos para um programa de conservação da biodiversidade. Fonte: extraído de Darrigran et al. (2012) de acordo com Cowie (2004).

Controle populacional de bivalves invasores

O controle das espécies invasoras pode ser realizado via métodos físicos, químicos e biológicos (Mansur et al., 2012). O controle físico envolve o uso de radiações e ondas ultrassonoras (Zurita, 2012, Santos et al., 2012a, 2012b), enquanto o controle químico utiliza substâncias oxidantes (Rodriguez, 2012). O controle biológico utiliza inimigos naturais que competem, predam ou causam doenças específicas ao organismo alvo (Paz e Pereira, 2012).

Os métodos utilizados no controle do mexilhão dourado foram desenvolvidos para ambientes fechados, como plantas de tratamento de água, sistemas de refrigeração e tubulações de indústrias e hidrelétricas. Quando o sistema é aberto, os efeitos dos controladores afetam diretamente a biota e, em contrapartida se for fechado, esses efeitos podem ser contidos (Figura 11). A maioria desses métodos compreende controles utilizando substâncias químicas, com pouco conhecimento sobre os subprodutos e seus efeitos tóxicos sobre os ecossistemas. Até o momento inexistem pesquisas que visam o controle biológico do mexilhão dourado.

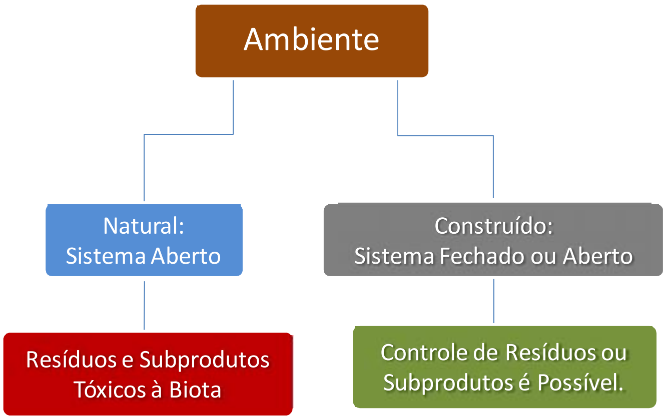


Figura 11. Efeitos do controle sobre o ecossistema. Diagrama: D. Pereira.

Dentre os métodos químicos, o sulfato de cobre foi muito utilizado em ETAS (estações de tratamento de água) e indústrias pela adição de sulfato de cobre diluído na água bruta em concentrações de 0,5 a 2 mg/L (Colares et al., 2002). Esta aplicação foi realizada sem estudo prévio dos resíduos resultantes deste tipo de tratamento químico. O cobre se acumula gradativamente nos organismos vivos e no sedimento. Soares et al. (2009) realizou testes estáticos de bancada, com sulfato de cobre ($CuSO_4.5H_2O$) objetivando avaliar a toxicidade deste sal sobre o mexilhão dourado e encontraram a concentração efetiva necessária para causar a mortalidade de 50% da população testada ($CE_{50} = 8{,}48$ mg/L (limite inferior, 6,69 mg/L e limite superior, 10,42 mg/L). As concentrações efetivas de cobre necessárias para causar a mortalidade de 50% da população do mexilhão dourado, em testes de bancada, são superiores aos padrões permitidos para lançamentos de efluentes líquidos (0,5 mg/L de cobre) em águas superficiais segundo resolução n. 128 do CONSEMA (2006) e os padrões para águas de classe 3 (0,013 mg L^{-1} de cobre) segundo resolução n. 357 do CONAMA (2005), portanto extremamente tóxica para o ambiente, não permitida de acordo com as leis ambientais brasileiras. Muitos outros métodos químicos são discutidos em Campos et al. (2012) e Campos e Fernandes (2012).

Outro tratamento largamente utilizado para evitar as incrustações em embarcações são as tintas antiincrustantes (Bergmann et al., 2010a; Bergmann et al., 2010b). No entanto, estes revestimentos podem causar toxicidade à biota aquática, principalmente aqueles desenvolvidos com base em óxidos de cobre e zinco.

Dentre os métodos físicos, experimentos com radiação ultravioleta foram realizados por Santos et al. (2012), que demonstraram 90% de eficiência no controle das larvas do mexilhão dourado em experimento realizado numa unidade piloto.

O controle biológico não a priori é menos impactante que os demais métodos de controle físico e químico, pois é mais específico ao organismo alvo e gera menos resíduos tóxicos em comparação aos inseticidas químicos. É mais estável e pode ter custo reduzido em comparação aos demais métodos. O controle biológico, de acordo com Baker & Cook (1974) é a redução de populações de organismos alvo ou de seus efeitos a um sistema natural ou construído, realizados naturalmente ou pela manipulação de inimigos naturais (Figura 12), com a finalidade de reduzir danos provocados por estas populações. São utilizados no controle biológico de insetos pragas vários inimigos naturais dos mesmos, tais como: vírus, bactérias e fungos. Os microrganismos são normalmente chamados de agentes de controle biológicos (ACBs)

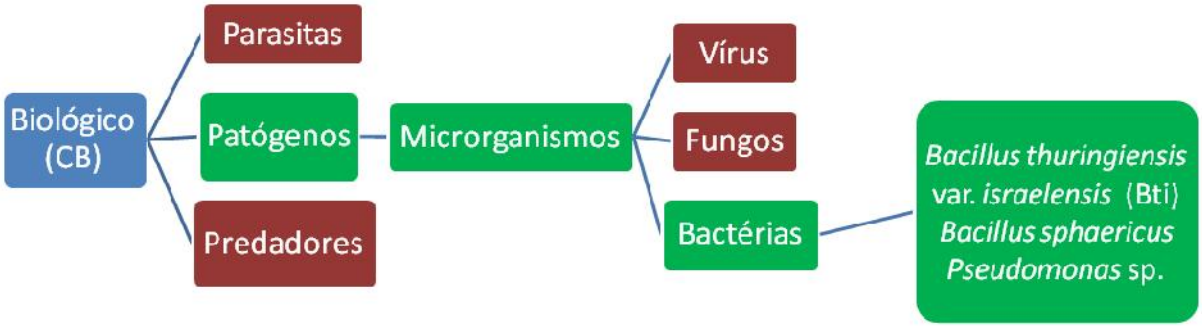
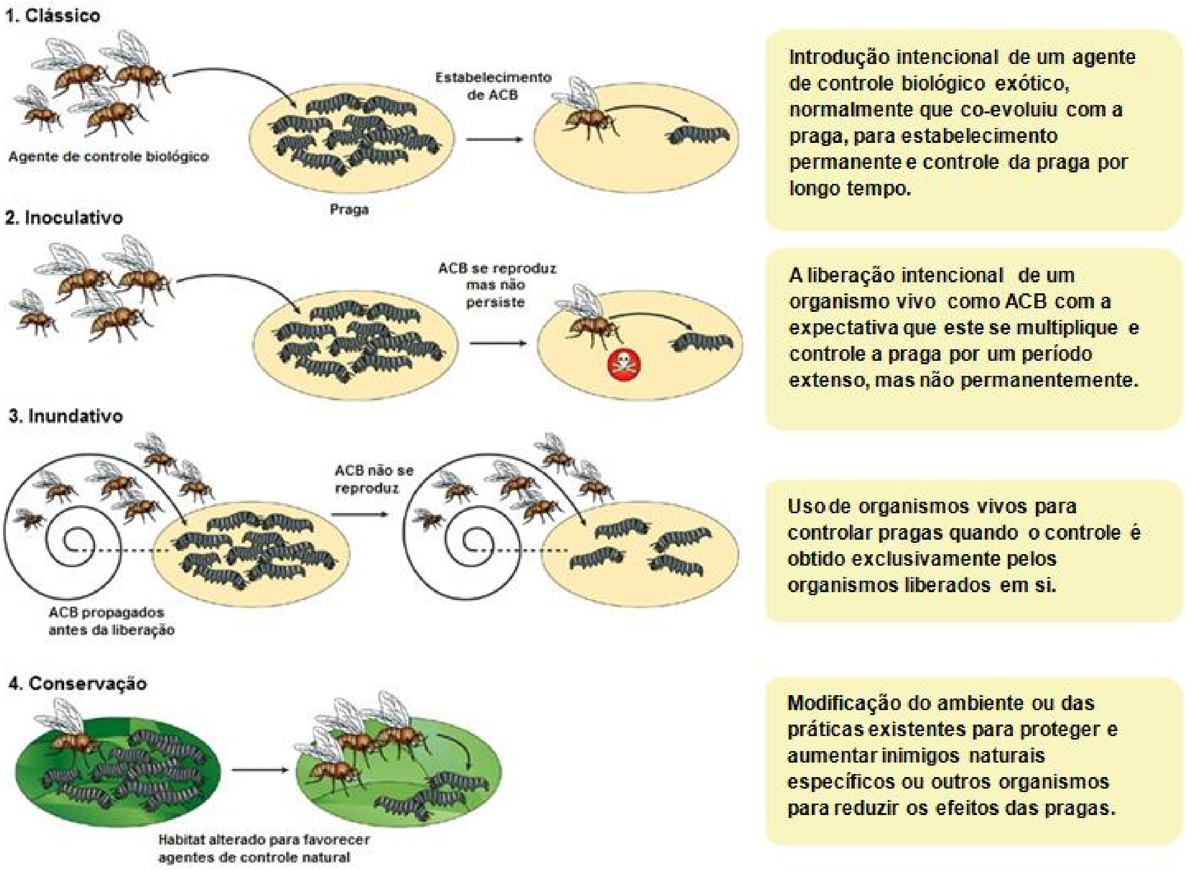


Figura 12. Tipos de inimigos naturais utilizados em controle biológico. Diagrama: D. Pereira.

A forma de aplicação dos ACBs no manejo de organismos-praga pode ser didaticamente dividida em quatro tipos, os quais são descritos na Figura 13. As vantagens e desvantagens deste tipo de controle são descritas na Tabela 3.



Introdução intencional de um agente de controle biológico exótico, normalmente que co-evoluiu com a praga, para estabelecimento permanente e controle da praga por longo tempo.

A liberação intencional de um organismo vivo como ACB com a expectativa que este se multiplique e controle a praga por um período extenso, mas não permanentemente.

Uso de organismos vivos para controlar pragas quando o controle é obtido exclusivamente pelos organismos liberados em si.

Modificação do ambiente ou das práticas existentes para proteger e aumentar inimigos naturais específicos ou outros organismos para reduzir os efeitos das pragas.

Figura 13. Tipos de controle biológico. Fonte: extraído de Paz & Pereira, 2012.

Tabela 3. Vantagens e desvantagens do uso de agentes de controle biológico (ACB) e químico (AQ). Fonte: extraído de Paz & Pereira, 2012, adaptado de Alves et al (1998).

Agente	Vantagens	Desvantagens
ACB	1. Automultiplicação e dispersão do ACB 2. Especificidade e seletividade ao organismo alvo 3. Permite uso associado com outras técnicas de controle de pragas 4. Permite melhoramento genético convencional e via transgenia, no caso de agentes microbianos 5. Riscos menores de poluição e de toxicidade aos organismos não alvos 6. Baixo risco de desenvolvimento de resistência nas populações de pragas.	1. Espectro de ação limitado ao organismo alvo ou aos organismos relacionados 2. Requer mais tempo para o controle efetivo da praga 3. Requer condições ambientais adequadas para introdução e estabelecimento na área de aplicação 4. Necessita estratégias de aplicação compatíveis com habitat e características da praga alvo 5. Necessidade de armazenamento adequado à espécie de ACB, por se tratar de organismos vivos
AQ	1. Amplo espectro de ação 2. Ação rápida e eficaz 3. Não dependente de fatores ambientais 4. Necessidade de poucos cuidados com armazenamento	1. Necessidade de reaplicação a cada ressurgência da praga 2. Baixa seletividade 3. Alto risco de poluição ambiental e de impacto sobre organismos não alvo, muitas vezes seus resíduos persistem em diferentes níveis da cadeia trófica 4. Alto risco de seleção de populações resistentes

Bacillus thuringiensis (Bt) foi descoberto em 1901 e a partir o uso de ACBs se tornou uma prática mundial, sendo que novas linhagens de *B. thuringiensis* foram descobertas e aplicadas no controle de ampla gama de grupos de insetos. *B. thuringiensis* var. *israelensis* (Bti) é altamente tóxico aos mosquitos dos gêneros *Aedes*, *Culex*, *Anopheles* e para Simulidae), enquanto *B. sphaericus* tem efeitos sobre *Culex*, *Anopheles* e *Psorophora* (Rabinovitch et al., 2008).

Segundo Molloy (1998), dois grupos de organismos têm potencial de controle de *Dreissena polymorpha*, bivalve invasor na América do Norte: microrganismos produtores de toxinas seletivas e inimigos naturais. O autor ressalta que técnicas utilizadas para controle de mosquitos borrachudos com *Bacillus thuringiensis* var. *israelensis* (Bti) podem ser adaptadas para o controle de *D. polymorpha*. Inúmeros trabalhos testaram efeitos tóxicos de microrganismos sobre moluscos (Genthner et al, 1997; Singer et al, 1997; Gu & Mitchell, 2001; Oliveira et al, 2004; Molloy et al, 2013), mas até agora nada foi feito visando o controle do mexilhão dourado.

Em sua obra de revisão sobre a "Avaliação da Periculosidade Ambiental de Bioinseticidas como uma Nova Perspectiva para a Ecotoxicologia no Brasil", Oliveira-Filho (2008) comenta que para fins de registro no país, o IBAMA, como representante do Ministério do Meio Ambiente, executa a avaliação e classificação da periculosidade ambiental de todos os produtos regidos pela

Lei no 7.802/89, entre os quais os bioinseticidas, por meio da observação de parâmetros físico químicos, de comportamento ambiental e de estudos toxicológicos e ecotoxicológicos. Segundo este autor, de acordo com a Instrução Normativa (IN) Conjunta N. 03/06, os principais estudos ecotoxicológicos solicitados são: fase I – ensaios de toxicidade aguda para invertebrados de água doce, peixes de água doce, insetos não-alvo, abelhas e toxicidade oral aguda para aves; fase II – estudos de comportamento dos agentes no ambiente terrestre, no ambiente de água doce e no ambiente estuarino; fase III – ensaios de toxicidade com organismos silvestres terrestres e aquáticos, patogenicidade e reprodução em aves, especificidade para invertebrados, ciclo biológico de peixes e plantas não-alvo. Essa IN ainda prevê a fase IV, que contempla os testes simulados em ambientes naturais. Oliveira-Fillho (2008) ressalta ainda que tais testes são igualmente solicitados pela ANVISA como subsídio para a avaliação de perigo à saúde humana, sendo que nesse caso, já na primeira fase de avaliação, têm grande importância o estudo dos potenciais patogênico e infectivo dos microrganismos além do estudo de possível toxicidade devido à presença de toxinas. Segundo ele, embora os agentes de biocontrole candidatos sejam patógenos naturais das espécies-alvo, a aplicação desses organismos no meio antrópico gera, também, preocupação com a segurança ambiental, pois a utilização desses patógenos no ambiente tem por objetivo causar danos somente à espécie-alvo.

Segundo Ignoffo (1973), questionamentos desse tipo têm motivado experimentos desde o desenvolvimento dos primeiros agentes de biocontrole, com principal enfoque na observação de efeitos sobre inseto não alvo, algumas aves e peixes. No entanto, muito pouco foi realizado neste sentido no Brasil.

Buscando responder as lacunas no conhecimento contextualizado na introdução desta tese de doutorado, alguns objetivos e hipóteses foram traçados e são descritos não próxima seção deste documento.

Objetivos e Hipóteses

Objetivo geral

- Determinar os fatores ambientais que explicam os padrões de riqueza e composição de espécies de bivalves límnicos em macro escala na América do Sul (AS), bem como o recrutamento do mexilhão-dourado, e selecionar agentes microbianos para o seu controle.

Objetivos Específicos

1) Categorizar as regiões hidrográficas (RH) e ecorregiões de água doce quanto à riqueza de bivalves límnicos e reconhecer as linhas filogenéticas de bivalves predominantes nas RH.

2) Determinar os fatores ambientais que explicam os padrões de riqueza e composição de espécies de bivalves límnicos em macro-escala, especialmente nas ecorregiões de água doce da AS.

3) Avaliar a relação entre a distribuição de espécies invasoras e à riqueza de espécies de bivalves límnicos nativos na AS.

4) Determinar as variáveis limnológicas que influenciam o recrutamento do mexilhão-dourado ao longo de um ciclo hidrológico

5) Avaliar a sobrevivência de *L. fortunei* ao pH.

6) Avaliar a toxicidade de cepas e formulações comerciais de *B. thuringiensis* e *B. cereus* sobre o mexilhão-dourado, visando selecionar potenciais agentes de controle populacional.

7) Avaliar a toxicidade das formulações comerciais selecionadas para o controle do mexilhão-dourado aos organismos não alvo.

8) Fornecer subsídios para a conservação da fauna de bivalves nativos e controle de espécies invasoras.

Hipóteses

1) A distribuição de espécies invasoras *Limnoperna fortunei*, *Corbicula fluminea*, *Corbicula fluminalis* e *Corbicula largillierti* está relacionada às assembleias de bivalves com menor riqueza de espécies – ARTIGO 1

2) Macrofatores ambientais, como atributos fisiográficos e indicadores da química da água, e a riqueza de peixes influenciam a composição de espécies de bivalves nas ecoregiões sulamericanas – ARTIGO 2

3) Variáveis limnológicas influenciam o recrutamento e a sobrevivência de *Limnoperna fortunei* – ARTIGO 3

4) Isolados e formulações comerciais de *Bacillus thuringiensis* e *B. cereus* podem ser utilizados no controle de *Limnoperna fortunei* sem causar danos a biota aquática e aos bivalves nativos – ARTIGO 4

Capítulo 1

Bivalve distribution in hydrographic regions in South America: historical overview and conservation

Bivalve distribution in hydrographic regions in South America: historical overview and conservation

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Abstract

Based on literature review and malacological collections, 168 native freshwater bivalve and five invasive species have been recorded for 52 hydrographic regions in South America. The higher species richness has been detected in the South Atlantic, Uruguay, Paraguay, and Amazon Brazilian hydrographic regions. Presence or absence data were analysed by Principal Coordinate for Phylogeny-Weighted. The lineage Veneroida was more representative in hydrographic regions that are poorer in species and located West of South America. The Mycetopodidae and Hyriidae lineages were predominant in regions that are richest in species toward the East of the continent. The distribution of invasive species *Limnoperna fortunei* is not related to species richness in different hydrographic regions there. The species richness and its distribution patterns are closely associated with the geological history of the continent. The hydrographic regions present distinct phylogenetic and species composition regardless of the level of richness. Therefore, not only should the richness be considered to be a criterion for prioritizing areas for conservation, but also the phylogenetic diversity of communities engaged in services and functional aspects relevant to ecosystem maintenance. A plan to the management of this fauna according to particular ecological characteristics and human uses of hydrographic regions is

needed.

Literature review

Earlier works on the freshwater bivalves of South America (from ~1800 to ~1890) are descriptive and consist of illustrated catalogs of species collected by naturalists during exploratory expeditions along river basins (Spix, 1827; Orbigny, 1835, 1846; Hupé, 1857). Shells acquired from travelers or merchants, or through exchange with colleagues or amateurs, have been described and cataloged by collectors and naturalists such as Maton (1811), Lamarck (1819), Lea (1834, 1838, 1852, 1857, 1860, 1863, 1869, 1874), Philippi (1847), Küster (1842), Sowerby (1864, 1867, 1868, 1869a, b), among others. Most scientific collections were private and would be eventually sold or donated to European museums (Dance, 1966; Olazarri, 1975; Haag, 2012). At that time, descriptions of new species were extremely poor, largely vague, and based on outdated concepts containing few illustrations and mostly from single specimens. Some of these catalogs were more iconographic than descriptive. In some cases, with the intent of showing the beauty shells, some conchological features were overlooked by designers.

This fact led to misunderstandings and wrong identification at the genus or species levels. Very often, collecting localities were unknown or poorly documented, consisting of vague references such as the continent or country name where a species was collected. Sometimes, old local names of rivers and lakes are no longer used, making the collection site difficult to locate.

In a subsequent period (~1890 to ~1960), special attention was given to the works of Simpson (1900, 1914) who published a summary and a catalog of World Unionoida, including South American species. This publication includes redescriptions, lists of synonyms, and significant taxonomic comments, with many species being labeled as incertae sedis. Hermann von Ihering emigrated from Germany to Brazil and lived there for many years, where he studied and collected bivalve mollusks, starting in the State of Rio Grande do Sul. Some years later, he moved to São Paulo to open the Museu de Zoologia da Universidade de São Paulo in 1895. Ihering organized the malacological collection and published over 35 articles on mollusks (Vaz, 1986), including checklists and identification keys of taxa from several drainages from Brazil and neighboring countries (Ihering, 1890, 1893, 1910). He also revisited the bivalve species described by Spix and Lamarck (Ihering, 1890, 1910) by examining the types. He was the first researcher to see and describe the lasidium (Ihering, 1891) larvae of Mycetopodidae, which is very similar to the haustorium of African species of the same Etherioidea superfamily (Wächtler et al., 2001). Unfortunately, due to political problems during WWI, Ihering was forced to leave both the museum and the country, and ended up selling his collection to European museums. In the early twentieth century, a pioneering initiative by local researchers attempted to catalog bivalves.

Among them, we can mention Formica-Corsi (1900) who looked at Uruguayan bivalves, as well as Morretes (1949, 1953) who worked with the mollusks from Brazil. Ortmann (1921) was the first researcher to include anatomical traits of the soft parts of adults and the glochidia larvae in the descriptions of his species. He proposed the first studies on phylogenetic relationships among Unionoida. However, his studies were not given the right recognition by his future fellow scholars.

Many Unionoida and Veneroida species were described for hydrographic basins located in Patagonia, Venezuela, Colombia, and Uruguay by Pilsbry (1896, 1897) and Marshall (1916, 1922, 1924, 1927a, b, 1928, 1930). Many new species were described (Baker, 1914, 1930) after conducting North American expeditions in the Amazon region, Brazil, and Venezuela. The 433 species of Unionoida described from South America were reduced by Haas (1930, 1931a, b, 1969) to 124, based primarily on shell characteristics. He mentioned 70 species and subspecies of Hyriidae and 54 Mycetopodidae.

With Argentino Bonetto and his team from Argentina, a new period (from ~1960 to present) pioneered by South American morphologists and taxonomists began. A series of morphological and taxonomic studies were published including the description of many species of glochidia and lasidia of South American freshwater bivalves (Bonetto, 1961a, b, 1962, 1963, 1964, 1965, 1966, 1967a, b, 1972, 1997); Bonetto & Ezcurra-de-Drago, 1966; Bonetto et al., 1986).

At the end of the last century, malacology was consolidated in many South American universities, mainly Argentina, Brazil, Chile, Uruguay, and in other research institutions like: Instituto Miguel Lillo at Tucuman and Instituto Nacional de Limnología at Santa Fé (both in Argentina), Plataforma de Investigación en Ecohidrología y Ecohidráulica at Santiago (Chile), Museo Nacional de Historia Natural de Montevideo (Uruguay), and Fundação Zoobotânica do Rio Grande do Sul at Porto Alegre (Brazil). From there, the study of freshwater bivalve became more consolidated resulting in several important scientific publications (Olazarri, 1963, 1966, 1975; Mansur, 1970, 1972, 1974, 1999; Veitenheimer, 1973a, b; Hebling & Penteado, 1974; Mansur & Veitenheimer, 1975; Hebling, 1976; Veitenheimer & Mansur, 1978a, b; Mansur &

Veitenheimer-Mendes, 1979; Alvarenga & Ricci, 1979a, b, 1989; Mansur & Anflor, 1981; Mansur et al., 1987, 1988, 1991, 1994; Mansur & Garces, 1988; Mansur & Campos-Velho, 1990, 2000; Mansur & Silva, 1990, 1999; Ricci et al., 1990; Mansur & Valer, 1992; Simone, 1994, 1997, 1999, 2006; Mansur & Olazarri, 1995; Avelar & Mendonça, 1998; Serrano et al., 1998; Pereira et al., 2000, 2011, 2012; Callil & Mansur, 2002, 2005, 2007; Mansur & Pereira, 2006; Scarabino & Mansur, 2007; Mansur & Pimpão, 2008; Pimpão et al., 2008, 2012; Lasso et al., 2009; Pimpão & Mansur, 2009). Chilean researchers carried out multiple studies on *Diplodon chilensis* documenting its ecology (Lara & Parada, 1991, 2009; Lara & Moreno, 1995; Lara et al., 2002a, b; Grandón et al., 2008), taxonomy (Parada & Peredo, 2002), morphology (Parada et al., 1989a; Valdovinos & Pedreros, 2007), reproduction (Peredo & Parada, 1984, 1986, Parada et al., 1987, 1990; Peredo et al., 1990), life history (Parada et al., 1989b, Parada & Peredo, 1994), genetics (Jara-Seguel et al., 2000; Peredo et al., 2003), distribution (Lara & Parada, 1988, 2008; Parada et al., 2007), and relocation (Parada & Peredo, 2005; Peredo et al., 2005). This intensive effort propelled *D. chilensis* as the best known species of Hyriidae in the continent.

Considering the order Veneroida, Spix (1827), Orbigny (1835, 1846), Anton (1837), Baker (1930), Clessin (1879, 1888), Josseaume (1889), Pilsbry (1897, 1911), described the first species of Sphaeriidae from South America. Later, South American researchers described and cataloged several species for that continent: Doello-Jurado (1921), Meier-Brook (1967), Ituarte (1989, 1994a, 1995, 1996, 1999, 2000, 2001, 2004, 2005, 2007), Ituarte & Mansur (1993), Ituarte & Korniushin (2006), Klappenbach (1962), Mansur & Meier-Brook, (2000), and Mansur et al. (2008).

Parodiz & Hennings (1965) reviewed the 30 species of Corbiculidae described for the Paraná/Paraguay and Uruguay basins. The authors concluded that only *Cyanocyclas* (= *Necorbicula*) *limosa* (Maton, 1811) and *Cyanocyclas paranensis* (Orbigny, 1835) would be valid species, whereas the others would be synonymized. Nevertheless, the species cited for the Amazon [*Cyanocyclas amazonica* (Prime, 1870) and *Cyanocyclas brasiliana* (Deshayes, 1854)], and more to the North of South America [*Cyanocyclas bavayi* (Ancey, 1880); *Cyanocyclas cuneata* (Jonas, 1844); *Cyanocyclas rotunda* (Prime, 1860) and *Cyanocyclas surinamica* (Clessin, 1879)] need revision. Later, Ituarte (1994b) presented important publications that provided diagnostic morphological and reproductive data of invasive species *Corbicula fluminea* (Müller, 1774) and *Corbicula largillierti* (Philippi, 1884) compared to native species *C. limosa*. Martins et al. (2004)

reviewed the Corbiculidae invasive species in Southern Brazil looking at morphological and conchological characters. Two known Dreissenidae species and *Anticorbula fluviatilis* (Adams, 1860), the last placed with doubts inside Myoida, requires taxonomic revisions. Darrigran & Damborenea (2009) and Mansur et al. (2012c) compiled a series of studies on *Limnoperna fortunei* (Dunker, 1857) after the invasion in South America since 1991.

Recently, Simone (2006) has published an illustrated catalog of the continental mollusks of Brazil and neighboring countries, which cited 120 species of freshwater bivalves. Despite this massive effort, many genera and species were listed without the proper taxonomic revision. Furthermore, synonyms of different species were brought together without considering advances in the study of the larvae.

Biological characterization

In South America, there are three lineages of freshwaters Bivalvia: Mytiloida, Unionoida, and Veneroida. According to Simone (1999), the systematic definition of *A. fluviatilis* into Lyonsiidae and Myoida was used as a temporary suggestion.

Mytiloida is represented by the invasive species *L. fortunei* commonly known as golden mussel. *L. fortunei* is native from Asia, and was probably brought to South America via ballast water in 1991 (Darrigran & Pastorino, 1995; Mansur et al., 2003b, 2004a, b; Santos et al., 2012). With morphological characteristics similar to marine mussels (Mansur, 2012), it presents the complete larval cycle in the plankton (Mansur et al., 2012a) and after recruitment forms macroclusters. *L. fortunei* is very aggressive to the environment since it modifies the landscape, the flora, and benthic fauna as an ‘‘ecosystem engineer’’ (Darrigran & Damborenea, 2011). In built environments that use untreated water for cooling, the golden mussel causes clogging with considerable economic losses (Darrigran et al., 2007).

The Unionoida are commonly known as freshwater mussels or only mussels, without marine members. They can be found all over the world except for Antarctica. In South America, this order is represented by two families, Hyriidae and Mycetopodidae, comprising of only native species. They normally have from 2 to 10 cm in length though they can be longer, but according to Castellanos & Landoni (1990), *Mycetopoda soleniformis* (Orbigny, 1835) can reach up to 22 cm in length. They are considered to be good biological (Pereira et al., 2011) and paleoenvironment (Wesselingh, 2006) indicators. During geological time, these bivalves were the first to adapt to freshwater. Fossil record of freshwater bivalve *Anthraconauta* Pruvost, 1930, from the Carboniferous and Permian (late Paleozoic era) (Pellant, 1996), hold many similarities to the current species (Parodiz, personal communication). The unionids are very biodiverse. They have an amazing life cycle and strategies allowing survival in extreme situations, such as waterfalls, drought, and flood pulses. In the larval stage, most are temporary fish parasites. The larvae form cysts on the gills, scales, and fish fins. After 1 month, the larvae evolve to the juvenile stage breaking the cysts and falling to the substrate. This strategy helps the bivalves to overcome the problems of dispersion in upstream rivers. The South American unionoids show two basic larval types: the lasidium of Mycetopodidae, and glochidium of Hyriidae (Mansur et al., 2012a). Both the larval types are modified veligers and act as temporary ectoparasites on fish. As fish parasites, the lasidium triples in size and sends haustorium that penetrates the host tissues and remove its nutrients. The larval shell consists of a single helmet-shaped piece which involves the dorsal part of a body. This is formed by an anterior tongue-shaped ciliated lobe or a bilobated one, a central body with ventral lobes, a bilobated posterior tail with terminal hooks, and an anterior transparent adhesive organ. Depending on the species, this can be either stripshaped (genus *Monocondylaea* Orbigny, 1835), scourgeshaped (*Leila blainvilliana* Lea, 1834), or flower-shaped with a micro hook at one end, as *Anodontites* Bruguière, 1792, *Mycetopoda* Orbigny, 1835 and *Acostea rivolii* Deshayes, 1827) (Bonetto, 1997). The lasidia of other species and genera of the family, as *Mycetopodella* Marshall, 1927, *Diplodontites* Marshall, 1922, *Fossula* Lea, 1870, *Haasica* Strand, 1932, *Bartlettia* A. Adams, 1866, and *Tamsiella* Haas, 1931 are unknown.

The larval body of glochidia is protected by two valves with an edge on the ventral border, a hook and a basal callus on the internal side of the ventral edge. Internally, there is an adhesive flagellum (absent in *Castalia* Lamarck, 1819), sensory cilia, cirrus, a central adductor muscle, a very rudimentary velum, and phagocytic cells lining inside the valves. With the flagellum and hooks, the glochidium is enabled to get attached to the gills, fins, or scales of the fish that develop a cyst covering the larva. However, there are exceptions among species of the genus *Diplodon* Spix (1827). Hook and adhesive filament are absent on glochidia of the subgenus *Rhipidodonta* Morch, 1853. So the respective species are not fish parasites. Larval development until the juvenile stage is complete inside parental marsupium. In general, the glochidia of Hyriidae does not present spinules at the edges of the valves and on the base of the hook like other species of Unionoidea (Unionidae and Margaritiferidae) (Mansur et al., 2012a). Bonetto (1961b) described glochidia of several species of *Diplodon* genus. Based on morphological studies, Pimpão et al. (2012) reviewed and standardized the terminology of glochidia shells from South American Hyriidae, thus facilitating the differentiation between several species of Amazonian Basin.

The order Veneroida includes the following families: Corbiculidae, Sphaeriidae, and Dreissenidae. They are too considered to be good indicators of trophic environments (Lanzer & Schäfer, 1987). The Corbiculidae native genera are represented by *Cyanocyclas* Blainville, 1818, and *Polymesoda* Rafinesque, 1828 with pallial sinus. The invasive Corbiculidade are represented by four species of the genus *Corbicula* Mergele von Muehlfeld, 1811. The incubation of larvae is complete in *Cyanocyclas* until it reaches an advanced stage inside the marsupium, a case of euvivipary. The number of embryos is small, ranging from 25 to 45 per gill, and the release is not synchronized. Two species of *Polymesoda* occur in brackish waters in the Northern part of the continent. The pallial sinus is absent in the invasive species of Corbiculidae. Only *C. fluminea* and *C. largillierti* have their larval and life cycles known; their embryos are incubated in marsupial gills until the end of stage veliger or pediveliger, and liberated synchronously (Mansur, 2012; Mansur et al., 2012a, b).

In Sphaeriidae, species of the genera *Sphaerium* Scopoli, 1777 and *Musculium* Link, 1807 show sequential development of broods into independent marsupial brood sacs. In *Pisidium* Pfeiffer, 1821 a synchronized development in a single marsupial brood sac occurs (Cooley & O´ Foighil, 2000). An exception was observed in *Pisidium punctiferum* (Guppy, 1867) which form one brood at a time, but with different sizes of embryos which suggest unsynchronized release (Anflor & Mansur, 2001). *Eupera* Bourguignat, 1854 has the most primitive system of reproduction. Embryos have synchronized development, but there is no brood sac inside the marsupium (Cooley & O´ Foighil, 2000). The species of this genus produce delicate byssus threads that facilitate adherence to pebbles, plants, or floating aquatic vegetation. The great expansion of its excretory sac may explain its adaptation and resistance to prolonged periods of drought. Among Dreissenidae, we only know of the biology of *Mytilopsis lopesi* Alvarenga & Ricci, 1989. In this species, the embryos grow attached to the mantle in the pallial cavity until the juvenile stage, with no synchronous release (Mansur et al., 2012a). *A. fluviatilis* is known from the Amazon River in Brazil and Peru (Simone, 1999). It is a nestling bivalve that lives attached to sandy grains and litter underneath (Beasley, pers. communication). Simone (1999) described its morphology for the first time including it with doubts in Lyonsiidae (Pandoroidea). According to him, this species has been reported by various authors also in Corbulidae (Myoida), sharing some similaritie with Myidae, Hiatelloidea, and Thraciidae as well.

The purpose of this paper is to survey freshwater bivalve species from South America, to classify and rank hydrographic regions based on species richness, composition, and phylogenetic lineages in order to facilitate the identification of region-specific conservation needs of this highly threatened fauna.

Compilation of species records and analysis

South America, with an area of 17,819.100 km^2, represents 12% of the world land area and is home to 6% of the world population. It has several major river systems such as the Amazon, Orinoco, Parana, and La Plata River basins, with a total drainage area of 9,583.000 km^2. Both these systems and other smaller ones show areas of endemism, diversity hotspots, and unique landscapes.

Data on the occurrence of bivalve species in hydrographic regions in South America (Fig. 1; Table 1) were compiled from the scientific literature and examinations of the following scientific collections: Academy of Natural Sciences of Philadelphia (ANSP; Philadelphia, USA); Carnegie Museum of Natural History (CM; Pittsburgh, USA); Coleção de Moluscos da Universidade do Estado do Rio do Janeiro (UERJ; Rio de Janeiro, Brazil); Coleção de Moluscos da Universidade Federal do Mato Grosso (UFMT; Cuiabá, Brazil); Fundación Miguel Lillo (FML; Tucumán, Argentina); Instituto Nacional de Pesquisas da Amazônia (INPA; Manaus, Brazil); Musée d'Histoire Naturelle Bâle (MHNB; Basel, Switzerland); Musée de Zoologie (ZML; Lausanne, Switzerland); Musée d'Histoire Naturelle de la Ville de Genève (MHNG; Geneva, Switzerland); Museo Argentino de Ciencias Naturales Bernadino Rivadávia (MACN; Buenos Aires, Argentina); Museo de La Plata (MLP; La Plata, Argentina); Museo Nacional de Historia Natural de Chile (MNHNC; Santiago, Chile); Museo Nacional de Historia Natural de Montevideo (MNHM; Montevideo, Uruguay); Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP; Porto Alegre, Brazil); Museu de Ciências Naturais Fundação Zoobotânica do Rio Grande do Sul (MCN; Porto Alegre, Brazil); Museu de Zoologia da UNISINOS (MZU; São Leopoldo, Brazil); Museu de Zoologia da Universidade de São Paulo (MZUSP; São Paulo, Brazil); Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ; Rio de Janeiro, Brazil); Museu Paraense Emilio Goeldi (MPEG; Belém, Brazil); Museum für Naturkunde (ZMB; Berlin, Germany); Museum National d'Histoire Naturelle

(MNHN; Paris, France); National Museum of Natural History, Smithsonian Institution (USNM; Washington D.C., USA); Natural History Museum of United Kingdom (NHMUK; London, United Kingdom); Naturhistorisches Museum (NMW; Wien, Austria); Senckenberg Forschungsinstitut und Naturmuseum (SMF; Frankfurt a.M., Germany); Staatliches Museum für Naturkunde (SMNS; Stuttgart, Germany); and Zoologische Sta- atssammlung München (ZSM; Munich, Germany). Part of the data on the occurrence of species in Peru, Ecuador, and Colombia were extracted from Mussel Project (mussel-project.uwsp.edu/). All records of species (presence or absence) were tabulated for each country according to the main hydrographic regions.

In order to recognize the phylogenetic composition of Bivalvia in the main hydrographic regions in South America (Fig. 1; Table 1), the following phylogenetic relationships were looked at (Mytilidae ((Hyriidae + Mycetopodidae) (((Sphaeriidae + Corbiculidae) Dreissenidae) Anticorbula fluviatilis))))) and supported by the molecular and morphological analyses according to Walker et al. (2006) and Giribet & Wheeler (2002).

A pairwise phylogenetic distance matrix (DP) for the presence or absence of bivalve species in hydrographic regions included in the dataset was generated using Mesquite software (available at http://mesquiteproject. org/mesquite/mesquite.html). Hence, tree branch lengths were fixed to 1.0, as clade age estimates for bivalves were not available, and patristic distances between species were computed. The phylogenetic composition of each hydrographic regions was addressed using the phylogenetic fuzzy-weighting method developed by Pillar & Duarte (2010), and implemented in the software SYNCSA v. 2.5.22 (Debastiani & Pillar, 2012, available at http://www.cran.org). Pairwise phylogenetic distances in D_P were transformed into a phylogenetic similarity matrix ($S_P = 1 - D_P$). Then, phylogenetic similarities in S_P were used to weigh species composition in hydrographic regions, using a fuzzy set algorithm (see Pillar & Duarte, 2010 for details). This procedure generates a matrix describing the phylogeny-weighted species composition for each hydrographic region in South America in the dataset. That is, the presence of each species *i* in a given hydrographic region is shared with each species *j* occurring in the array of hydrographic regions, taking into account the phylogenetic similarity between *i* and *j*. Accordingly, those species *j* that are more phylogenetically related to *i* (e.g., from the same genus) will receive a proportionally higher fraction of the presence of *i* in those hydrographic regions than more phylogenetically distant species (e.g., from a different family), which will receive a proportionally lower fraction, and so on. Note that the sum of species presences (i.e., species richness) in each hydrographic region will remain exactly the same after phylogenetic fuzzy-weighting. After defining a multivariate matrix describing phylogenetic composition of hydrographic regions, we conducted a principal coordinates analysis (Gower, 1966; Legendre & Legendre, 1998) on that matrix to generate principal coordinates of phylogenetic structure (PCPS) for each hydrographic regions (Duarte, 2011; Duarte et al., 2012). This analysis was conducted on square-rooted Bray-Curtis dissimilarities between hydrographic regions. Then, we plotted the two first PCPS in a scatter plot to evaluate the association between the hydrographic regions and major bivalve lineages. PCPS analysis was conducted using the PCO statistical software (by M. Anderson, available at http:// www.stat.auckland.ac.nz/*mja/Programs.htm). The Mantel test was used to assess the possible relationship of the distribution of invasive species with species richness in hydrographic regions. The test verified the possible correlation between two arrays: presence and absence of *L. fortunei* or *Corbicula* species (obtained from *Jaccard* index) and richness species of freshwater bivalves (chord distance).

Species richness and distribution

Based on the survey of presence and absence, 168 native limnic bivalves and 5 invasive species were recorded for the 52 hydrographic regions of 12 South American countries, and one territory (Table 2).

Hyriidae (36.42%) accounts for the highest percentage of species, followed by Mycetopodidae (27.75%) and Sphaeriidae (24.86%), Corbiculidae (8.09%), Dreissenidae (1.73%), and Mytilidae and Lyonsiidae (0.58%). The Unionoida represents 64.18% of the species richness of freshwater bivalves in South America while Veneroida 35.26% and Mytilioida 0.58%.

The country that has the highest species richness is Brazil (117 species), followed by Argentina (60), Venezuela (49), and Uruguay (46) (Table 2). Hydrographic regions with the greatest species richness (Fig. 2) are in Brazil followed by Argentina and Uruguay, Venezuela and Peru. In Brazil, the richest hydrographic regions are in the South and Southeast Atlantic, Uruguay, Paraguay, and Amazon Rivers (> 40 species). In Uruguay, the continuation of the Uruguay River basin presents the greatest wealth, followed by the basin of the La Plata River. In Argentina, the Uruguay River and the rivers of Paranoplatense System are the richest in species. Further North of this continent, the Orinoco River in Venezuela and Amazon River, in Peru are quite relevant. In rivers, generally there is a greater species richness in the middle and lower zones (Mansur & Pereira, 2006; Pereira et al., 2011), where the primary production is higher. Moreover, in these areas, a floodplain with oxbow lakes containing many species of bivalves (Colle & Callil, 2012) is very common. Very low richness is probably related to small Pacific drainages, to arid domains from the Andes, to the semiarid at Brazilian Northeast Atlantic or salty endorheic systems in Argentina (Fig. 2).

Only 43 native species occur in more than 10% of the hydrographic regions inventoried, while the other species occur in only 5 of 131 hydrographic regions inventoried (10%) (Fig. 3). It means that there is an expressive and large zone of endemisms forming mosaics with different richness levels and taxocenosis compositions. *Anodontites* (*A*). *trapesialis* (Lamarck,1819) and *C. fluminea* are widely distributed in South American hydrographic regions. The respective frequency of occurrence figures for these species in the basins analyzed are 59.6 and 53.8%. The following species should also be mentioned: *M. siliquosa* (Spix, 1827) (44.2%); *Anodontites* (*A*). *elongatus* (Swainson, 1823); *Anodontites* (*A*). *trapezeus* (Spix, 1827) and *C. largillierti* (32.7%); *Anodontites* (*A*). *patagonicus* (Lamarck, 1819) (28.8%); *Anodontites* (*L*). *ensiformes* (Spix, 1827) (26.9%); *L. fortunei* (25.7%); *Anodontites* (*A*). *crispatus* Bruguie`re, 1792; *Anodontites* (*A*). *tenebricosus* (Lea, 1834) and *Pisidium sterkianum* Pilsbry, 1897 (25.0%); *M. soleniformis* and *Castalia ambigua* Lamarck, 1819 (21.1%).

A. *trapesialis* is widely spread in hydrographic regions of the South America, occurring in sandy/ muddy or muddy only sediment, with deposits of silt and clay, in regions of lower water velocity as side channels or in marginal lakes, where it finds food (phytoplankton) in abundance (Bonetto & Di Persia, 1975; Hebling, 1976; Simone, 1994; Pereira et al., 2011; Colle & Callil, 2012). The species had dispersed further due to fish farming. The lasidia of this species appear not to show specificity with hosts (Callil et al., 2012), facilitating the dispersion in the fish farms, causing damage on fish production (Guardia-Felipi & Silva-Souza, 2008). *C. fluminea*, which has been reported in South America since the 70s has invaded all the large basins of the continent from Colombia to the North of Patagonia where it became quickly dominant (Santos et al., 2012). *M. siliquosa* is not abundant but present in most of the South American basins living in small aggregate populations that prefer compacted substrate of marginal areas. *A*. (*A*). *elongatus* is present in many basins from the North at the Magdalena, Orinoco, and Amazon basins to the South in the Uruguay River. It usually occurs together with *A*. (*A*). *trapesialis* and *Castalia* spp. sharing the same habitat in areas of marginal lakes and side channels, especially in the region of the Pantanal on the upper Paraguay River (Colle & Callil, 2012). *A*. (*A*). *trapezeus* is very common in the basins of the Eastern and Southern Atlantic, Paraná, Paraguay, and

Uruguay, and is rare in Tocantins, Amazonas, and Orinoco.

The distribution of two *Corbicula* species does show no significant (P = 0.01) correlation with species richness in the different hydrographic regions in South America: *C. fluminea* (r = 0.11; P = 0.012) and *C. fluminalis* (r = 0.07; P = 0.31). However, *C. largillierti* demonstrates significant and poor positive correlation (r = 0.32; P = 0.0001) with species richness. *C. largillierti* was the first species of the genus to invade South America through the La Plata River. Subsequently, *C. largillierti* decreased in density and distribution after the arrival of another invasive species, *C. fluminea*. *A*. (*A*). *patagonicus* is very common in the Southern American hydrographic regions as Paraná, Uruguay, and South Atlantic River basins. *A.* (*L.*) *ensiformis* is common in the middle Paraná in Argentina, in Paraguay River of Brazil and Paraguay and in a small part of middle Uruguay River bordering Argentina and Brazil. Northwards, it is observed in the Madeira River in Bolivia, in the Amazon, Tocantins, and Orinoco basins. Like *M. siliquosa*, it lives in small populations on muddy river margins.

The distribution of *L. fortunei* does show no significant correlation (r = 0.02; P = 0.69) with species richness in different hydrographic regions in South America. After the first record of *L. fortunei* in the La Plata River near Buenos Aires, the species was rapidly dispersed with the help of the boats that flow through waterways of the Uruguay, Paraná, and Paraguay rivers invading Argentina, Brazil, Uruguay, Paraguay, and Bolivia. So far it has not been reported in the Amazon River Basin despite the proximity. It has been recorded in the upper Paraná River, downstream of the dam of St. Simon at Paranaiba River, bordering the state of Goiás, Brazil. This region is very close to the headwaters of the Tocantins River which flows in the delta of the Amazon River (Santos et al., 2012).

A. (*A*). *crispatus* is more frequent in the basins of the Northern part of the continent, and the upper tributaries of the Paraguay river. *A.* (*A*). *tenebricosus* is very common on the lower part of the Uruguay river, where it appears in a very robust form. It also occurs in the south Atlantic drainage of Brazil but at a lower extent, and in the basins of Plata and Paraná becoming more scarce to the north. The record of this species for the Orinoco must be revised because it may have been confused with the related species *A.* (*A*). *crispatus* or *A. elongatus*.

Pisidium sterkianum is often present and abundant in sandy bottoms of lakes and lower parts of the rivers of Paraguay, Paraná, upper Paraná in Brazil, and Uruguay basins. It has also been reported for the Amazon Basin in Brazil and Bolivia.

Mycetopoda soleniformis just like the other species of this genus, lives in clusters forming small populations. It is most frequently found in the basin of the Paraná River, and much less common in the Uruguay River. As for the Amazonas River, there are records for Peru, Bolivia near the Madeira River, and in the state of Acre in Brazil. *C. ambigua* is common in large parts of the Orinoco and the Amazon Rivers even along the Andes in Peru and Ecuador, and has been reported for the Pacific basin in Ecuador. It occurs also in the rivers of Suriname and Guyana. The citations of *C. ambigua* to La Plata, Paraná and Paraguay rivers, and the lower reach of the Uruguay River must be carefully studied with the support of genetics considering the similarities to *Castalia inflata* Orbigny, 1835 which predominates in these Southern hydrographic regions. It is possible that both species could be considered as synonyms.

Endemisms can be easily observed in some species that live on stones in running waters like: *A. rivolii* (Magdalena River at Colombia), *Bartlettia stefanensis* (Moricand, 1856) (High Amazon and Paraguay rivers), *Byssanodonta* (Ihering, 1893) (Middle Paraná River), and *M. lopesi* (lower part of Amazon and Tocantins rivers). *Triplodon*, *Paxyodon* Schumacher, 1817 and *Prisodon* Schumacher, 1817 only appear in the Amazon and Orinoco rivers. *H. balzani* lives in very restricted areas of the Paraguay River that present calcareous water. Endemisms are even more evident among Sphaeriidae. *Eupera iguazuensis* Ituarte, 1989 is restricted to Iguazú falls (area bordering Brazil and Argentina) and *Pisidium pipoensis* Ituarte, 2000 found only in the region of Missiones (Argentina). In the region of Patagonia in Argentina and Chile, there are many proper species of *Pisidium* and at Lake Titicaca (area bordering between Peru and Bolivia) some endemic species of *Sphaerium* can be found.

Regarding *Dreissenidae*, the native *M. lopesi*, from the lower part of the Amazon River and Tocantins/ Araguaia Rivers is adapted to freshwater forming small and low clusters on submerged rocks (Alvarenga & Ricci, 1989). Embryos and larvae develop outside the gills, inside the pallial cavity, fixed to the mantle of parental individuals, and are released as they are young (Mansur, 2012). They differ considerably from estuarine dreissenids as *Mytilopsis sallei* (Recluz, 1849) and *Mytilopsis leucophaeata* (Conrad, 1831) with planktotrophic larvae. Both species are from North America: the former was detected in Venezuela and the latter has been most recently collected in the mangroves of Recife (Souza et al., 2005). *A. fluviatilis* is an endemic species of Amazonas River occurring from Peru to river mouth on the main channel (Simone, 1999, 2006).

Phylogenetic composition and origin of the hydrographic regions

The principal coordinate's analysis for phylogeny-weighted species composition generated 51 PCPS. The first two PCPS contained, respectively, 53.6 and 33.8% of the total variation in the phylogenetic composition matrix. The ordination scatter plot (Fig. 4) shows that the first PCPS was positively related to hydrographic regions characterized by the predominant occurrence of Veneroida + *A. fluviatilis*, and negatively related to predominant occurrence of Mycetopodidae and Hyriidae. On the other hand, the second PCPS split hydrographic regions characterized by predominant occurrence of Hyriidae (positive values) and Mycetopodidae (negative values).

The Veneroida had higher species richness in the hydrographic regions located in the Andes Mountains on the far Southwest, and coastal areas of the continent. This order is represented basically by several species of *Pisidium* genus concentrated mainly in Andean area. These are cooler regions, where rivers are born in mountainous areas. These are very similar environments to the frozen rivers of the Paleartic Region, where many species of *Pisidium* are sympatric. However, the species of *Pisidium* are rarely sympatric in South America and show a great variation within populations (Kuiper, 1983). In streams and lakes of the Andean highlands, they are more numerous and concentrated (Kuiper & Hinz, 1984; Ituarte, 2007). Species of *Sphaerium*, are practically only present in the Andean highlands. An exception is *Sphaerium* cambaraense Mansur et al., 2008, which occurs in the highlands (above 800 m) in Southern Brazil at the *Araucaria angustifolia* forest (Mansur et al., 2008). Fitkau (1981) mentioned that the Amazon does not have habitats suitable for the occurrence of Sphaeriidae except for E. simoni, which is adapted to the fluctuations of the water level and long drought periods. In the coastal environment of Northern Brazil and Venezuela, species of *Cyanocyclas* and *Polymesoda* genus are predominant.

Parodiz & Bonetto (1963) presented distribution maps of Hyriidae and Mycetopodiade in South America which coincide with the distribution of species observed in this study. Some species of Hyriidae and Mycetopodidae have also been reported in rivers located in mountainous areas which are not so elevated like Andes area. *D. chilensis* is the only species of Unionoida inhabiting Andine Rivers and lakes in the Patagonian region found in Chile, Argentina, and Peru. This is the most frequent species in lakes near the cities of Temuco, Valdivia, and Puerto Montt at Chile (Parada & Peredo, 2002; Parada et al., 2007).

A. (*A*). *tenebricosus*, *B. stefanensis*, and *A. rivoli* are typical waterfall species. However, the highest richness of Mycetopodidae and Hyriidae is to be found in lowland rivers, oxbow lakes,

lakes, and costal lakes. Very inflated species, such as *Castalia inflata*, float over the mud of river margins and lakes. The elongated forms like *Mycetopoda*, *Mycetopodella falcata* (Higgins, 1868), *A.* (*L*). *ensiformis* bury themselves in the compacted substrate of wet river banks.

To understand the patterns of distribution of species, it is necessary to know the geological events that gave rise to the current configuration of the landscape and hydrographic regions in South America. According to Leal (2011), during the breakup of the Gondwana Paleocontinent in the Mesozoic (Cretaceous period, ~100 Ma), the main drainage of the South American plate was directed to the West. This pattern changed due to geotectonic episodes like: separation of South America from Africa with the opening of the South Atlantic Ocean, the Andean uplift, and the closure of the Panamanian Isthmus. Since the upper Mesozoic era (83–67 Ma), three separate large river basins were present, two located at the current Amazon River Basin (one part which flowed East and another West), and another drainage which flowed South and originated the Paraná–Paraguay river system.

According to Hubert & Renno (2006), successive geological events determined the genesis of the current South American basins in the Cenozoic era (Tertiary period) as follows: (1) 15 and 10 Ma: the last event of great marine incursion, before the final establishment of the Amazon, previously dated between and was postulated to lead to a 150-m marine highstand forming a big sea called Pebas. At least one continental sea, the Paranean Sea between Southern Brazil and Northern Argentina, was formed. The Magdalena basin was isolated after the uplift of the Northwestern Andes changing the direction of river flow to the west; (2) 10 and 8 Ma: marine regressions and Andean foreland dynamics are associated with the final establishment of the Amazon basin. The Paraná–Paraguay split from the protoAmazon at 10 Ma; (3) 8 and 5 Ma: separation of the Orinoco occurred on the Vaupes arch. The modern course of Amazon River appeared with the final uplift of the central Andean cordillera related to the rise of the Purus arch. The Maracaibo Lake was formed after the final uplift of the Northwestern Andes. The Upper Amazon was isolated from the remainders of the Orinoco and Paraná rivers; and (4) 4 Ma: after marine regressions and Andean dynamics, the Upper Amazon was fragmented. The formation of the Pebas sea got several rivers isolated and consequently got their populations of freshwater bivalves isolated, too. According to Wesselingh (2006), the Western Amazonian became a mosaic of lakes, swamps, and meander belts splitting the mains river in different subsystems. According to Wares & Turner (2003), the freshwater habitats are typically connected in a hierarchical, fractal geometric fashion with low-order streams draining into larger streams and rivers. This physical configuration offers a great diversity of habitats for freshwater clams. According to the same authors, ‘‘the patchy nature of freshwater habitats, may in some respects account for the high species diversity encountered there considering that opportunity for geographic isolation (and presumably alopatric speciation) is greater than in marine habitats’’. The compartmentation of hydrographic regions in South American basins promoted different ways to diversification of both invertebrate and vertebrate fauna like fishes, and this fact is closely associated with hydrogeological history of the continent (Hubert & Renno, 2006). For million years in the Mioceno, there was also probably sufficient time for diversification of freshwater bivalves. By virtue of the formation of Pebas, the Andean uplift and erosion changed the fluvial landscapes of South America again resulting in more intensive diversification of freshwater bivalves. Events similar to the formation of Pebas occured in the Southern part of the continent in the Paraná–Paraguay with formation of Paranean Sea. Events like these probably promoted the fauna diversification in water courses as Rivers of the South and Southeast Atlantic, and coastal lakes. Lanzer (2001) verified that the distribution of freshwater clams in lake systems of the coast of Rio Grande do Sul, in Southern Brazil, is related to the genesis of those systems that resulted from the processes of marine transgressions and regressions.

In addition to the geological events, other factors are important for the distribution of bivalves. Freshwater clams cited for South America can also be scattered across the stomach contents of fish, but are limited to the distribution areas of these vectors. They can also be transported over long distances by birds, crossing geographical barriers. These birds eat large bivalves, but normally they break the shell eating only the soft part. However, smaller bivalves can remain unscattered through the gut, mainly Corbiculidae, and Mytilidade, or transported fixed on feathers, mainly Corbiculidae and Sphaeriidae.

Knowledge gaps

The lack of basic knowledge on freshwater clams is a reality that hinders the categorization of species conservation status in South America. This paucity is in part due to the lack of organized and representative collections of the freshwater bivalves species of the main hydrographic regions in South America, difficulties in obtaining type material or respective good illustrations, lack of identification keys and publications on the reproduction, ecology, morphology, and on the affinity of the species with the host fish of gloquidia and lasidia, besides the scarcity of limnological institutions or biological stations dealing with mussels. Many hydrographic regions are underrepresented in scientific collections, especially those located in the Northern part of the continent.

By comparing the study of freshwater bivalves in South America with the one developed in other continents, especially Europe and North America, we can see that in the period of the early naturalists (Haag, 2012), the difficulties encountered there, such as the scarcity of morphological data and the lack of sampling locality of the species, were similar to ours. But in South America, we have aggravating circumstances that type material and additional collections were donated or sold to museums in Europe or North America. In the subsequent periods, the first museums and scientific collections were formed in the countries of the Northern hemisphere. At that time, studies on mussels compared morphologies, ecology, and phylogeny saw a period of major development (Haag, 2012). In South America, the studies leave something to be desired by the lack of comparative material, and again, important collections as the one from Ihering were still sold to Europe. Ortmann (1921), who started and strongly encouraged malacology and mussel ecology in North America (Haag, 2012), did not collect in our watersheds. He described relatively few species from some basins, mainly those mussels collected by his colleague Ichthyologist J. D. Hasemann, with their testimonies reported at the Carnegie Museum, Pittsburgh, again outside South America.

In recent decades, genetic studies have shed light on the phylogenetic and evolutionary relationships inside Unionoida. However, the presence of unionoidean doubly uniparental inheritance of mtDNA (DUI) make evolutionary interpretations difficult mainly by the South American Hyriidae that are scarcely evaluated. Genetic studies are also necessary in order to differentiate similar or cryptic species of Mycetopodidae as, *Anodontites* (*A.*) *iheringi* (Clessin, 1882), and *Anodontites ferrarisii* (Orbigny, 1835); *A. tenebricosus* and *A. soleniformis*; and of Hyriidae as, *D. granosus* and *D. multistriatus*; *C. ambigua*, and *C. inflata*. Many species are morphologically unknown and rare in scientific collections like, *Anodontites* (*A.*) *aroanus* Baker, 1930; *Anodontites (A.) carinatus* (Dunker, 1858); *Anodontites* (*A.*) *colombienses* Marshall, 1922; *Anodontites* (*A.*) *guanarensis* Marshall, 1927; *Anodontites* (*A.*) *puelchanus Orbigny*, 1835; *Monocondylaea costulata* (Moricand, 1858); *Monocondylaea franciscana* (Moricand, 1837); *Monocondylaea guarayana* (Orbigny, 1835); *Tamsiella amazonica* Bonetto, 1972 and, *Tamsiella schroeteriana* (Lea, 1852). It would be necessary to conduct new expeditions in the type localities in order to obtain topotypes to support the redescription of these species.

Many species of *Diplodon* genus cited for the basins of the Eastern Atlantic, Upper Paraná River, and North and Northeast Atlantic are hardly differentiated. Until now, the diagnostic criteria are not well established, thus requiring adequate morphological studies for the recognition of their taxonomic status: *Diplodon* (*D.*) *caipira* (Ihering, 1893); *Diplodon* (*D.*) *expansus* (Kuester, 1856); *Diplodon* (*D.*) *ellipticus* (Spix, 1827); *Diplodon* (*R.*) funebralis (Lea, 1860); *Diplodon* (*D.*) *multistriatus* (Lea, 1831); *Diplodon* (*D.*) *granosus* (Bruguie`re, 1792); *Diplodon* (*D.*) *paulista* (Ihering, 1893), and *Diplodon* (*D.*) *rhombeus* (Spix, 1827). In addition, *Diplodon* (*D.*) imitator Ortmann, 1921 was described from the Jacuí River in the South Atlantic Basin; however, it has not been found ever since. Some species of genus *Diplodon* were not yet framed within subgenera due to lack of knowledge of glochidia morphology (Table 2).

The species, *C. ambigua*, *C. inflata*, *Castalia quadrata* Sowerby, 1869, *Castalia schombergiana* Sowerby, 1869 and *Castalia sulcata* (Krauss, 1849) show a wide morphological variation, with a particular shape of the shell for each different basin, which also hampers the recognition of these species by nonspecialists. The internal anatomy is unknown for the most part of the species and the glochidium is not a good intraspecific character in this genus.

Prisodon obliquus Schumacher, 1817 and *Paxyodon syrmatophorus* (Gmelin, 1791) are very similar species with winged hinge, no umbonal sculpture and the same color and periostracum brightness. The upper Amazon River sees a predominance of *P. obliquus*, whereas in the low Amazon River, *P. syrmatophorus* prevails. However, intermediate forms occur in sympatry in some parts of the lower Amazon River. Therefore, questions remain to be answered about the identity of both species, raising suspicions of the existence of only one species with a wide morphological variation along the basin. Pimpão et al. (2012) observed that the glochidia of both species are also very similar.

All species of the genus *Cyanocyclas* should be reviewed. Mainly species of northern part of the continent and *C. limosa*, which shows a wide morphological variation and may represent a large number of species.

Considering Sphaeriidae in the Southern hemisphere, Kuiper (1983) emphasizes the fact that the paucity of species with conspicuous interpopulational variation in the same environment is regarded as a rule. This morphological variation makes difficult the definition of diagnostic criteria and consequently the species recognition. The species of the *Pisidium* genus cited for Argentina, Bolivia, Chile, Peru, and Uruguay were reviewed by Ituarte (2007), and all other hydrographic regions in South America require similar revisions and more collections.

Considering the above mentioned amount of gaps of knowledge, we can recognise that *D. chilensis* is one exception and probably the best known species of Hyriidae in the continent.

Risks for the biodiversity of freshwater bivalves

The main threats to the conservation of freshwater bivalves are related to habitat destruction, water pollution, and the invasion of exotic bivalves (Mansur et al., 2003a; Machado et al., 2008; Pereira et al., 2012). Among the causes of habitat destruction, we can highlight the deforestation of riparian vegetation, damming and channeling rivers, wetland drainage, siltation of rivers and lakes, sand mining, etc. The bivalves are filter feeders that have little or no mobility in adulthood. As a consequence, they are very sensitive to changes in river flow, sediment grain size, water level, slope and shading on the margins. The destruction of the terrestrial environments entails drastic consequences to hydrographic regions. Until today, the practice of burning forests and savannah environments are common in many South American countries and territories despite the restrictions imposed by environmental agencies sponsored by the government. This practice disrupts the soil, facilitating erosion and siltation. Thus, all processes that modify and destroy the vegetation cover also have a negative impact on hydrographic regions, affecting the assemblage of bivalves.

Miyahira et al. (2012a, b) made some comments on the habitat degradation and their effects on freshwater mussels in the state of Rio de Janeiro. Water pollution is an important factor in the population decline of native bivalves. The high organic contamination decreases the oxygen dissolved in the water, keeping these mollusk from surviving. Contamination from industrial effluents and solid waste generates metals that are incorporated by the bivalves and accumulated in the food chain. The agricultural activity also impacts on this fauna which is poisoned by pesticides.

In South America, the main source of energy is provided by hydroelectric plants. In Brazil, the construction of reservoirs to meet the energy demands required for the accelerated development of this country is encouraged by the government. However, when it comes to mollusks, the terms of reference that guide the implementation of the environmental studies for licensing ventures require only a survey of the snails vector of zoonosis. In addition to that, the construction of dams causes environmental changes in making a river into a lake. This fact changes the patterns of connectivity of the wet drainage and affects the structure of the fish fauna (composition and abundance of fish), and their migratory routes. The majority of the Unionoida use fish as dispersal vectors. With the interruption of the migration route of host fishes, the dispersion of mollusks is compromised.

Historical data (Takeda et al., 2005; Pereira et al., 2012) revealed that the construction of 70 reservoirs in a system of waterfalls along the most populated area of Brazil, in Upper Paraná River, changed the lotic environment to lentic, favoring the colonization of the Corbiculidae invasive species and *L. fortunei*, as well as the gastropod *Melanoides tuberculata* (Müller, 1774). The river segments that allow the survival of native bivalves in their natural habitats are rare. Furthermore, the fish that dispersed bivalve larvae are unable to move upstream along rivers. Consequently, all Unionoida species reported in this area are endangered, though many of them do not appear on official red lists.

The freshwater bivalves have been adapted to drought and flood of the rivers for millions of years. With the construction of reservoirs, the natural flood pulse that occurred in the floodplains of the rivers has become artificially regulated. In many of those rivers, the overflow of the channel during the rainy season is stopped, so there is no more communication with floodplain lakes. This change in water dynamics of rivers impacts the life cycle of bivalves that depend on fish for their dispersal. The disconnection of these environments limits the lasidia and glochidia dispersion through the fish.

Moreover, the bivalves can not keep up with sudden emptying of reservoirs in times of intense rainfall. Two types of impacts are known to be related to that. One occurs in the reservoir when it is quickly emptied by opening the floodgates. The water level decreases dramatically exposing the entire bank, resulting in the death of bivalves that can not keep up with the speed of emptying. The same impact can be observed in the Northeast of Brazil at the times of severe droughts, when reservoirs became empty due the absence of rains. The other impact occurs downstream the reservoir when the water is released at high speed dragging all the marginal fauna and flora, often throwing the bivalves out of the system.

The dispersion of the invasive bivalve species in several hydrographic regions of South America constitutes a threat to the conservation of native clams. The golden mussel produces byssus threads that enable the incrustation on the various types of hard substrates forming macrofouling. This structure of aggregates alter different types of substrate-forming mussel beds on sediment and between rhizomes of the *Schoenoplectus californicus* (C.A. Mey.) Palla (Cyperaceae), a kind of emergent shoreline vegetation common in South America (Santos et al., 2012). Also, it forms macroclusters over other types of free-floating and amphibious macrophytes, such as species of trees from the banks of rivers and lakes. All these habitats are modified and so is the entire benthic fauna composition. In addition to the habitat loss, the bivalves are choked by the incrustation of mussels on their shells, keeping the valves from opening, and in some cases, from closing, too. So the native bivalves can not perform filtering and become exposed to predators.

The golden mussel occurs predominantly on hard substrates, and to a lesser extent on sandy bottoms. On the other hand, the Corbiculidae invasive species occurs predominantly on sandy bottoms dominating the benthic communities. Thus, the pressure of invasive species on native clams is intense. *L. fortunei* can reach 500,000 ind.m^{-2} (Bergonci et al., 2009) and *C. fluminea* just to 5,295 ind.m^{-2} (Mansur & Garces, 1988).

L. fortunei form macrofouling on hard substrate covering great areas of rivers and lake bottoms altering the benthic fauna structure. The great density of *L. fortunei* related to the high filtration rates have an impact on the planktonic community and food chain (Darrigran & Damborenea, 2011). The macrofouling also impact the equipments of hydroelectric and thermoelectric plants. However, until now new designs for power plants do not present solutions to minimize the effects of biofouling.

Conservation strategies

Since the 1990s there has been a great effort from most South American countries for the preparation of their official lists of endangered species of their fauna. However, most of these lists include only vertebrate species. Out of the 12 South American countries and 1 territory, only 4 have published lists of endangered species of mollusks: Brazil, Colombia, Paraguay, and Uruguay. The Brazilian list of threatened fauna (Machado et al., 2008) includes the following species: *Diplodon* (*R.*) *koseritzi* (Clessin, 1888) (critically endangered, CEN); *A.* (*A.*) *ferrarisi*, *A.* (*A.*) iheringi, *D.* caipira, *D.* (*D.*) *dunkerianus*, *D. fontainianus*, *D. pfeifferi*, *D. rotundus*, *C. undosa*, *A.* (*A.*) *trapezeus*, *Fossula fossiculifera* (Orbigny, 1835), *L. blainvilliana* (endangered, EN); *A.* (*A.*) *elongatus*, A. (L.) ensiformis, *A.* (*A.*) soleniformis, *A.* (*A.*) *tenebricosus*, *A.* (*A.*) trapesialis, *M. legumen*, *M. siliquosa*, *Monocondylaea paraguayana* (Orbigny, 1835), *Leila esula* (Orbigny, 1835), *B. stefanensis*, *D.* (*D.*) *expansus* (Vulnerable, VU). The species *A.* (*A.*) *soleniformis*, *A.* (*A.*) *trapezeus*, *F. fossiculifera*, *H. balzani*, *B. stefanensis*, *D.* (*D.*) *expansus*, *C.*

inflata and *C. nehringi* were considered in the Paraguayan list (Ministerio de Agricultura y Ganaderia, 1998) in only one category defined as ‘‘endangered’’. *Polymesoda solida* (Philippi, 1946) was considered to be a vulnerable species in the threatened fauna list of Colombia (Ardila et al., 2002). The list of the IUCN (2012) includes only *D.* (*D.*) *dunkerianus* and *D. fontainianus* (endangered, EN); *Diplodon* (*D.*) *expansus*, *D. pfeifferi*, and *Castalia martensi* (Ihering, 1891) (vulnerable, VU). The National list of priority species (Scarabino & Clavijo, 2009) recognized that 93% of the species of bivalves (37) from the freshwater environments from Uruguay are priority for conservation. Later Clavijo et al. (2010) prioritized three other species for conservation.

Pereira et al. (2012) listed all species of freshwater bivalves from Brazil and their conservations status based on an official list. According to the authors, 1% of species is critically endangered, 10% are endangered, 9% are vulnerable, and 37% need a new evaluation and should be included in the revised list. Many other species need more information for the adequate determination of their conservation status. The quotation of *A.* (*A.*) *trapesialis* in the list of Brazilian threatened fauna should be revised because this species has dispersed through aquaculture systems as well as invasive species. *A.* (*A.*) *trapesialis* adapts to different environmental conditions and probably does not fit into any category of endangered species.

The lack of basic knowledge on freshwater clams is a general reality that hinders the categorization of the conservation status of the species. There are too many gaps in collection records in Northern South America. These regions are underrepresented in scientific collections; however, in better represented South regions that are many gaps, too.

For the purposes of conservation and management, Parada & Peredo (2005) and Peredo et al. (2005) made an experience with relocation of two populations of *D. chilensis* through a long-term evaluation of survival and recruitment. After 18 years, the relocated population remained at the same site. At one site, the authors did not found recruits but the individuals were greater than at the original site. At the other site, the recruitment has resulted from the dispersion of larvae by the host fish. The size of the juveniles suggested that recruitment took place in the previous reproductive season.

In Brazil, Beasley et al. (2000) studied the reproductive cycle of the harvested salmon pink mussel *P. syrmatophorus*, giving strategies for conservation and management of the species in the Tocantins River Basin, in Brazil. Later, Beasley (2001) studied the density, size frequency distribution, the habitat structure, and the impact of exploitation of these bivalves by industries of pearl buttons aiming to define management strategies. Initiatives on relocation, translocation, and repopulation of the freshwater mussels are unknown in Brazil.

There is little information on the conservation status of freshwater bivalves in Uruguay. Scarabino & Mansur (2007) listed the species of bivalves in Uruguay with the intent of supporting the conservation of this fauna. Scarabino (2004) reviewed for the first time the conservation status of Uruguayan malacofauna and highlighted the priority actions to be taken in order to conserve this fauna. Currently, there are several initiatives to improve and disseminate the knowledge base and implement conservation measures for freshwater bivalves in Uruguay (Clavijo et al., 2010). The first and only experience of relocation was held in Uruguay in 2010 based on a private initiative. As a result of this experience, a total of 133 specimens of *D.* (*R.*) *charruanus*, *D.* (*D.*) *rhuacoicus* (Orbigny, 1835), *A.* (*A.*) *trapesialis* and *A.* (*A.*) *patagonicus* ended up endangered by a dam construction were relocalized to a natural place (Clavijo et al., 2012).

The concern on bivalve conservation in Argentina begins with the implementation of database systems for the malacological scientific collections. Rumi et al. (2008) evaluated the richness of mollusk species in continental Argentina, and mapped their distribution. The authors offered subsidies for prioritizing areas for conservation.

Final considerations

The number of 111 Uninoid species places South America as a very rich continent, but not richer than North America. According to Graf & Cummings (2007), North America presents the highest diversity of mussels on Earth (~300 species). Our results came to 63 mussel species of Hyriidae and 48 Mycetopodidae, a number which is a bit higher than the figures presented by Graf & Cummings (2007) for both families (40 and 32 species, respectively) in South America.

The most diverse hydrographic regions in South America are: (1) very high richness, Amazon River, Paraguay River, Uruguay River, and Rivers of the South and Southeast Atlantic in Brazil; (2) high richness, Orinoco River in Venezuela; Paranoplatense System in Argentina; Uruguay River, La Plata River, and Negro River in Uruguay; and (3) medium richness (Amazon River in Peru, Upper Parana River in Brazil, and Paraguay River in Paraguay). These hydrographic areas are located within the two richest South American macroregions identified by Graf & Cummings (2007): Amazon–Orinoco (on the Peba System) and Paraná–Paraguay (on the Paranean System).

The hydrographic regions present distinct phylogenetic and species composition regardless of the level of richness. Therefore, not only should the richness be considered to be as a criterion for prioritizing areas for conservation, but also the phylogenetic diversity of communities engaged in services and functional aspects relevant to ecosystem maintenance.

The wide distribution of some native species can be attributed to their high tolerance to environmental factors, transposition of geographical barriers, and persistence in face of geological events in the past. Native species with wide distribution, such as *Anodontites trapesialis*, may have similar properties to invasive species, which would explain its wide distribution along to hydrographic regions and success in its current dispersion in the fish farms. However, more studies are needed on the biology of this species for us to understand their mechanisms of dispersion and whether these mechanisms are related to a certain degree of invasiveness.

Another issue to be considered is that the small number of invasive species seems not to interfere in the patterns of species composition and phylogenetic lineages in the different hydrographic regions looked at. *L. fortunei* does not contribute to the dominance of Mytilidae lineage in none of the hydrographic regions assessed with complex assemblages of native mollusks. On that line, it can be inferred from the occurrence of Corbiculidae invaders, among the Veneroida, which are widely distributed in South America, that they appear also in areas dominated by Mycetopodidae and Hyriidae. It is also to consider that the number of corbiculid invaders is much smaller than the total number of species of Veneroida recorded in the continent. However, it is important to raise awareness to the potential impact of invasive species that are dispersing by South American water courses. The golden mussel invasion may result in the reduction of the diversity of bivalve mollusks in the different addressed areas with the capacity to modify the patterns of species richness, species composition, and phylogenetic lineages. Considering this possibility, efforts should be made in order to control the dispersion and population growth of invasive species. The control of the spread of invasive species depends primarily on educational actions intended to raise awareness of boatmen, fishermen, and farmers, who use the water for irrigation; their procedures and equipment must be revised in an attempt to minimize the danger of contamination of new bodies of water.

The distribution of invasive species *L. fortunei*, *C. largillierti*, *C. fluminea*, and *C. fluminalis* is not related to species richness in the different hydrographic regions in South America. This distribution does not corroborate to the assumption that the poorest com- munities in species would be more susceptible to bioinvasion (Wolfe, 2002; Bohn et al., 2004).

However, the Andean region does not seem to be inviting to the invasion of *L. fortunei* according to Darrigran et al. (2011). The same authors identified three environmental parameters that are barriers to invasion in this region: salinity, river flow intermittence (in different sectors of Pilcomayo and Salado del Norte Rivers), and concentration of suspended sediments (in the Bermejo River and in the upper reaches of the Salado del Norte and Pilcomayo Rivers).

Detailed inventories of native bivalve fauna in different hydrographic regions are also needed, as well as the identification of habitats, with the environmental variables that govern the distribution of the species, the patterns of diversity, and the provision of deeper insights into the reproductive cycle and morphological characters which are determinants for species recognition. This is essential for the establishment of management strategies, identification of potential areas for the conservation, breeding and relocation of endangered species. The species composition and phylogenetic patterns identified in this study will contribute to the definition of priority actions for the conservation of the native mollusks fauna and the control of invasive species. They can also help to direct more studies in order to understand this diversity and to review the lists of endangered species.

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Fig. 1. Hydrographic regions in South American countries and territory. Respective codes on Table 1.

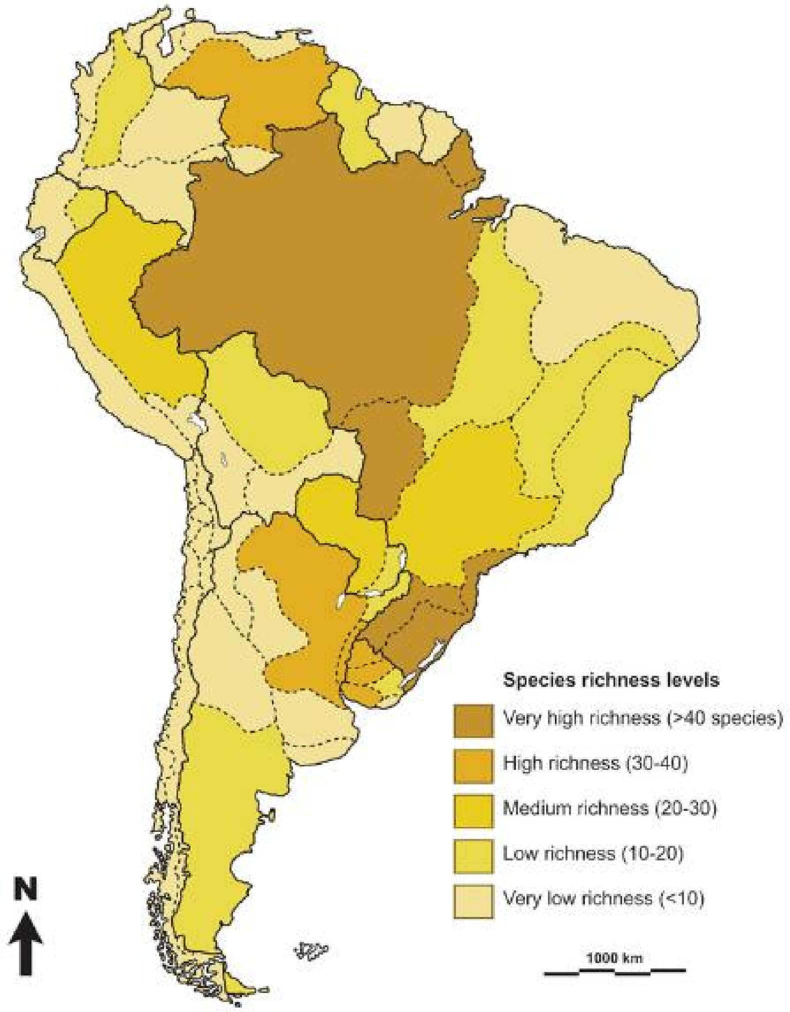

Fig. 2. Species richness (S) zonation of freshwater bivalves in the hydrographic regions in South America.

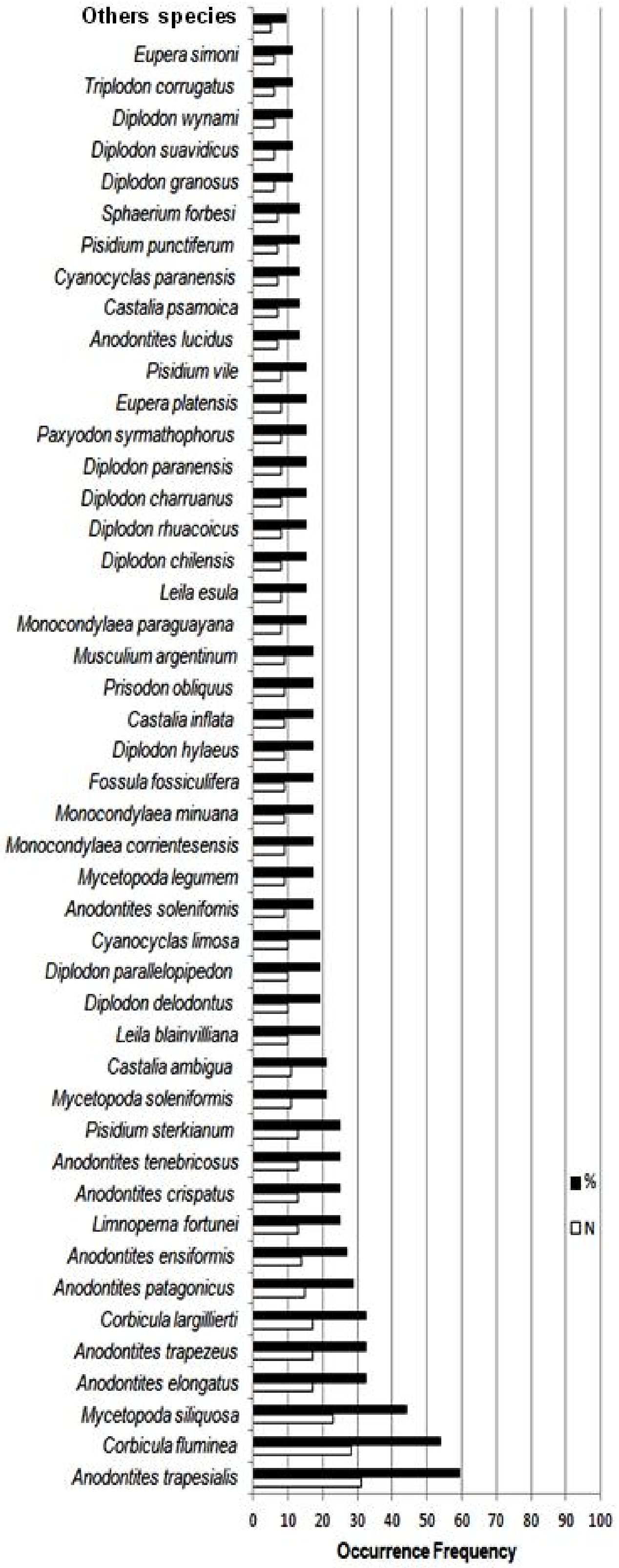

Fig. 3. Occurence frequency (N and %) of freshwater bivalves in hydrographic regions of South America.

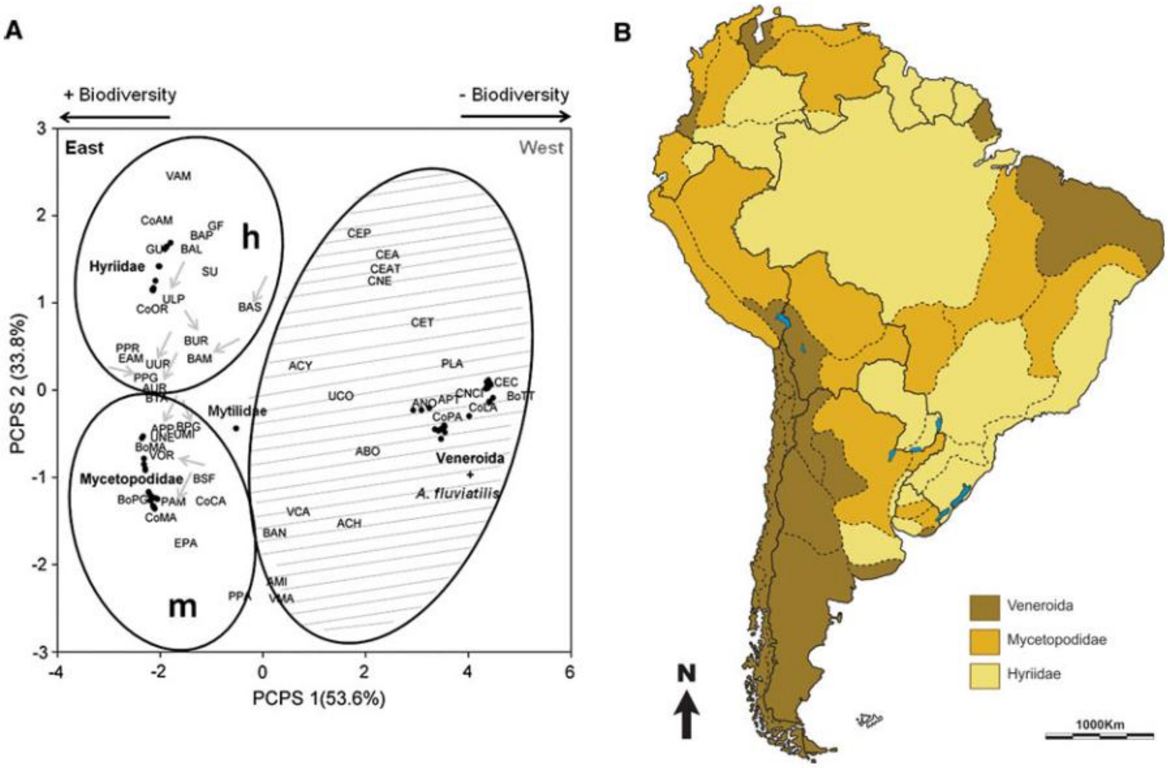

Fig. 4. Principal coordinates analysis of phylogenetic structure (PCPS) for each hydrographic regions of South America. A) Ordenation scater plot; B) phylogenetic structure of hydrographic regions. → very high richness. Mycetopodidae (m), Hyriidae (h), Veneroida (striped area).

Table 1. Hydrographic regions in South America.

Countries	Hydrographic Regions	Codes
Argentina (AR)[1]	Patagonico System	APT
	Endorreico Central System	ACH
	Cuyano Subandino System	ACY
	Bonaerense	ABO
	Paranoplatense System	APP
	Misionero System	AMI
	Uruguay River System	AUR
	Salado del Sur System	ASS
	Noa System	ANO
Brazil (BR)[2]	Amazonas River	BAM
	Tocantins/Araguaia River	BTA
	Rivers of the North and Northeast Atlantic	BAN
	São Francisco River	BSF
	Rivers of the East Atlantic	BAL
	Upper Paraná River	BAP
	Paraguay River	BPG
	Uruguay River	BUR
	Rivers of the South and Southeast Atlantic	BAS
Bolivia (BO)[3]	Madeira River	BoMA
	Titicaca Lake – Endorheic Basins	BoTT
	Paraguay River	BoPG
Chile (CH)[4]	Atlantic Exorheic Basins	CEAT
	Trans-Andean Exorheic Basins	CET
	Andean Exorheic Basins	CEA
	Pre-Andean Exorheic Basins	CEP
	Coastal Exorheic Basins	CEC
	Endorheic Basins of Alta Puna	CNE
	Endorheic Basins of Intermediate Elevations	CNCI
Colombia (CO)[5]	Rivers that flow into the Caribbean Sea	CoCA
	Magdalena River	CoMA
	Orinoco River	CoOR
	Rivers that flow into the Pacific Ocean	CoPA
	Amazon River	CoAM
Guyana (GU)[6]	Rivers that flow into the Atlantic Ocean	GUA
French Guiana (GF)[7]	Rivers that flow into the Atlantic Ocean	GFA
Ecuador (EQ)[8]	Rivers that flow into the Pacific Ocean	EPA
	Amazon River	EAM
Paraguay (PY)[9]	Paraguay River	PPG
	Paraná River	PPR
Peru (PE)[10]	Rivers that flow into the Pacific Ocean	PPA
	Andine Lakes	PLA
	Amazon River	PAM
Suriname (SU)[11]	Rivers that flow into the Atlantic Ocean	SUA
Venezuela (VE)[12]	Rivers that flow into Caribbean Sea	VCA
	Maracaibo Lake	VMA
	Orinoco River	VOR
	Amazon River	VAM

Table 1. Hydrographic regions in South America (continuation).

Countries	Hydrographic Regions	Codes
Venezuela (VE)[12]	Uruguay River	UUR
Uruguay (UY)[13]	Negro River	UNE
	La Plata River	ULP
	Mirim Lake	UMI
	Coastal Lagoons	UCO

The Hydrographic Regions were delimited and adapted according to the following sources:

[1] IADIZA - Instituto Argentino de Investigaciones de las Zonas Áridas (www.cricyt.edu.ar/ladyot/lava_carto/mapas/argentina_cuencas/index.html).

[2] ANEEL - Agência Nacional de Energia Elétrica (www.aneel.gov.br/area.cfm?id_area=104).

[3] Mondaca (2011).

[4] IGM - Instituto Geografico Militar del Chile (www.igm.cl/).

[5] IGAC - Instituto Geográfico Agustín Codazzi (www.igac.gov.co)

[6, 7, 11] Each country is one Hydrographic region considering that all rivers flow into the Atlantic Ocean.

[8] IGM - Instituto Geográfico Militar del Ecuador (www.igm.gob.ec)

[9] Paraguay Biodiversidad (www.pybio.org/)

[12] MINEM - Ministerio de Energia Y Minas del Peru (www.minem.gob.pe/minem/archivos/file/DGAAM/mapas/mapas_cuencas.htm)

[12] IGVSB - Instituto Geográfico de Venezuela Simon Bolívar (www.igvsb.gob.ve/#)

[13] IA - Instituto de Agrimensura Facultad de Ingeniería UdelaR (www.fing.edu.uy/ia/deptogeom/libro/capitulo8/hidrografia.htm)

Table 2. Freshwater bivalves species of South American Countries and territory.

Species	South American Countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
MYTILOIDA													
Mytilidae													
Limnoperna fortunei (Dunker, 1857)	1	1	1	1	1	0	0	0	0	0	0	0	0
UNIONOIDA													
Mycetopodidae													
Anodontites (*Anodontites*) *aroanus* H.B. Baker, 1930	0	0	0	0	0	0	0	0	0	0	0	0	1
Anodontites (A.) carinatus (Dunker, 1858)	0	0	0	0	0	0	1	1	1	0	0	0	1
Anodontites (*A.*) *colombiensis* Marshall, 1922	0	0	0	0	0	0	1	0	0	0	0	0	0
Anodontites (*A.*) *crispatus* Bruguière,1792	0	1	0	0	1	0	1	1	1	1	1	1	1
Anodontites (*A.*) *elongatus* (Swainson, 1823)	1	1	1	1	1	0	1	1	1	0	0	0	1
Anodontites (*A.*) *ferrarisii* (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *guanarensis* Marshall, 1927	0	0	0	0	0	0	0	0	0	0	0	0	1
Anodontites (*A.*) *iheringi* (Clessin, 1882)	0	1	0	0	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *infossus* H.B. Baker, 1930	0	0	0	0	0	0	0	0	0	0	0	0	1
Anodontites (*A.*) *irisans* Marshall, 1926	0	0	0	0	0	0	0	0	0	0	0	0	1
Anodontites (*A.*) *lucidus* (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *moricandii* (Lea, 1860)	0	1	0	0	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *obtusus* (Spix in Wagner, 1827)	0	1	0	0	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *patagonicus* (Lamarck, 1819)	1	1	1	1	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *puelchanus* (Orbigny, 1835)	1	0	0	0	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *pittieri* Marshall, 1922	0	0	0	0	0	0	0	0	0	0	0	0	1
Anodontites (*A.*) *schomburgianus* (Sowerby, 1870)	0	1	0	0	0	0	0	0	1	1	0	0	1
Anodontites (*A.*) *soleniformis* (Orbigny, 1835)	1	1	0	1	1	0	0	0	1	0	0	0	0
Anodontites (*A.*) *tenebricosus* (Lea, 1834)	1	1	1	1	1	0	0	0	1	0	0	0	1

Table 2. Freshwater bivalves species of South American Countries and territory (continuation).

Species	South American Countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Anodontites (*A.*) *tortilis* (Lea, 1852)	0	0	0	0	0	0	1	1	1	0	0	0	1
Anodontites (A.) trapesialis (Lamarck, 1819)	1	1	1	1	1	0	1	1	1	0	0	0	1
Anodontites (A.) trapezeus (Spix in Wagner, 1827)	1	1	1	1	1	0	0	0	0	0	0	0	1
Anodontites (*Lamproscapha*) *ensiformis* (Spix in Wagner, 1827)	1	1	1	1	1	0	0	1	1	1	0	0	1
Anodontites (*L.*) *falsus* (Simpson, 1900)	0	0	0	0	0	0	0	0	0	0	0	0	1
Mycetopoda legumen (Martens, 1888)	1	1	1	1	0	0	0	0	0	0	0	0	0
Mycetopoda siliquosa (Spix in Wagner 1827)	1	1	1	1	1	0	1	1	1	0	1	0	1
Mycetopoda soleniformis Orbigny, 1835	1	1	1	1	1	0	1	0	1	0	0	0	1
Mycetopodella falcata (Higgins, 1868)	0	1	0	0	0	0	1	0	1	0	0	0	0
Monocondylaea corrientesensis (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
Monocondylaea costulata (Moricand, 1858)	0	1	0	0	1	0	0	0	1	0	0	0	0
Monocondylaea franciscana (Moricand, 1837)	0	1	0	0	0	0	0	0	0	0	0	0	0
Monocondylaea guarayana (Orbigny, 1835)	0	0	0	1	1	0	0	0	0	0	0	0	0
Monocondylaea jaspidea (Hupé, 1857)	0	1	0	0	0	0	0	0	0	1	0	0	1
Monocondylaea minuana (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
Monocondylaea paraguayana (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
Monocondylaea parchappii (Orbigny, 1835)	1	1	0	0	0	0	0	0	0	0	0	0	0
Fossula fossiculifera (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
Tamsiella amazonica Bonetto, 1972	0	1	0	0	1	0	0	0	1	0	0	0	0
Tamsiella schroeteriana (Lea, 1852)	0	1	0	0	0	0	0	0	1	0	0	0	0
Tamsiella tamsiana (Dunker, 1858)	0	0	0	0	0	0	1	0	0	0	0	0	1
Diplodontites cookei Marshall, 1922	0	0	0	0	0	0	1	1	1	0	0	0	0
Diplodontites olssoni Pilsbry, 1933	0	0	0	0	0	0	1	0	0	0	0	0	0
Diplodontites pilsbryana Olsson & Wurtz, 1951	0	0	0	0	0	0	1	0	0	0	0	0	0

Table 2. Freshwater bivalves species of South American Countries and territory (continuation).

Species	South American Countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Haasica balzani (Ihering, 1893)	0	1	0	0	0	0	0	0	0	0	0	0	0
Leila blainvilliana (Lea, 1834)	1	1	1	1	0	0	0	0	0	0	0	0	0
Leila esula (Orbigny, 1835)	0	1	0	1	1	0	1	0	1	1	0	0	1
Acostaea rivolii (Deshayes, 1827)	0	0	0	0	0	0	1	0	0	0	0	0	0
Bartlettia stefanensis (Moricand, 1856)	0	1	0	1	1	0	0	1	1	0	0	0	0
Hyriidae													
Diplodon (*Australis*) *solidulus* (Philippi, 1869)	0	0	0	0	0	1	0	0	0	0	0	0	0
Diplodon (*Diplodon*) *aethiops* (Lea, 1860)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *berthae* Ortmann, 1921	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *besckeanus* (Dunker, 1848)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *caipira* (Ihering, 1893)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *chilensis* (Gray, 1828)	1	0	0	0	0	1	0	0	1	0	0	0	0
Diplodon (*D.*) *delodontus* (Lamarck, 1819)	1	1	1	1	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *dunkerianus* (Lea, 1856)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *ellipticus* Spix in Wagner, 1827	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *expansus* (Küster, 1856)	0	1	0	1	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *granosus* (Bruguière, 1792)	0	1	0	0	0	0	0	0	0	1	1	1	1
Diplodon (*D.*) *guaranianus* (Orbigny, 1835)	0	0	0	1	1	0	0	0	0	0	0	0	0
Diplodon (*D.*) *imitator* Ortmann, 1921	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *martensi* (Ihering, 1893)	0	1	0	1	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *multistriatus* (Lea, 1831)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *obsolescens* Baker, 1913	0	1	0	0	0	0	0	0	0	1	0	0	1
Diplodon (*D.*) *parallelopipedon* (Lea, 1834)	1	1	1	1	1	0	0	0	0	0	0	0	0

Table 2. Freshwater bivalves species of South American Countries and territory (continuation).

Species	South American Countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Diplodon (*D.*) *parodizi* Bonetto, 1960	1	1	0	1	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *paulista* (Ihering, 1893)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *piceus* (Lea, 1860)	0	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *rhombeus* Spix in Wagner, 1827	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *rhuacoicus* (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *suavidicus* (Lea, 1856)	0	1	0	0	0	0	1	0	0	1	0	0	1
Diplodon (*D.*) *vicarius* Ortmann, 1821	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *wymanii* (Lea, 1860)	1	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*Rhipidodonta*) *burroughianus* (Lea, 1834)	1	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *charruanus* (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *deceptus* Simpson, 1914 sensu Ortmann, 1921	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *funebralis* (Lea, 1860)	0	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *koseritzi* (Clessin, 1888)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *hildae* Ortmann, 1921	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *hylaeus* (Orbigny, 1835)	1	1	1	0	1	0	0	1	1	0	0	0	0
Diplodon (*R.*) *iheringi* Simpson, 1914	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *peraeformis* (Lea, 1860)	1	0	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *variabilis* (Maton, 1811)	1	0	1	0	0	0	0	0	0	0	0	0	0
Diplodon fontainianus (Orbigny, 1835)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon greeffeanus (Ihering, 1893)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon paranensis (Lea, 1834)	1	1	1	1	0	0	0	0	0	0	0	0	0
Diplodon pfeifferi (Dunker, 1848)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon rotundus Spix in Wagner, 1827	0	1	0	0	0	0	0	0	0	0	0	0	0

Table 2. Freshwater bivalves species of South American Countries and territory (continuation).

Species	South American Countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Diplodon solisianus (Orbigny, 1835)	0	0	1	0	0	0	0	0	0	0	0	0	0
Diplodon uruguayensis (Lea, 1860)	0	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon voltzi Vernhout, 1914	0	0	0	0	0	0	0	0	0	0	1	1	1
Castalia ambigua Lamarck, 1819	0	1	0	0	1	0	1	1	1	1	1	0	1
Castalia cordata Swainson, 1840	0	1	0	0	0	0	0	0	0	0	0	0	0
Castalia crosseana Hidalgo, 1865	0	0	0	0	0	0	0	1	0	0	0	0	0
Castalia duprei (Récluz, 1842)	0	1	0	0	0	0	0	0	0	0	0	0	0
Castalia ecarinata Mousson, 1869	0	0	0	0	0	0	1	1	0	0	0	0	0
Castalia inflata Orbigny, 1835	1	1	1	1	1	0	0	0	0	0	0	0	0
Castalia martensi (Ihering, 1891)	0	1	1	0	0	0	0	0	0	0	0	0	0
Castalia multisulcata Hupé, 1857	0	0	0	0	0	0	1	0	0	0	0	0	1
Castalia nehringi (Ihering, 1893)	0	1	0	1	0	0	0	0	0	0	0	0	0
Castalia orbignyi (Deville & Hupé, 1850)	0	1	0	0	0	0	0	0	0	0	0	0	0
Castalia orinocensis Morrison, 1943	0	0	0	0	0	0	1	0	0	0	0	0	1
Castalia psammoica (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
Castalia quadrata (Sowerby, 1869)	0	1	0	0	0	0	0	0	0	1	0	0	1
Castalia schombergiana Sowerby, 1869	0	1	0	0	0	0	0	0	0	0	0	0	1
Castalia stevensi (H.B.Baker,1930)	0	0	0	0	0	0	1	0	0	1	0	0	1
Castalia sulcata (Krauss, 1849)	0	1	0	0	0	0	0	0	0	1	1	1	1
Castalia undosa Martens, 1885	0	1	0	0	0	0	0	0	0	0	0	0	0
Paxyodon syrmathophorus (Meuschen, 1781)	0	1	0	0	1	0	1	0	1	1	0	0	1
Prisodon obliquus Schumacher, 1817	0	1	0	0	0	0	1	1	1	1	0	0	1
Triplodon corrugatus (Lamarck, 1819)	0	1	0	0	0	0	1	1	1	0	0	0	1

Table 2. Freshwater bivalves species of South American Countries and territory (continuation).

Species	South American Countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Triplodon chodo Mansur & Pimpão, 2008	0	1	0	0	0	0	0	0	0	0	0	0	0
VENEROIDA													
Dreissenidae													
Mytilopsis lopesi Alvarenga & Ricci,1989	0	1	0	0	0	0	0	0	0	0	0	0	0
Mytilopsis trautwineana (Tryon, 1866)	0	0	0	0	0	0	1	1	0	0	0	0	0
Congeria hoeblichi Schütt, 1991	0	0	0	0	0	0	1	0	0	1	0	0	1
Corbiculidae													
Cyanocyclas amazonica (Prime, 1870)	0	1	0	0	0	0	0	0	0	0	0	0	0
Cyanocyclas bavayi (Ancey, 1880)	0	0	0	0	0	0	0	0	0	0	0	1	1
Cyanocyclas brasiliana (Deshayes, 1854)	0	1	0	0	0	0	0	0	0	0	0	0	0
Cyanocyclas cuneata (Jonas, 1844)	0	0	0	0	0	0	0	0	0	0	0	0	1
Cyanocyclas limosa (Maton, 1811)	1	1	1	0	0	0	0	0	0	0	0	0	0
Cyanocyclas paranaensis (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
Cyanocyclas rotunda (Prime, 1860)	0	0	0	0	0	0	0	0	0	1	1	0	1
Cyanocyclas surinamica (Clessin, 1879)	0	0	0	0	0	0	0	0	0	0	1	0	1
Corbicula fluminalis (Müller, 1774)	0	1	0	0	0	0	0	0	0	0	0	0	1
Corbicula fluminea (Müller, 1774)	1	1	1	0	0	0	1	0	1	0	0	0	1
Corbicula largillierti (Philippi, 1844)	1	1	1	0	0	0	0	0	0	0	0	0	0
Corbicula sp.	0	1	0	0	0	0	0	0	0	0	0	0	0
Polymesoda solida (Phillipi, 1846)	0	1	0	0	0	0	1	0	0	0	0	0	1
Polymesoda aequilatera (Deshayes, 1854)	0	1	0	0	0	0	0	0	0	1	1	1	1
Sphaeriidae													
Byssanodonta paranensis Orbigny, 1846	1	1	0	0	0	0	0	0	0	0	0	0	0

Table 2. Freshwater bivalves species of South American Countries and territory (continuation).

Species	South American Countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Eupera bahiensis (Spix in Wagner, 1827)	0	1	0	0	0	0	0	0	0	0	0	0	1
Eupera doellojuradoi Klappenbach, 1962	1	1	1	0	0	0	0	0	0	0	0	0	0
Eupera elliptica Ituarte & Dreher-Mansur, 1993	1	1	0	0	0	0	0	0	0	0	0	0	0
Eupera guaraniana Ituarte, 1994	1	1	0	0	0	0	0	0	0	0	0	0	0
Eupera iguazuensis Ituarte, 1989	1	1	0	0	0	0	0	0	0	0	0	0	0
Eupera klappenbachi Mansur & Veitenheimer, 1975	0	1	1	0	0	0	0	0	0	0	0	0	0
Eupera modioliforme (Anton, 1837)	0	0	0	0	0	0	0	0	0	0	0	0	1
Eupera platensis Doello-Jurado, 1921	1	1	1	1	0	0	0	0	0	0	0	0	0
Eupera primei Klappenbach, 1967	0	0	0	0	0	0	0	0	1	0	0	0	0
Eupera simoni (Jousseaume, 1889)	0	1	0	0	0	0	0	0	1	0	0	0	1
Eupera tumida (Clessin, 1879)	0	1	0	0	0	0	0	0	0	0	0	0	1
Musculium argentinum (Orbigny, 1835)	1	1	1	0	0	1	0	0	0	0	0	0	0
Musculium patagonicum Pilsbry, 1911	1	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium bejumae H.B. Baker, 1930	0	1	0	0	0	0	0	0	0	0	0	0	1
Pisidium boliviense Sturany, 1900	0	1	0	0	0	0	0	1	1	0	0	0	0
Pisidium chicha Ituarte, 2005	1	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium chilense (Orbigny, 1846)	0	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium chiquitanum Ituarte, 2001	1	0	0	0	1	0	0	0	0	0	0	0	0
Pisidium dorbignyi Clessin, 1879	0	1	1	0	0	0	0	0	0	0	0	0	0
Pisidium forense Meier-Brook, 1967	0	1	0	0	0	0	0	0	0	0	0	0	0
Pisidium globulus Clessin, 1888	0	1	0	0	0	0	0	0	0	0	0	0	0
Pisidium huillichum Ituarte, 1999	1	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium inacayali Ituarte, 1996	1	0	0	0	0	0	0	0	0	0	0	0	0

Table 2. Freshwater bivalves species of South American Countries and territory (continuation).

Species	South American Countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Pisidium iquito Ituarte, 2004	0	0	0	0	0	0	0	0	1	0	0	0	0
Pisidium lebruni Mabille, 1884	1	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium llanquihuense Ituarte, 1999	0	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium magellanicum (Dall, 1908)	1	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium meierbrooki Kuiper & Hinz, 1984	0	0	0	0	1	1	0	0	1	0	0	0	0
Pisidium ocloya Ituarte, 2005	1	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium omaguaca Ituarte, 2005	1	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium patagonicum Pilsbry, 1911	1	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium pipoense Ituarte, 2000	1	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium plenilunium (Melvill & Standen, 1907)	1	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium punctiferum (Guppy, 1867)	0	1	0	0	0	0	0	0	0	0	0	0	1
Pisidium sterkianum Pilsbry, 1897	1	1	1	1	1	0	0	0	0	0	0	0	0
Pisidium taraguyense Ituarte, 2000	1	1	1	0	0	0	0	0	0	0	0	0	0
Pisidium vile Pilsbry, 1897	1	1	1	1	1	0	0	0	0	0	0	0	0
Sphaerium aequatoriale Clessin, 1879	0	0	0	0	0	0	0	1	0	0	0	0	0
Sphaerium cambaraense Mansur, Meier-Brook & Ituarte, 2008	0	1	0	0	0	0	0	0	0	0	0	0	0
Sphaerium forbesi (Philippi, 1869)	0	0	0	0	1	1	1	0	1	0	0	0	0
Sphaerium lauricochae (Philippi, 1869)	0	0	0	0	0	1	0	0	1	0	0	0	0
Sphaerium titicacense (Pilsbry, 1924)	0	0	0	0	1	0	0	0	1	0	0	0	0
MYOIDA (?)													
Lyonsiidae (?)													
Anticorbula fluviatilis (H. Adams,1860)	0	1	0	0	0	0	0	0	0	0	0	0	0
Species Richness (S)	60	117	46	31	27	12	29	18	33	17	9	6	49

Capítulo 2

Environmental factors and fish richness influencing the bivalve assemblies in freshwater ecoregions in Brazil and bordering countries

Environmental factors and fish richness influencing the bivalve assemblies in freshwater ecoregions in Brazil and bordering countries

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Abstract

The species composition of the assemblies of bivalves in South American ecoregions, as well as environmental factors, was not known until now. Aiming to evaluate the environmental factors that influence the structure of bivalves assemblies of these biogeographical units, 24 ecoregions located in Brazil and part of neighboring countries were selected due to the greater availability of environmental data and greater number of mollusk material deposited in scientific collections. The presence and absence of species in each polygon area of each ecoregion was obtained through literature review and examination of the scientific collections of renowned museums. Physiographic attributes, such as slope, elevation, polygons area, precipitation, air temperature, as well as indicators of water chemistry, were evaluated through several univariate and multivariate methods. Index of species rarity was calculated for each region in order to quantify the endemicity of the areas. We observed greater species richness of bivalves in large areas of lower slope and high richness of fishes. The high richness of Unionoida with parasitic larval stage was also related to polygon area and high fishes richness. Most environmental factors that explained the structure of the bivalve assemblies were physiographic attributes and the fish species richness. Moreover, geological events of the past that shaped the South American landscapes contributed to the present distribution and composition of bivalve species in the evaluated ecoregions. This one first step to understanding the structure of bivalve assemblies in macroscale is an important basis for the management and conservation of native species and the control of invasive ones.

Introduction

In South America, the highest species richness of freshwater bivalves is found in Brazil, especially in the tropic zone in the Amazon and Paraguay River basins, and also in temperate climatic zones, in the Uruguay River Basin and in rivers of South and Southeast Atlantic (Pereira et al., 2013). However, the environmental macrohabitat factors that influence the distribution of bivalve species in South America watersheds and freshwater ecoregions are poorly known. A few references addressed this issue, conducting an analysis of the distribution of bivalves and gastropods in coastal lacustrine environmental gradients (Lanzer and Shafer, 1985, 1987, 1988, Lanzer, 2001), and several types of wetlands systems, at different altitude levels, orders of magnitude and hydroperiods (Maltchick et al., 2010), both cases in Southern Brazil. Regarding the relation between the bivalve fauna and microhabitat factors, many studies were conducted in South America: in rivers (Bonetto & Di Persia, 1975), creeks and dams (Pereira et al., 2001), dams (Mansur et al., 1994, Mansur & Garces, 1988), reservoirs (Henry & Simão, 1984 e 1986, Suriani et al., 2007, França et al, 2007, Pereira et al., 2012), and coastal lakes (Duarte & Diefenbach, 1994, Duarte et al., 1996).

According to Haag (2012), the main macrohabitats factors that influence the distribution of freshwater bivalves (Unionoida) in the North America are climatic features, physiographic attributes, tidal effects, and water chemistry, mainly pH, Ca^{++} availability and salinity (Na^{+}). Strayer (1993) highlights the importance of stream size, hydrologic variability, calcium concentration and physiographic provinces in the prediction of mussels in North America. In Europe, strong influence of altitude, latitude and depth on the distribution of freshwater bivalves (Unionoida and Veneroida) in 23 French lakes were observed by Mouthon (1990).

Other important issue is the relationship between species richness and the ecosystem or habitat area. This is the first general pattern of biological communities to be discovered in biogeographic and ecological studies in large scale (Triantis and Bhagwat, 2011). The increase of species richness of Unionoida with increasing watershed area (Waters, 1992, Haag, 2010) and stream size (Ortmann, 1923, Coker et al, 1921, Hornbach, 2001), was also observed in the U.S.A. Larger areas have a higher diversity of habitats and consequently a highest richness of fish hosts (Strayer, 2008).

According to Haag & Warren (1998), the structuring of mussels community is closely related to density and fish-hosts richness in sites with stable numbers of hosts, and also with reproductive strategies of mussels. The difference is that all Unionoida species in North America have a parasitic larval stage on fish, while in South America some species of Hyriidae of *Diplodon* (*Rhipidodonta*) subgenus do not parasitize fishes. Different strategies of incubation, larval release and dispersal are found among South American bivalve fauna (Mansur et al, 2012), which possibly determines the species distribution across the hydrographic regions of continent. Unfortunately, most studies describe only fish diseases caused by infestation of the *Anodontites trapesialis* (Lamarck, 1819) lasidia in fish farming (Guardia-Felipi & Silva-Souza, 2008), and little is known about the relations between mussels and fish-hosts from natural conditions in South America.

According to Olson et al. (2001), ecoregions comprise finite spatial areas with environmental conditions and communities rather homogeneous and distinct when compared to the heterogeneity observed in larger areas. Abell et al. (2008) delineated 830 freshwater ecoregions for all continent based on fish richness, among which 51 are located in South America. This delineation of ecoregions has directed scientific research and conservation strategies in South America. Most of these areas have suffered progressive anthropogenic pressure due to deforestation, agriculture and damming. Until now, they are not known on patterns of richness, species composition, endemism levels and environmental macrofactors determining the bivalve community structure in South American ecoregions. Pereira et al. (2013) reported bivalve community data about species richness and phylogenetic composition only for large hydrographic basins.

The purpose of this paper is to survey freshwater bivalve species from freshwater ecoregions in Brazil and bordering countries and identify the macrohabitat factors that influence the distribution and species composition in these biogeographical units, in order to guide conservation strategies.

Material and Methods

Study Area

The 24 ecoregions selected for this survey (Fig. 1) and their respective major habitats are described in table 1 according to Abell et al. (2008). The set includes all ecoregions concentrated in the large polygon area of Brazil and partial areas of bordering countries such as Venezuela, Colombia, Peru, Bolivia, Paraguay, Argentina and Uruguay. The total area surveyed is 9822386.7 km^2, of which 86.7% is located in Brazil. These areas were selected because of the vast repository of malacological material deposited in scientific collections and the largest number of bivalve species records in the literature. Most of ecoregions assessed are located in hydrographic regions with high species richness of limnic bivalves (Pereira et al., 2013).

Compilation of species records

Data on the occurrence of bivalve species in hydrographic regions in South America (Fig. 1; Table 1) were compiled from the scientific literature and examinations of the following scientific collections: Academy of Natural Sciences of Philadelphia (ANSP; Philadelphia, USA); Carnegie Museum of Natural History (CM; Pittsburgh, USA); Coleção de Moluscos da Universidade do Estado do Rio do Janeiro (UERJ; Rio de Janeiro, Brazil); Coleção de Moluscos da Universidade Federal do Mato Grosso (UFMT; Cuiabá, Brazil); Fundación Miguel Lillo (FML; Tucumán, Argentina); Instituto Nacional de Pesquisas da Amazônia (INPA; Manaus, Brazil); Musée d'Histoire Naturelle Bâle (MHNB; Basel, Switzerland); Musée de Zoologie (ZML; Lausanne, Switzerland); Musée d'Histoire Naturelle de la Ville de Genève (MHNG; Geneva, Switzerland); Museo Argentino de Ciencias Naturales"Bernadino Rivadávia" (MACN; Buenos Aires, Argentina); Museo de La Plata (MLP; La Plata, Argentina); Museo Nacional de Historia Natural de Chile (MNHNC; Santiago, Chile); Museo Nacional de Historia Natural de Montevideo (MNHM; Montevideo, Uruguay); Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP; Porto Alegre, Brazil); Museu de Ciências Naturais Fundação Zoobotânica do Rio Grande do Sul (MCN; Porto Alegre, Brazil); Museu de Zoologia da UNISINOS (MZU; São Leopoldo, Brazil); Museu de Zoologia da Universidade de São Paulo (MZUSP; São Paulo, Brazil); Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ; Rio de Janeiro, Brazil); Museu Paraense Emilio Goeldi (MPEG; Belen, Brazil); Museum für Naturkunde (ZMB; Berlin, Germany); Museum National d'Histoire Naturelle (MNHN; Paris, France); National Museum of Natural History, Smithsonian Institution (USNM; Washington D.C., USA); Natural History Museum of United Kingdom (NHMUK; London, United Kingdom); Naturhistorisches Museum (NMW; Wien, Austria); Senckenberg Forschungsinstitut und Naturmuseum (SMF; Frankfurt a.M., Germany); Staatliches Museum für Naturkunde (SMNS; Stuttgart, Germany); and Zoologische Staatssammlung München (ZSM; Munich, Germany). Part of the data on the occurrence of species in Peru, Ecuador, and Colombia were extracted from Mussel Project (musselproject.uwsp.edu/). All records of bivalve species (presence or absence) were tabulated for each ecoregion.

The rarity was evaluated using the uniqueness of the set of species in freshwater ecoregion and the average originality of species in each sample (Boix et al., 2008).

$$S = e/E \cdot 100$$

where *e* is the number of species only reported in a given freshwater ecoregion (endemic species), whereas *E* is the total number of species reported in that freshwater ecoregion.

Environmental descriptors of the freshwater ecoregions

Measures of physiographic attributes of the freshwater ecoregions such as Altitude and Slope were obtained using Digital Elevation Model (MDE) of South America (spatial resolution of 15 arc seconds -. 450 mts), generated by Hydrological data and maps based on SHuttle Elevation Derivatives at multiple Scales (HydroSHEDS) of the World Wildlife Fund (2006). Average altitude, maximum, minimum, range and standard deviation values were obtained using Zonal Statistics from Spatial Analyst package of ArcGis, calculated from the MDE. Average slope, maximum, minimum, range and standard deviation values were obtained from the Model Slope also using Zonal Statistics. The Model Slope was derived from MDE through the Slope tool package of ArcGIS Spatial Analyst.

The average values of water chemistry indicators were obtained from dataset of all freshwater ecoregions sampled during 2004 by Brasil das Águas Project (brasildasaguas.com.br/). The following variables were considered: water temperature (°C), pH, turbity (NTU) (multiparameter probe YSI), total phosphates (μg-P/L), TCD – total dissolved carbon (mg/L), K^+ (mg/L), Na^+ (mg/L), Mg^{++} (mg/L) and Ca^{++} (mg/L) (atomic absorption spectrophotometry).

The values of minimum and maximum annual rainfall, mean annual temperature and richness of fish species from all freshwater ecoregions were compiled from WWF/TNC (2013) according to Köppen (1936), and the fish richness were compiled Abell (2008).

Statistical analysis

Species-area curve for bivalve richness, UPLS (Unionoida with parasitic larval stage) richness, and fish richness were obtained by regression analysis (power function) according to (Haag, 2010, Waters, 1992, Albert et al., 2011) using SPSS 13. Bivalve richness-environmental factors curve, UPLS richness-environmental factors curve, Bivalve richness-fish richness curve, and UPLS richness-fish richness curve were obtained through regression analysis (linear function) using the same software. Predictive equations of bivalve richness (response variables) depending on environmental factors and fish richness (predictors) were obtained through models generated by multiple regressions, considering all dataset from each freshwater ecoregions. Models were generated considering the assumptions of normality, homoscedasticity, errors independence, multicollinearity, and linearity. The For the multiple regression analysis SPSS 13.0 software was used. The dataset of bivalve, UPLS, and fish richness, as well environmental factors were transformed using log (x+1) for all analysis above, except for species-area curve.

The ordination of freshwater ecoregions was conducted by Principal Coordinates Analysis (PCoA) on an array of species dissimilarity (distance of Gower) using MULTIV software (Pillar, 1998). The exclusion of rare species increased only 2% of the explanation of the axes. Thus it was decided to keep them in this analysis. In order to characterize the influence of environmental variables on the distribution of freshwater ecoregions in the PCoA analysis, a (*Spearman's rho*) correlation analysis was conducted on the first two axes of the PCoA and the environmental variables (physiographic attributes and water chemistry indicators) and fish richness using the SPSS 13.0 software. The following physiographic attributes were considered: polygon area, average values of altitude and slope, values of minimum and maximum annual rainfall, mean annual temperature. The median values of all water chemistry indicators were considered in this analysis. The Mantel test was used to assess the possible relation of species composition with environmental factors. The test verified the possible correlation between two arrays: bivalve records (presence or absence) *versus* environmental factors and fish richness (log (x+1)) both obtained from Gower index.

Results

Physiographic attributes (Table 2)

Amazon Lowland (1,911,985.8 km^2), Upper Paraná (834,088.7 km^2) and Laguna dos Patos (270,059.8 km^2) show the highest polygon areas among the freshwater ecoregions. The Fluminense contrasts with all the other ecoregions showing the lowest polygon area (11059.0 km^2). Regarding the slope attribute, the coastal areas from Rio de Janeiro to Santa Catarina states showed the highest average slope value among all other freshwater ecoregions as follow: Southeastern Mata Atlantica and Ribeira do Iguapé (9.8%), Tramandaí - Mampituba (8.6%), Fluminense (8.3%), Paraiba do Sul (8.1%), and Northeastern Mata Atlantica (6%). The Amazonas Lowlands contrasts with all other ecoregions showing the lower average slope value (1.0%). Minimum and maximum values of average annual precipitation are higher in the Amazon Lowland (2400-3900 mm), Rio Negro (1850-3500 mm) and Amazon Estuary (2000-3500 mm). The Northeastern Caatinga & Coastal Drainages contrasts all others ecoregions showing the lowest values of average annual precipitation (350-1140 mm). Laguna dos Patos and Tramandaí - Mambituba ecoregions show the lowest values of average annual temperatures (17°C) contrasting with higher values in Amazonas Guiana Shield (27°C).

Water Chemistry (Figs. 2 to 4)

Acid waters were found in the Rio Negro (average values ± standard error, 5.7±0.1 (ranging from 4.3 to 8.0), N=46) while very alkaline water was reported in the Iguassu (8.4±0.2 (7.4 to 10.4), N=12) (Fig 2). The Guapore - Itenez shows turbid waters (73.1±85.3 NTU (1.1 to 294.3), N=223) contrasting with Iguassu River (10.2±3.7(0 to 38.3), N=12) (Fig 2). Regarding to total phosphate, higher values were reported in Ribeira do Iguape (109.3±46.6 µg-P/L (28.3 to 198.6), N=4) and lower values in Rio Negro (19.4±0.9 (7.2 to 32.3), N=46) (Fig 3). Potassic waters (49.7±23.0 mg/L (0.8 to 221.1), N=13) were reported in the Southeastern Mata Atlantica, where many lacustrine water bodies connected to the Atlantic Ocean can be found, while lower potassic levels (0.4±0.04 mg/L (0.1 to 1.8), N=46) were reported in the Negro River (Fig 3). Sodic waters were reported in Northeastern Caatinga & Coastal Drainages (25.8±4.0 mg/L (0.4 to 92.0), N=41), while lower sodium levels in the Paraguay ecoregions (0.9±0.7 mg/L (0.1 to 3.9), N=66) Fig 3). Northeastern Caatinga & Coastal Drainages also shows higher leves of magnesium (6.7±1.0 mg/L(0.1 to 23.6), N=41), and calcium (10.8±1.3 mg/L(0.2 to 26.8), N=41) (Fig 4). In opposition, the Rio Negro ecoregion shows lower levels of magnesium (0.4±0.05 mg/L (0.1 to 1.4), N=46) and calcium (1.1±0.3 mg/L (0.2 to 9.0), N=46) respectively (Fig 4).

Fish species richness

The dynamic Amazon Lowland is a species-rich area (910 species) regarding fish assemblage while the Iguassu characterized by intermittent streams is species-poor area (68 species) (table 2).

Bivalve species richness and distribution

Based on this survey, 115 native limnic bivalves and 5 invasive species were recorded for the 24 freshwater ecoregions located in Brazil and bordering countries (table 3). Among Major habitats, the highest values of average species richness was observed in tropical and subtropical floodplain rivers and wetland complexes (Fig. 3). Bivalve species richness was higher in two major habitats of the freshwater ecoregions in Brazil and bordering countries: temperate coastal rivers (TCR) and tropical-subtropical floodplain rivers and wetlands complexes (TSFRWC) (Fig 5). Lower Uruguay is the freshwater ecoregion with the highest species richness (48 species) (Fig. 6), followed by Laguna dos Patos (42), Amazonas Lowlands and Paraguay (40), and Upper Parana (35). Regarding the invasive species richness, the highest values were observed in

Laguna dos Patos (5 species) and Tramandaí – Mampituba (4) ecoregions (Fig. 6). The highest rarity index value (Fig. 6) was observed in the Iguassu River ecoregion, where the species richness (7 species) is lower than all other ecoregions, but two endemic species were recorded. The second highest value was observed in the Lower Uruguay ecoregion, due to three endemic species. The highest values of invasives species richness were observed in Laguna dos Patos ecoregion (Fig. 6). So far, no invasive species are reported in the Xingu, Tapajos – Juruena and Madeira Brazilian Shield.

Hyriidae (44%) accounts for the highest percentage of species, followed by Mycetopodidae (28%), Sphaeriidae (17%), Corbiculidae (8%), Dreissenidae (1%), and Mytilidae and Lyonsiidae (1%). The Unionoida represents 72% of the species richness of freshwater bivalves in South America while Veneroida 27%, Mytilioida and Myoida 1%. The species number of bivalve families for each freshwater ecoregions are shown in Fig. 7.

Only two bivalve species are reported in more than 75% of the freshwater ecoregions inventoried (table 3), one native and one invasive species, *Anodontites* (*A*). *trapesialis* and *C. fluminea* respectively. The following species with larger distribution in the ecoregions (50 to 75%) should also be mentioned: *M. siliquosa* (Spix, 1827) (71%) and *C. largillierti* (54%). All other species showed the following distribution patterns: presence at 5 to 50% of freshwater ecoregions (20 species) and <25% (97 species). A high number of species (25 species) was reported in only one ecoregion, corresponded to 4% of all ecoregions.

Bivalves, fishes and species-area curve

Bivalve richness were correlated to polygon area (r = 0.52, *P* = 0.01), but only 25% of richness values were explained by same factor (*P* = 0.02) (Fig. 8A). UPLS richness were correlated and area (r = 0.45, *P* = 0.02), but only 23% of richness values were explained by same factor (*P* = 0.049) (Fig. 8B). On the other hand, the polygon area showed a larger explanation (r^2 = 0.49, *P* = 0.0001) of the fish richness values in the ecoregions (Fig. 8C). Bivalve richness were correlated to fish richness (r = 0.54, *P* = 0.006), but only 24% of bivalve richness values were explained by fish richness values (*P* = 0.014) (Fig. 9A). UPLS richness were correlated to fish richness (r = 0.41, *P* = 0.04), but only 17% of UPLS richness values were explained by fish richness values (*P* = 0.042) (Fig. 9B)..

Species richness and ecoregions relief

Bivalve richness and UPLS richness were correlated to average slope (r = -0.50, *P* = 0.01; r = -

0.46, *P* = 0.02). The average slope explain 28% of bivalve richness values (*P* = 0.03) in ecoregions (Fig. 9C), and 22% of UPLS richness values (*P* = 0.07) (Fig. 9D). The multiple regression analysis considering all data set showed that the variable that best explained the variation of bivalve richness values were slope and altitude (Table 4).

Bivalve assemblies versus environmental factors and fishes

Regarding to the ordination, the axis 1 contained 26.6% of the total variation in the species composition matrix, while the axis 2, 16.2% (Fig. 7). This axis splits two groups of ecoregions, one including Amazon river and its main tributaries, Tocantins-Araguaia and Parnaíba, and other with the remaining surveyed ecoregions. Along the second axis, an environmental gradient described by the sequence of species-poor ecoregions (positively related) to species-rich ecoregions (negatively related) was observed. The ordination shows that the first axis was positively related to water temperature (r = 0.66, *P* = 0,0004), polygon area (r = 0.54, *P* = 0.005), air annual temperature (r = 0.83, *P* < 0,0001), minimum annual precipitation (r = 0.47, *P* = 0,02), maximum annual precipitation (r = 0.53, *P*=0,007), and fishes richness (r = 0.43, *P*= 0,04). On the other hand, this axis was negatively related to pH (r=-0,39, *P*=0.05), total phosphate (r = -0,52, *P* = 0.007), K^+ (r = -0,60, *P* = 0.001), Mg^{++} (r = -0,61, *P* = 0.001), Ca^{++} (r = -0,76, *P* < 0.0001), altitude (r = -0,34, *P* = 0.09), and slope (r = -0,63, *P* = 0.001). The second axis was positively related to K^+ (r = 0,47, *P* = 0.02), altitude (r = 0,51, *P* = 0.01), and slope (r = 0,69, *P* = 0.0002). On the other hand, the second axis was negatively related to water temperature (r = -0.37, *P* = 0,07), polygon area (r = -0.38, *P* = 0.07), minimum annual precipitation (r = -0.38, *P* = 0,06), fishes richness (r = -0.54, *P* = 0,006). Mantel test showed positive correlation between bivalve composition (presence or absence) array and environmental factors + fish richness array (r=0.18; *P*=0. 1).

Discussion

Physiographic attributes

The physiographic attributes reflect the landscape features of South America described by A'b Sáber (2003, 2006). According to Ab'Sáber (2003), in these areas the following morphoclimatic domains predominate: Equatorial domain in the basin of the Amazon River; Cerrado domain in the Upper Parana and Upper Paraguay Rivers presenting humid tropical climate with two distinct seasons; Caatingas domain in semi-arid inter-plateau depressions with intermittent rivers and mangroves near the sea; Tropical Atlantic domain with seas of forested hills and plateaus in the tropical Atlantic coast of Brazil, where small rivers flow into the Atlantic, reaching sets of lakes and lagoons near the sea; Domain of the Southern Brazil Plateaus of Araucaria, in an area with pine forests, where subtropical climate has four distinct seasons; Domain of the Wet Pampa, characteristic by large Pampean plains covered by grasslands.

Water chemistry indicators

The cationic content of ecoregions corroborate data obtained by several authors: Upper Paraná and Ribeira do Iguape (Maier et al., 1986a, 1986b), Paraguay (data compilation by Maier et al., 1986a, Junk and Furch, 1980, Neto et al., 1993), Amazon region (data compilation by Maier et al., 1986a, Junk and Furch, 1980, Junk and Howard-Williams, 1984, Furch et al., 1983, Weber and Junk, 1998), Fluminense (Ovalle et al., 1990), and Lagoa dos Patos (data compilation by Maier et al., 1986a) ecoregions.

Bivalve species richness and distribution

Comparing the species richness observed in freshwater ecoregions with data reported by Pereira et al (2013) in hydrographic regions of the South American countries, we can make the following considerations: the total number of species (120) reported in all evaluated ecoregions represent 72% of the species richness recorded in South America; according to the authors above 117 species are recorded in Brazil, representing ≅98% of species richness in freshwater ecoregions assessed in this paper; the high levels of species richness reported for Laguna dos Patos, Amazon Lowlands, Paraguay and Upper Paraná ecoregions are congruent with the ones recorded in hydrographic regions of Amazon River, Paraguay River, Uruguay River and rivers of the South and Southeast Atlantic (very high richness, >40 species), and Upper Paraná River (high richness, 30-40 species); Hyriidae, Mycetopodidae (Unionoida) and Sphaeriidae (Veneroida) are more representative families in both freshwater ecoregions and hydrographic regions of South America. In African and Madagascar ecoregions, Graf and Cummings (2011) recorded 87 unionoid species from 90 freshwater ecoregions, whereas the highest richness is related to large rivers and lakes.

The largest number of invasive species in the Laguna dos Patos ecoregion is not a surprise. This ecoregion, especially in the Jacuí Delta, has been one of the important entrance gates to invasive species in South America since the 70s due to the navigation route stop in the area of the Porto Alegre harbor (Mansur et al, 1998, 2003, 2004, Santos et al., 2012). Other important gateway is the La Plata River estuarine system (Darrigran & Pastorino, 1995, Darrigran & Mansur, 2009, Santos et al., 2012) at Argentina.

The arrival of the golden mussel in ecoregions located in the hydrographic regions of Amazon River, Tocantins-Araguaia Rivers and San Francisco River may occur soon if urgent preventive measures are not undertaken by several sectors of societythat use these water resources. This species can cause extreme effects on benthic and planktonic, as on all trophic web (Darrigran et al., 1998, Darrigran & Damborenea, 2011). According to Pereira et al. (2013), the distribution of *Limnoperna fortunei* (Dunker, 1857) and all species of genus *Corbicula* in the hydrographic regions of South America is not correlated with species richness of native bivalve species. This suggests that the richest assemblages are not less susceptible to bioinvasion, which corroborates the presence of *L. fortunei* and some *Corbicula* species in Laguna dos Patos and Paraguay ecoregions, as well as the high possibility of the golden mussel reach the Amazon Lowlands and all connected Amazonian ecoregions by flood pulse of Amazon River, such as Xingu, Tapajos – Juruena and Madeira Brazilian Shield. Moreover, the wide range of pH tolerance (2-12 after 24 hours, and 4-11 after 144 hours) of the golden mussel possibly will facilitate the passage of the mussel through ecological barriers resulting from Amazonian acidic waters (Pereira et al, see Chapter 3). By means of modeling tools, Oliveira et al. (2010) predicted scenarios of dispersion of the golden mussel that suggest the invasiveness potential of the São Francisco and the Amazon basins, especially the Teles Pires, Tapajós and Araguaia rivers. Strategic projects of the Brazilian government for intensification and connection of waterways can accelerate the bioinvasion process if appropriate prevention measures, with establishment of barriers and checkpoints, are not deployed in an integrated manner.

Most Amazonian ecoregions have common species with wide distribution in these areas and bordering ecoregions such as Paraguay and Parnaíba. Most of these species show occurrence frequency between 25 and 50%, while the species of restricted distribution (<25%) predominate in ecoregions located in the south of the Paraíba do Sul, towards Laguna dos Patos ecoregion, often occurring in a single ecoregion (25 species). According to Pereira et al. (2013), in tropic and subtropical areas of South America there is an expressive and large zone of endemisms forming mosaics with different richness levels and taxocenosis compositions. Among the species widely distributed, it is worth noting that most are Unionoida with parasitic larval stage, lasidia or glochidia (species of subgenus *Diplodon* (*Diplodon*)), on fish-hosts. This species show three strategies of dispersion via plankton, fishes, and benthos (Mansur et al., 2012). Secondly, Spheriidae species showing reproductive and diapause mechanisms adapted to flood pulse stress and the invasive species have very small pediveliger easily carried by water flow. According Mansur & Meier-Brook (2000), *Eupera* species from Amazon and Paraguay regions survive long periods of drought due to the presence of large excretory sacs with structures like valves that avoid the water loss.

The species distribution patterns influenced the rarity index values, which were higher in ecoregions in southern direction. Although the bivalve fauna of ecoregions located in the Amazon Hydrographic Region and bordering basins is distinct from the other ecoregions, especially in the Lower Uruguay and the coastal basins such as Lagoa dos Patos, between the Amazonian ecoregions there is little differentiation due to their high connectivity among these areas. Nonetheless, in the ecoregions in the South high values of index of rarity were observed due to the high degree of endemism as result of the lack of connectivity of these areas featured by ground elevations that split watersheds.

Only two species are widely distributed in ecoregions, one with lasidia larvae (*A. trapesialis*) and other with very small pediveliger (*C. fluminea*), have easily carried by water flow. *A. trapesialis* was reported in 98% of the ecoregions surveyed, probably due to not showing specificity with hosts (Callil et al., 2012), which may facilitate its spread via different fish-host species. This species live in several types of substrate on the bed of lakes, rivers, creeks, dams, ponds and drainage channels of the rice irrigation systems, and fish ponds (Bonetto & Di Persia, 1975; Hebling, 1976; Simone, 1994; Pereira et al., 2011; Colle & Callil, 2012). So far, *C. fluminea* is the most successful invasive species of exotic bivalve in South America and also the oldest mollusk invasion in the 20th century, beginning in the 70s. Currently, this species is reported in large area from rivers of Colombia to the North of Patagonia (Santos et al., 2012).

Large number of endemic species versus a small number of widely distributed species seems to be a common pattern to the assemblies of African bivalve. Graf and Cummings (2011) observed that 55% (34 species) of bivalve species are known from only one or two ecoregions. In contrast, the authors observed that only three are reported to more than 20 ecoregions: *Etheria elliptica* (38 ecoregions), *Chambardia wahlbergi* (25), and *Mutela rostrata* (21). At Etheridae as Iridinidae (= Mutelidae) the larva is a haustorium very similar to the lasidium of South American Mycetopodidae (Parodiz & Bonetto, 1963). Probably the reproductive strategies of these mollusk lineages, together with other ecophysiological aspects contributed to the wide distribution of some species along to different types of habitats and ecoregions in Africa and South America.

Bivalves, fishes and species-area curve

Bivalve species richness were correlated or partly explained by area in south American ecoregions. However, Watters (1992) found a more consistent species-area curve from Unionoida species dataset of St. Joseph River system in North America ($r^2 = 0.84$). Haag (2012), compiled data from different authors founding different species-area curve of the bivalve assemblages in several river basins: Ohioan province ($r^2 = 0.77$), Interior Highlands province ($r^2 = 0.64$), and Upper Mississipi province ($r^2 = 0.38$). Larger areas have greater diversity of habitats and may harbor a large number of species. However, higher habitat diversity does not necessarily reflect high number of viable habitats for colonization and species dispersal, which is related to the connectivity of habitats.

Despite the Amazonian lowland presenting the largest area of polygon and highest fish richness values of all south American freshwater ecoregion (Albert et al., 2011), the greatest number of bivalve species was recorded in the Laguna dos Patos and Paraguay ecoregion. The Amazon River, on the stretch from frontier Peru - Colombia - Brazil to the Xingu River mouth comprises 87600km^2 of floodplain area (Junk, 1997). Nevertheless, the fluctuation of the water level in this area is very wide. The clearwater and blackwater present poor levels of cation content. Blackwater are an limiting factor to mollusks (Volkmer-Ribeiro et al., 1998).

The bivalve zonation in watersheds is not only related to the higher habitats diversity present in larger areas. Bivalve species richness was also related to fish species richness, which suggests the congruence of freshwater ecoregion delineation based on fish and bivalves assemblages. In North America, all freshwater Unionoida species present parasitic larval stage (Strayer, 1993), which probably make the relation with fish fauna more stronger. In the ecoregions assessed, the species richness of Unionoida with parasitic larval stage (UPLS) was related and partly explained by fishes richness. UPLS-fish curve is another well-known pattern in the mussel ecology (Haag, 2012). Watters (1992) found a very consistent UPLS-fishes curve from dataset of St. Joseph River system in North America ($r^2 = 0.92$). Haag (2012) assessed dataset from 113 Northern American river systems and also found a very consistent UPLS-fishes curve ($r^2 = 0.77$). In African ecoregions, the bivalve species richness was also related ($r = 0.71$) to fishes species richness (Graf and Cummings, 2011).

The UPLS-fishes curve from dataset of freshwater ecoregions assessed may represent a very generalized relation. According to Haag (2012) this relations are dependent on geographic scale. The ecoregions considered in this paper showed different area magnitudes, with particular drainage and microclimatic features, which possibly influences the composition patterns of UPLS assemblages in addition to fishes richness. Furthermore, the relationship between UPLS and their hosts in South America is poorly known, since the parasitic cycle of less than ten species was described (Bonetto, 1954, 1955, Bonetto and Ezcurra, 1963, Mansur, 1999). In North America, all freshwater Unionoida present parasitic larval stage and some species use amphibians-hosts for the development of their life cycle (Watters and O´Dee, 1998) and this parasitic relation may also exist in southern American ecosystems.

Species richness and ecoregions relief

The species-slope curve that showed inverse relationship between both variables corroborates distribution patterns observed in another survey on bivalve fauna in southern American watersheds. The highest bivalve and UPLS species richness were reported by several authors in the middle and lower zones of rivers and lakes such as Amazon Lowlands (Mansur & Valer, 1992, Pimpão & Mansur, 2009, Pimpão et al., 2008), Paraguay (Serrano et al., 1998, Colle and Callil, 2012), Lower Uruguay (Bonetto & Di Persia, 1975) and Laguna dos Patos ecoregions (Lanzer & Schafer, 1985, 1987, 1988, Anflor and Mansur, 2001, Mansur et al., 1988, 1991, 1994, Duarte et al., 1994, 1996, Pereira el al. 2000, 2011, Gallon and Pereira, 2005, Mansur & Pereira, 2006), where altitude and average slope are lower. Big rivers and its floodplains, with many marginal lakes, small tributaries, and secondary canals, are located low-altitude and low-slope areas. These areas presents a great diversity of aquatic habitats with high connectivity due to lack of physiographic barriers, that are more present in areas with sloping terrain, and embedded and isolated water bodies.

Bivalve assemblies versus environmental factors and fishes

The freshwater ecoregions ordered by PCOA regarding to bivalve assemblies showed a very clear pattern of species composition. This ordenation splits species-rich and species-poor areas, which are related to environmental gradient described by physiographic attributes and water chemistry indicators, as well fish richness. The firs axis 1 split Amazonian ecoregions from others. Regarding to Amazon ecoregions, despite the fact that these areas present different patterns of composition and species richness due to particular geomorphologic and hydrologic features, the connectivity of these areas in the flood phase can promote exchange of species. According to Junk and Furch (1993), these important major wetland types are reported for the Amazon River Basin: river floodplains in the Solimões, Purus and Amazonas Rivers (Amazon Lowlands ecoregion); periodically flooded forests in the Rio Negro (Rio Negro ecoregion) and Rio Branco (Amazonas Guiana Shield ecoregion); periodically flooded savannas in the Xingu and Araguaia rivers (Xingu and Tocantis-Araguaia ecoregions); and coastal wetlands in the lower Amazon River (Amazonas Estuary & Coastal Drainages). These wetlands systems are connected in wet phase of big rivers. The temperature and precipitation are very high in these areas and may vary from 2000 to 3600 mm (Sioli, 1983), promoting big inundantions. These different landscape aspects reflect on the structure of aquatic communities and their interspecific relations and evolutionary patterns. These features, combined with high species richness of fish and low average slope of these areas, support the differentiation of Amazonian ecoregions from other ones through ordination.

Moreover, bivalve species needs ecological and physiological adaptations to live in habitats that are directly connected to the Amazon River such as flood forest, marginal lakes and secondary channels. The Amazon river can rise 12 to 22 m above the normal level in the flood phase (Weber and Junk, 1998, Junk, 1999), and in the dry phase the lower water level decreases considerably the cation content, and also affect the survival of bivalves. According to Irmler (1975), *Eupera simoni*, *Eupera bahiensis* and *Psidium sterkianum* adapted their reproductive cycles to the drought and flood periods. *E. simoni* suspends its development at the end of the flood and resumes only after the beginning of the next flood (Irmler, 1976, 1977, 1981, Junk and Robertson, 1997). This clam can survive to drought through the diapause by sheltering below wet bark of trees of the floodplain forest (Irmler, 1975), and also by using floating logs to disperse the floodplain. According to the same author above, similar adaptation was recorded to *P. sterkianum*. This species has two reproductive peaks, one at the beginning of the flood pulse and another at the end. During periods of drought, the young bivalves survive by sheltering inside the valves of dead progenitors. Pereira et al. (2000, 2001) also found *P. sterkianum* at extreme water level conditions in intermittent creeks located in South Brazil affected by water catchment from rice irrigation system. In addition to Sphaeriidae, several species of Unionoida probably show morphological and functional adaptations on their shells. *Paxyodon*, *Prisodon* and *Triplodon* species from Amazon Basin show wings at hinge plate of shells, similar to symphynote species from North America. However, the wings of the southern America species are not glued, but possibly exert similar hydrodynamic effect on the soft substrate. According to Watters (1994), symphynote shells may function in two ways: "as a stabilizing shape in a current preventing the animal from being washed away if dislodged, and to attain a favorable orientation when righted; as a buyoance or “snowshoe” device in very soft substrata". The same author cited other shell adaptation such as globosity of shells, which also helps the animal to buy on soft substrata. Many species of *Castalia* and *Monocondylaea* from Paraguay and Amazon Lowlands ecoregions are very globose and buoy on soft substrate. These morphologic features play an important role for the success of life cycle and colonization of Unionoida at depositional areas from big rivers systems (Watters, 1994).

Analyzing the second axis of PCOa, two groups of ecoregions are clearly distinguished. One group consist in species-poor areas related with highest values of altitude, slope, and cationic content. These group are represented by all coastal ecoregions, except for Lagoa dos Patos ecoregion that is located in the extreme south of Brazil. From north to south, the Northeastern Caatinga & Coastal Drainages is a particular natural system. This area is located in the Brazilian semi-arid, where the precipitation is lower and irregular, so most rivers are intermittent and present two extreme hydrologic phases, flood and drought (Maltchik, 1999). The benthic communities show close relation with hiporreic waters and are resistant and resilient to extreme water levels (Maltchik & Silva-Filho, 2000). According to Walker et al. (2001), in Australian inland waters, Hyriidae species are widespread, except in ephemeral and saline waters, probably due to ecological and physiological limitations. Perhaps, the high cationic content in the rivers of Northeastern Caatinga & Coastal Drainages due to the input of saline water caused by wide tidal variation, modeling unique estuarine landscapes, is a limiting factor to the freshwater bivalve, added to the intermittency of streams in higher fields. Paraiba do Sul, Ribeira de Iguape and Southeastern Mata Atlantica, ecoregions located in the morphoclimatic “Tropical Atlantic domain with seas of forested hills (“mares de morros”) and plateaus in the tropical Atlantic coast of Brazil”, according to Ab´Sáber (2003). In these areas, small rivers flow into the Atlantic, reaching sets of lakes and lagoons near the sea. Most of river mouths and lagoons present wide tidal variation at different orders of magnitude, which affect the cationic content and salinity in these water bodies bordered by restinga vegetation (Tundisi & Tundisi, 2008). According to Junk & Furch (1993), these coastal environments are located into wide swath of mangroves distributed in the mouth of rivers from Surinam coast to Ararangua River at State of Santa Catarina (29°S), Southern Brazil. Some lakes present salinity levels due to the coastal rainwaters that are more saline than the inland rainwaters of continent (Rebouças, 2006) and influences of marine spray (Tundisi & Tundisi, 2008). A little set of lacustrine environments can support the establishment of freshwater bivalve fauna.

The second group consist in species-rich areas related with lowest values of altitude, slope, and cationic content. Lower Uruguay and Laguna dos Patos, are a complex of several types of rivers and coastal lakes at temperate zone of South America. The major tributary rivers of Laguna dos Patos system are Jacuí and Camaquã, which drain distinct geological and geomorphological unique landscapes such as mountains, valleys and plains. Headwaters of Jacuí River are located in the plateau of State of Rio Grande do Sul (Brazil) and its mouth in the central depression, where it is connected to Guaíba Lake through a complex delta system. These important hydrographic systems added to coastal lakes systems and several types of other wetlands represent high habitat diversity such as different grain size, aquatic macrophytes and bedrock favorable to the occurrence of mollusks (Lanzer and Schäfer, 1985, 1987, Mansur et al., 1988, 1991, 1994, Pereira et al., 2000, 2001, 2011, Gallon & Pereira, 2005). One of the main geomorphological features of the Lower Uruguay are the braided channels, with many depositional areas such as bars and vegetated islands, which offer a range of habitats for bivalve mollusks. Paraguay ecoregions is another complex environment that presents several types of habitats such as temporary or permanent shallow lakes, wetlands, flooded depressions, a large number of canals and rivers, and other water bodies subject to flooding (Tundisi et al., 2006) favorable to the occurrence of mollusks (Serrano, 1998, Callil and Mansur, 2005, 2007, Marçal and Callil, 2008, Callil et al, 2012, Colle and Callil, 2012). Pantanal wetland system receives waters from several geological formations, which give complex hydrogeochemical features to the aquatic ecosystem (Junk & Silva, 1995). The flood pulse of Paraguay River influence reproductive cycles of bivalves (Callil et al, 2012). Bivalve assemblies is influenced by organic matter and particle size resulting from the flood pulse of wetland system (Colle and Callil, 2012). The species composition of Paraguay ecoregion is a match of species from Amazon Hydrographic Region and La Plata System. The Pantanal is a remnant of a large intercontinental pond drained at the beginning of the Pleistocene after the formation of Madeira River (Por et al, 1997), which is tributary of Amazon River. Just as the species of Amazon Lowlands, many species have adaptations to wetland flood pulse in Paraguay ecoregion.

Addition to the direct relationship between bivalve richness and the polygon area, slope, and fish richness, the mantel test showed that the bivalve assemblies have a relationship with the environmental gradient, which was defined by set of physiographic attributes, water chemistry indicators, and climate variables.

Final considerations

Bivalve assemblies in the ecoregions assessed are structured under the influence of the polygon area, slope and fish richness. These results corroborate patterns observed in North America and Africa by several authors (Watters, 1992, Streyer, 1993, Haag and Warren, 1998 Haag, 2010, 2012, Hornbach, 2001).

In addition to the environmental macro factors, important biogeographic factors probably shaped the distribution patterns of bivalve species in the ecoregions assessed. Probably two major past geological events from Cenozoic era (Tertiary period) also influenced the current distribution patterns of the bivalve species in the ecoregions assessed. Isolation of many rivers by means the Pebas sea formation in Amazon region, followed by inversion of main flow of Amazon river promote many ways for diversification in this rich-species area (Wesselingh, 2006, Hubert and Renno, 2006). On the other hand, similar event also influenced the current species composition of bivalve assemblies of southeast and southern Brazil and bordering countries, where are also located the Lower Uruguay and Laguna dos Patos rich-species ecoregions. In this areas was formed the Paranean sea that isolated many water courses also promoting many ways for diversification (Leal 2011, Hubert and Renno, 2006). The Current "Pantanal" (Paraguay ecoregion) is a transitional area formed by means of the events described above, which corroborates by their mixed species composition of both Amazon and La Plata system. Successive marine transgressions along the Brazilian coast also modeled the bivalve assemblies from lakes and coastal rivers, especially in south Brazil where limnic species are more abundant than halophilic species.

The improved knowledge of relationships between the bivalves and fish, their vectors of spread, it is necessary for better understanding the distribution of bivalve species in these ecoregions. Understanding the influence of multiple factors in structuring bivalve assemblies in South American will subsidize the establishment of conservation strategies for the protection of ecoregion and their complex and dynamic communities.

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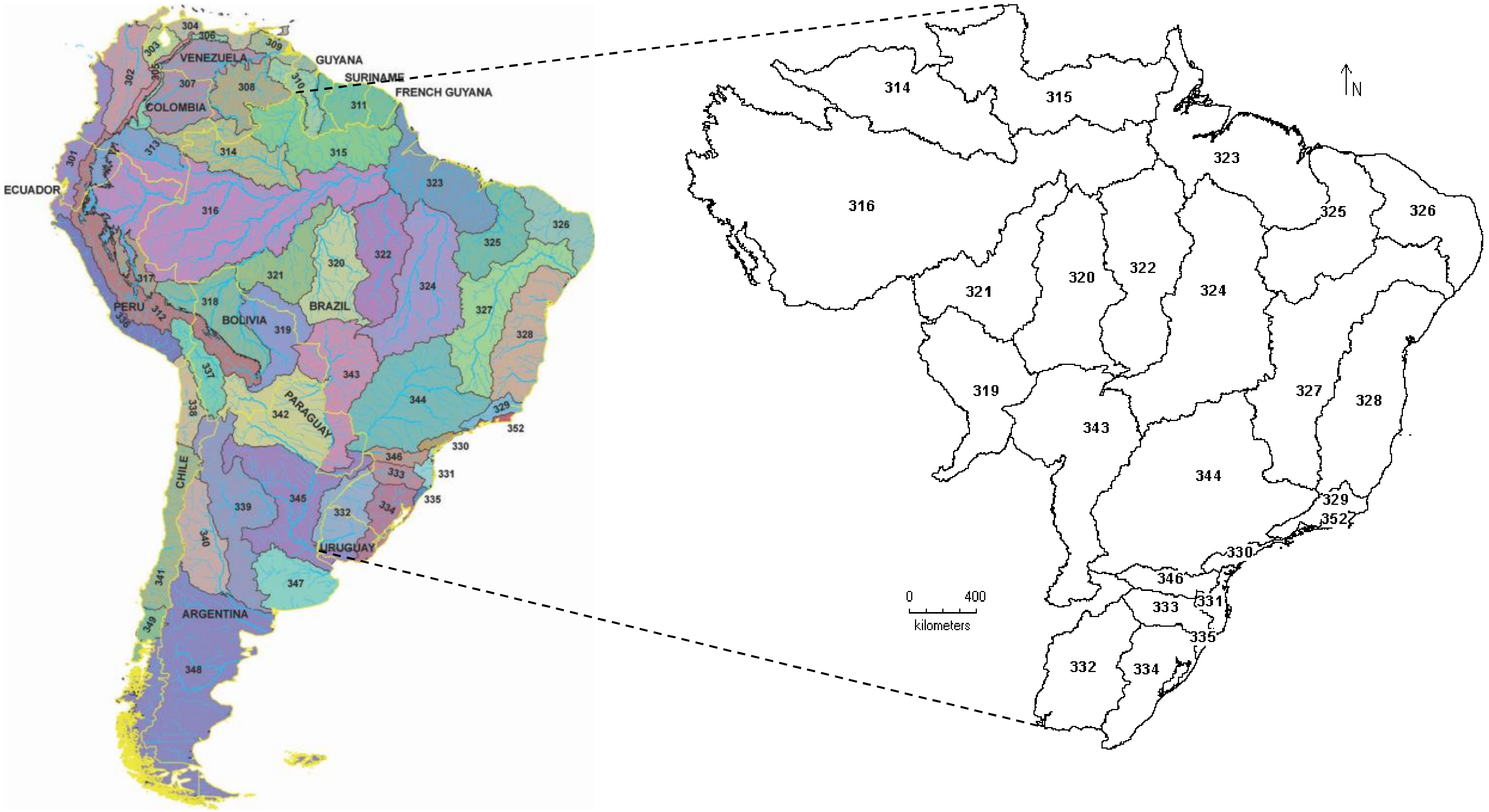

Figure1. Freshwater ecoregions of South America according to Abell et al. (2008) selected for the analysis of bivalve distribution. Map adapted from Albert et al (2011) and TNC/WWF (2013).

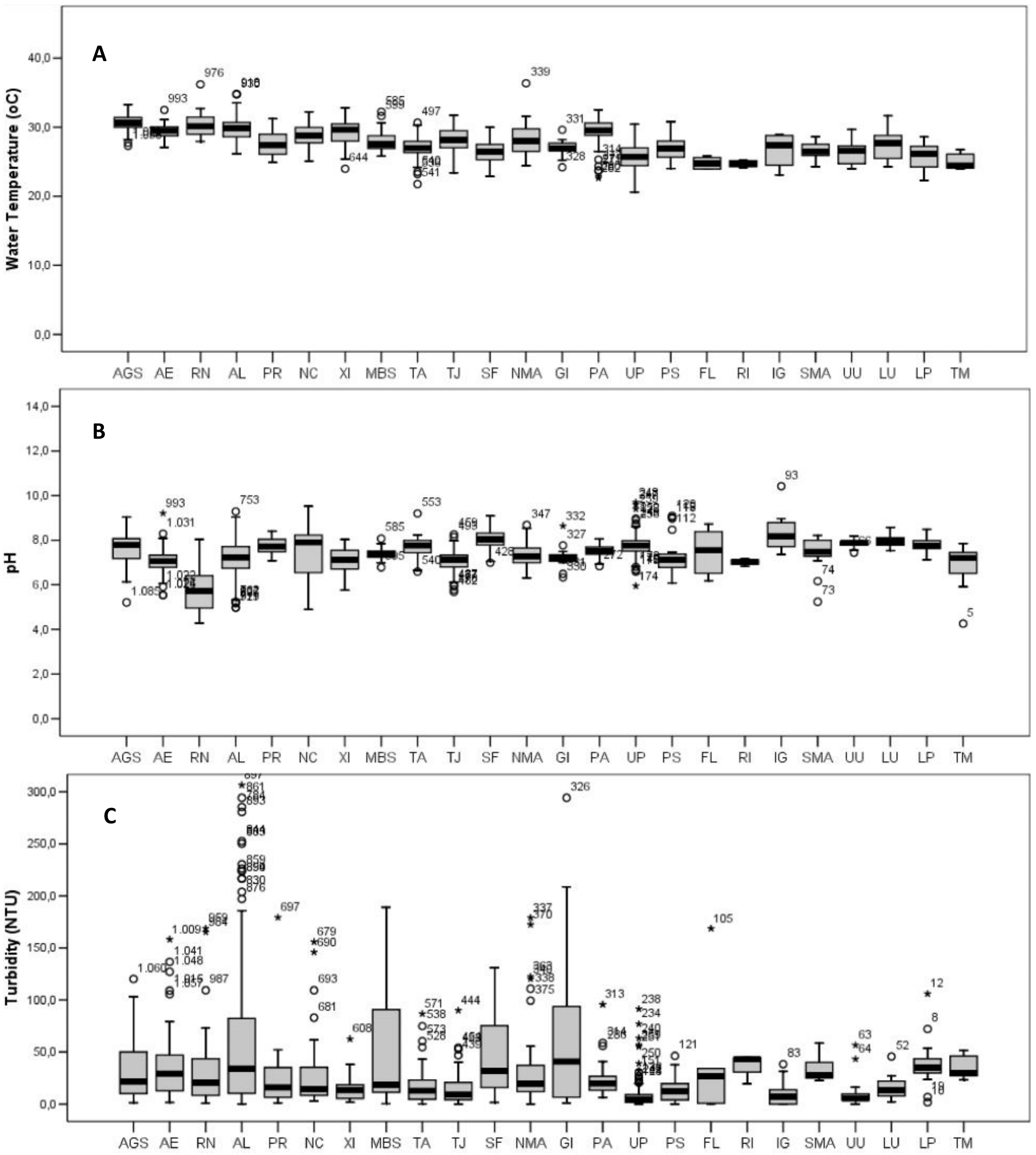

Figure 2. Box plots of water chemistry indicators in freshwater ecoregions in Brazil and bordering countries in South America, ordered from north to south and from west to east. Water temperature (A), pH (B), and Turbidity (C).

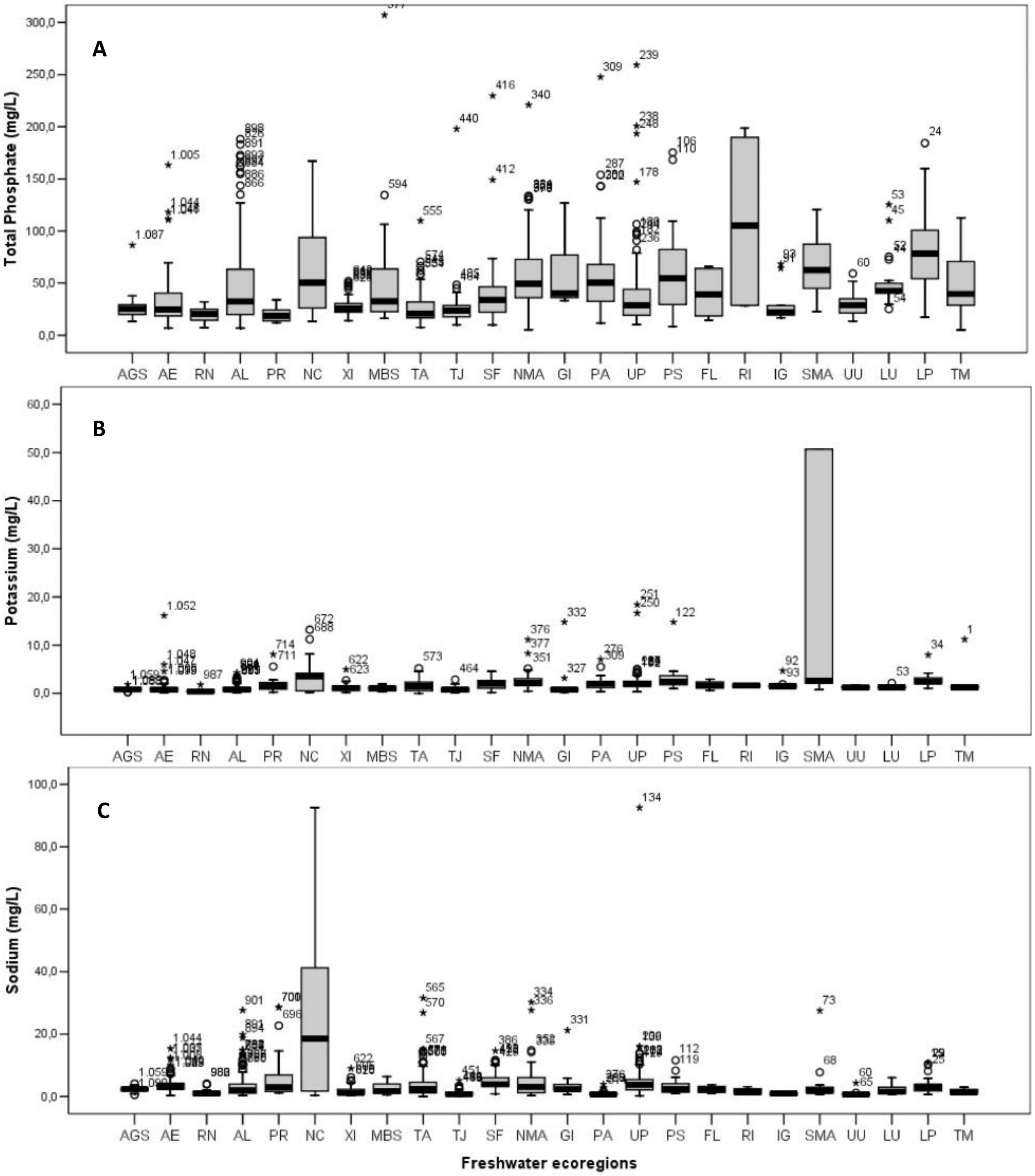

Figure 3. Box plots of water chemistry indicators in freshwater ecoregions in Brazil and bordering countries in South America, ordered from north to south and from west to east. Total phosphate (A), K^+ (B), and Na^+ (C).

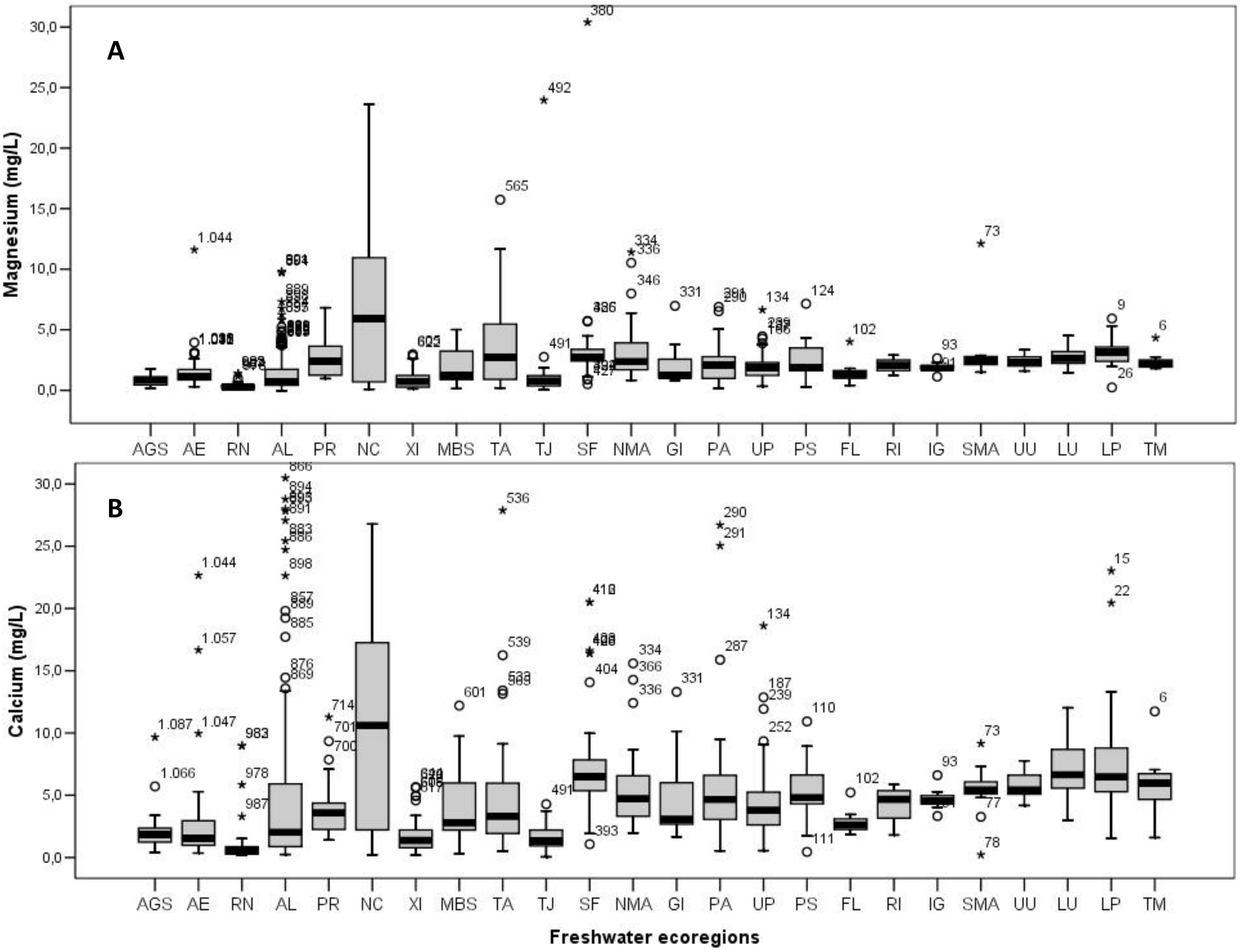

Figure 4. Box plots of water chemistry indicators in freshwater ecoregions in Brazil and bordering countries in South America, ordered from north to south and from west to east. Magnesium (A) and Calcium (B).

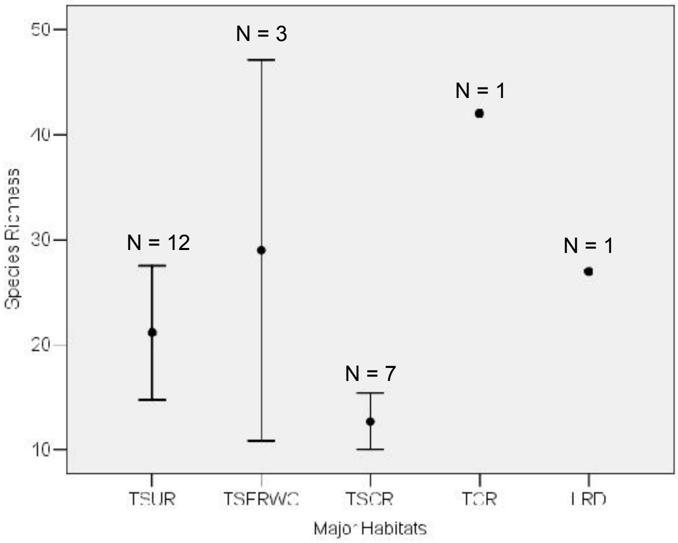

Figure 5. Bivalve species richness (average values and standard error), in major habitats of the freshwater ecoregions in Brazil and bordering countries. Tropical and subtropical upland rivers (TSUR), Tropical and subtropical floodplain rivers and wetland complexes (TSFRWC), Tropical and subtropical coastal rivers (TSCR), Temperate coastal rivers (TCR), Large river deltas (LRD). Number (N) of freshwater ecoregions in each major habitats.

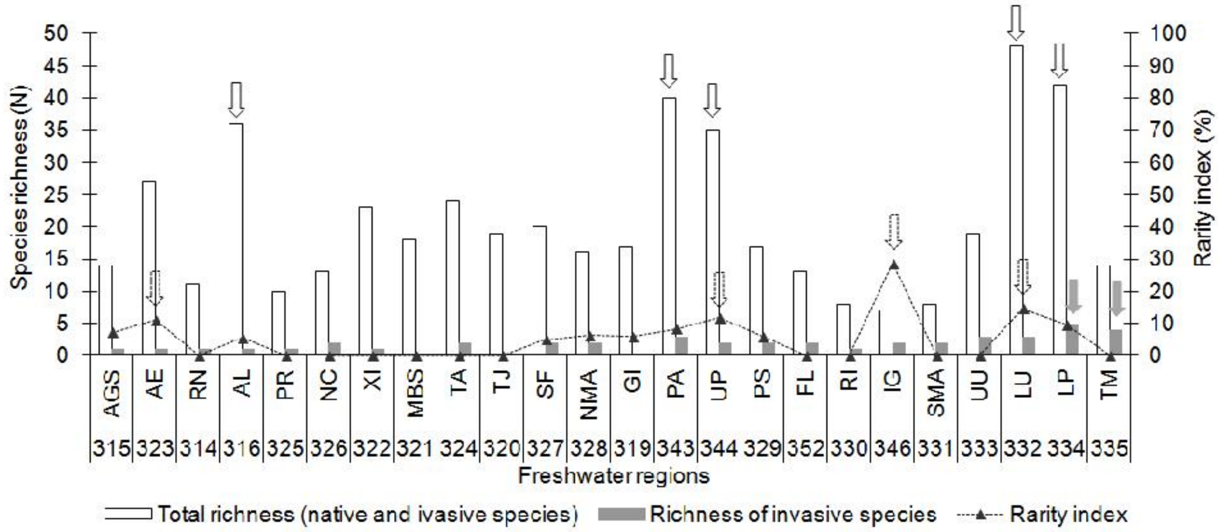

Figure 6. Species richness in the freshwater ecoregions in Brazil and bordering countries, in South America ordered from north to south and from west to east: total richness of native and invasive species, richness of invasive species and rarity index for each freshwater ecoregion. Arrows highlight the highest values.

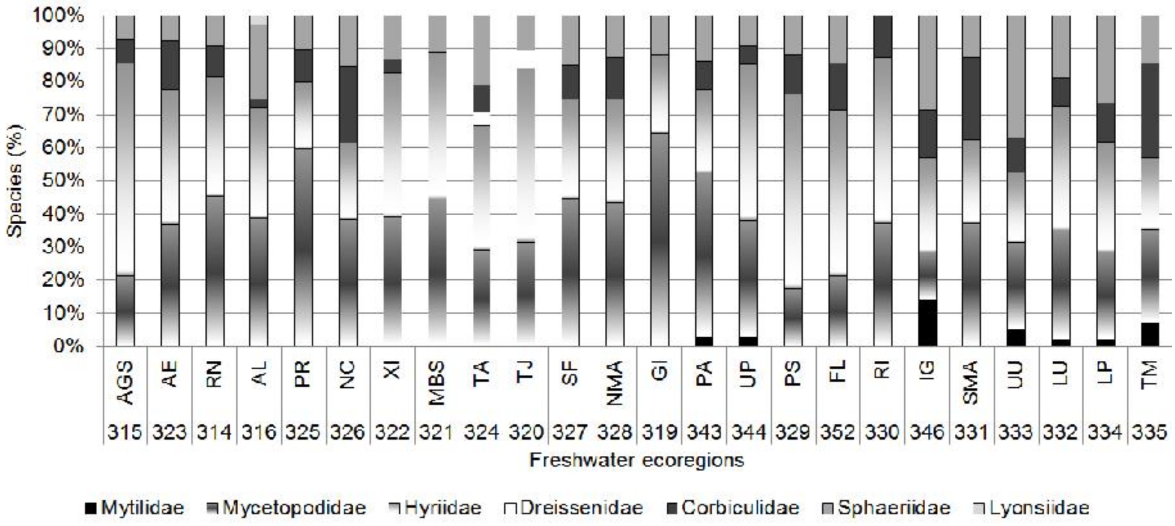

Figure 7. Species richness (%) of bivalve family in freshwater ecoregions in Brazil and bordering countries in South America, ordered from north to south and from west to east.

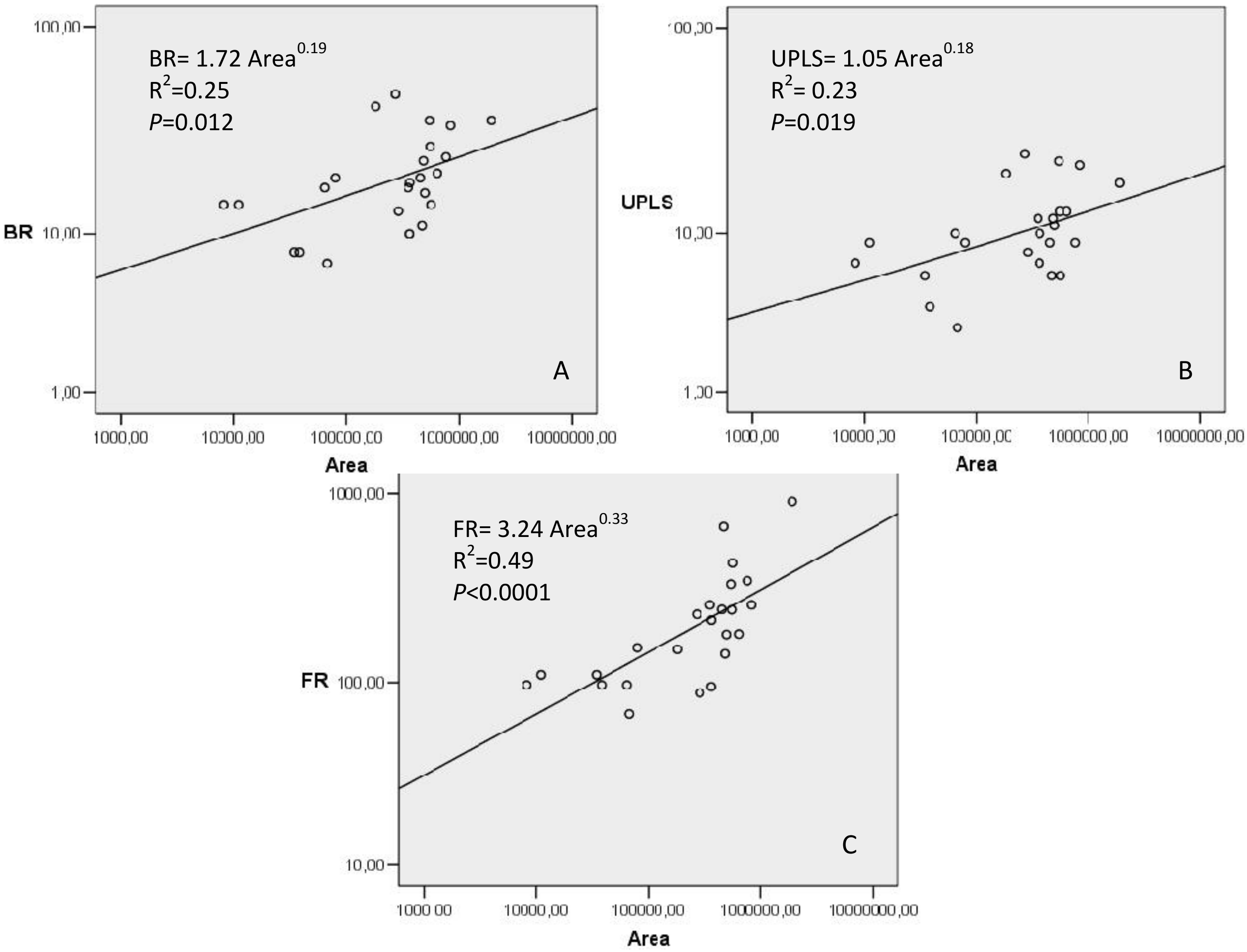

Figure 8. Species – area curve (power functions) in freshwater ecoregions in Brazil, and bordering countries, South America: bivalve richness (BR) – area curve (A), Unionoida with Parasitic Larval Stage (UPLS) – area curve (B), and fish richness (FR) – area curve.

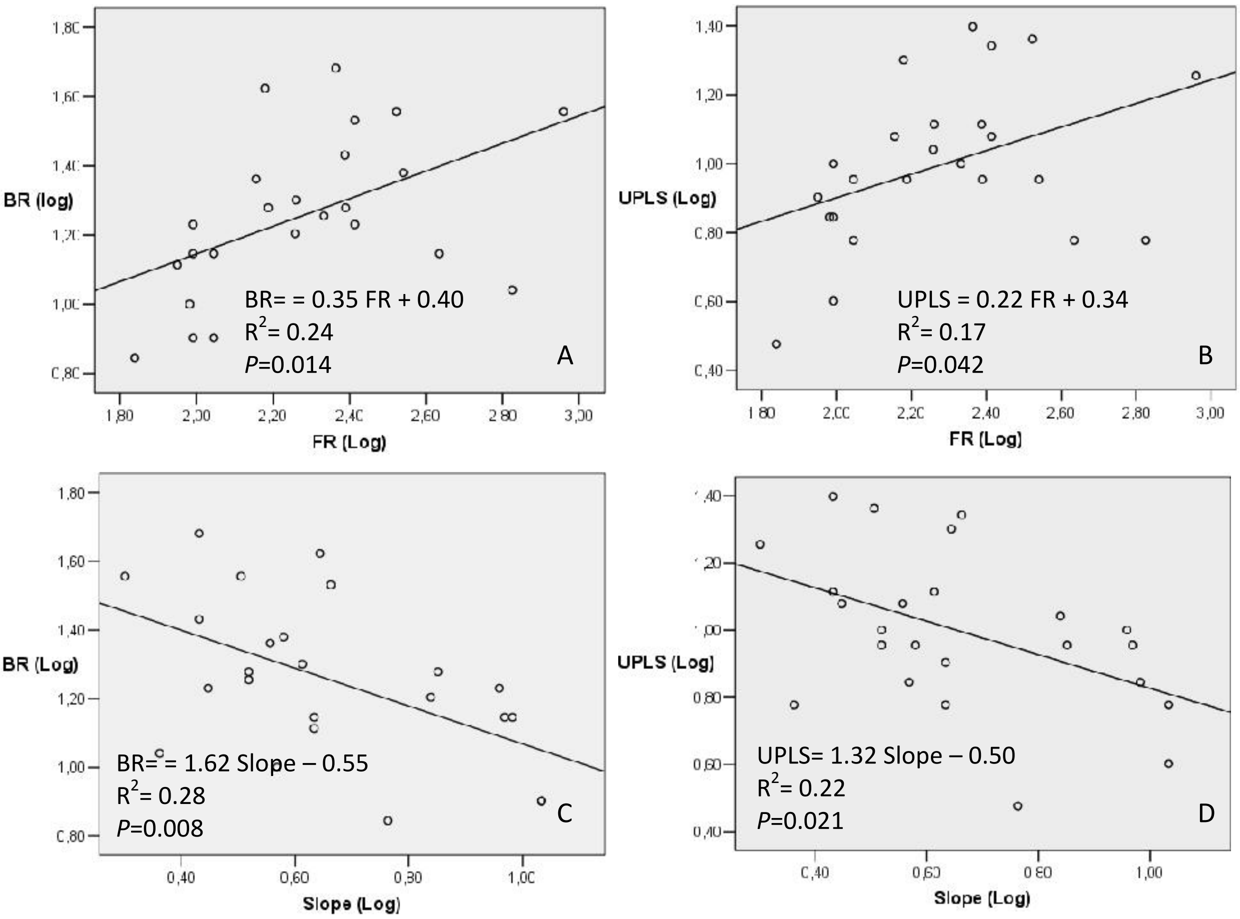

Figure 9. Bivalve richness - fish richness curve and bivalve richness – slope curve (linear functions) in freshwater ecoregions in Brazil, and bordering countries, South America: bivalve richness (BR) – fish richness (FR) curve (A), Unionoida with Parasitic Larval Stage (UPLS) – fish richness (FR) curve (B), bivalve richness (BR) – slope curve (C), and Unionoida with Parasitic Larval Stage (UPLS) – slope curve (D).

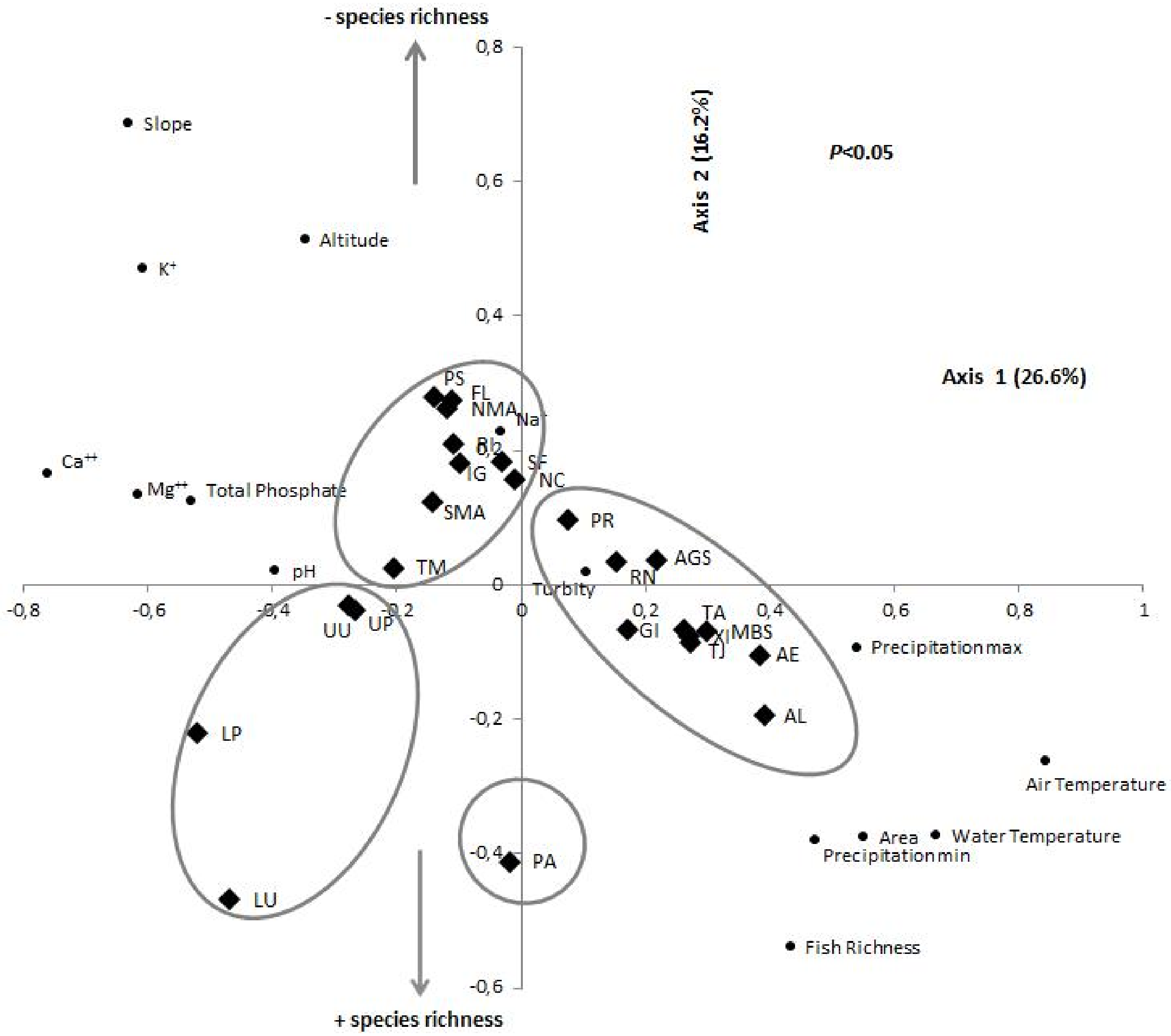

Figure 10. Principal coordinates analysis based on a dissimilarity matrix (Gower index) calculated using the presence and absence data of bivalve species recorded in the freshwater ecoregions: (A) without and (B) with rare species (presence in <5% of ecoregions). Rio Negro (RN), Amazonas Guiana Shield (AGS), Amazonas Lowlands (AL), Guapore - Itenez (GI), Tapajos - Juruena (TJ), Madeira Brazilian Shield (MBS), Xingu (XI), Amazonas Estuary & Coastal Drainages (AE), Tocantins - Araguaia (TA), Parnaiba (PR), Northeastern Caatinga & Coastal Drainages (NC), São Francisco (SF), Northeastern Mata Atlantica (NMA), Paraiba do Sul (PS), Ribeira de Iguape (RI), Southeastern Mata Atlantica (SMA), Lower Uruguay (LU), Upper Uruguay (UU), Laguna dos Patos (LP), Tramandai - Mampituba (TM), Paraguay (PA), Upper Parana (UP), Iguassu (IG), and Fluminense (FL), calcium (Ca^{++}), sodium (Na^{+}), magnesium (Mg^{++}), potassium (K^{+}).

Table 1. Freshwater ecoregions in Brazil and bordering countries according Abel et al. (2008), in South America.

Code	Freshwater ecoregion	Major Habitats
314	Rio Negro (RN)	Tropical and subtropical floodplain rivers and wetland complexes
315	Amazonas Guiana Shield (AGS)	Tropical and subtropical upland rivers
316	Amazonas Lowlands (AL)	Tropical and subtropical floodplain rivers and wetland complexes
319	Guapore - Itenez (GI)	Tropical and subtropical upland rivers
320	Tapajos - Juruena (TJ)	Tropical and subtropical upland rivers
321	Madeira Brazilian Shield (MBS)	Tropical and subtropical upland rivers
322	Xingu (XI)	Tropical and subtropical upland rivers
323	Amazonas Estuary & Coastal Drainages (AE)	Large river deltas
324	Tocantins - Araguaia (TA)	Tropical and subtropical upland rivers
325	Parnaiba (PR)	Tropical and subtropical upland rivers
326	Northeastern Caatinga & Coastal Drainages (NC)	Tropical and subtropical coastal rivers
327	São Francisco (SF)	Tropical and subtropical upland rivers
328	Northeastern Mata Atlantica (NMA)	Tropical and subtropical coastal rivers
329	Paraiba do Sul (PS)	Tropical and subtropical coastal rivers
330	Ribeira de Iguape (RI)	Tropical and subtropical coastal rivers
331	Southeastern Mata Atlantica (SMA)	Tropical and subtropical coastal rivers
332	Lower Uruguay (LU)	Tropical and subtropical upland rivers
333	Upper Uruguay (UU)	Tropical and subtropical upland rivers
334	Laguna dos Patos (LP)	Temperate coastal rivers
335	Tramandai - Mampituba (TM)	Tropical and subtropical coastal rivers
343	Paraguay (PA)	Tropical and subtropical floodplain rivers and wetland complexes
344	Upper Parana (UP)	Tropical and subtropical upland rivers
346	Iguassu (IG)	Tropical and subtropical upland rivers
352	Fluminense (FL)	Tropical and subtropical coastal rivers

Table 2. Physiographic attributes and fish richness of the freshwater ecoregions, ordered from north to south and from west to east. Area, altitude and slope obtained through Geographic information system (GIS). Precipitation and average annual air temperature (AT) compiled from (WWF/TNC, 2013). Fish richness (FR) according Albert et al (2011).

Ecoregions		Area (Km)	Polygon Centroids		Altitude (m)					Slope (%)					Precipitation (mm)			AT (°C)	FR
			x	y	Mean	STD	Min	Max	Range	Mean	STD	Min	Max	Range	Min	Max	Range	AM	
315	AGS	560636.7	58° 10' 53.02" W	1° 10' 0.84" N	255.0	191.3	8.0	2275.0	2267.0	3.3	4.8	0	69.1	69.1	1500	2500	1000	27.0	430
323	AE	552227.6	48° 8' 45.19" W	2° 39' 56.32" S	97.3	100.1	0.0	679.0	679.0	1.7	1.9	0	34.6	34.6	2000	3500	1500	26.6	243
314	RN	468524.5	65° 42' 27.09" W	0° 3' 15.94" N	126.5	143.1	7.0	2565.0	2558.0	1.3	4.2	0	106.0	106.0	1850	3500	1650	26.0	668
316	AL	1911985.8	67° 9' 49.07" W	4° 57' 49.35" S	131.2	73.9	0.0	1565.0	1565.0	1.0	1.1	0	63.8	63.8	2400	3900	1500	24.0	910
325	PR	363721.1	43° 17' 3.14" W	6° 55' 53.24" S	330.0	175.9	0.0	977.0	977.0	2.7	2.8	0	44.5	44.5	490	1970	1480	24.5	95
326	NC	286912.7	37° 54' 47.62" W	6° 9' 17.57" S	284.0	215.3	0.0	1152.0	1152.0	3.3	4.4	0	63.5	63.5	350	1140	790	23.7	88
322	XI	481628.8	53° 7' 20.69" W	8° 42' 56.05" S	307.2	89.2	72.0	843.0	771.0	2.6	3.1	0	37.7	37.7	1485	2547	1062	24.0	142
321	MBS	365474.1	61° 5' 14.42" W	9° 15' 58.26" S	186.7	94.8	13.0	1097.0	1084.0	2.3	2.5	0	49.0	49.0	1500	2700	1200	24.0	214
324	TA	760910.7	49° 29' 55.96" W	11° 24' 20.67" S	367.8	206.5	67.0	1637.0	1570.0	2.8	3.8	0	52.8	52.8	1200	2400	1200	25.5	346
320	TJ	451139.3	56° 58' 26.15" W	10° 9' 51.00" S	323.6	125.1	27.0	889.0	862.0	2.3	2.0	0	42.2	42.2	1500	2900	1400	24.0	244
327	SF	637494.7	43° 14' 50.57" W	13° 26' 52.76" S	634.0	205.6	0.0	1946.0	1946.0	3.1	3.8	0	66.9	66.9	400	1800	1400	22.5	181
328	NMA	495571.7	40° 45' 19.15" W	15° 32' 18.15" S	484.1	303.9	0.0	2773.0	2773.0	5.9	6.0	0	83.4	83.4	400	2400	2000	18.5	180
319	GI	353641.6	62° 6' 19.33" W	15° 7' 38.66" S	298.3	203.7	124.0	3501.0	3377.0	1.8	3.3	0	66.9	66.9	500	2000	1500	24.4	258
343	PA	543295.8	56° 41' 2.46" W	19° 16' 4.73" S	239.4	158.8	44.0	1275.0	1231.0	2.2	3.3	0	71.7	71.7	951	1700	749	23.0	332
344	UP	834088.7	50° 20' 23.17" W	21° 7' 16.66" S	615.8	242.2	105.0	2612.0	2507.0	3.6	3.2	0	60.0	60.0	1100	2000	900	21.0	258
329	PS	64353.9	43° 20' 56.89" W	22° 3' 48.76" S	564.7	356.7	0.0	2713.0	2713.0	8.1	8.2	0	81.4	81.4	960	2300	1340	17.5	97
352	FL	11059.0	42° 37' 4.00" W	22° 38' 39.79" S	169.8	292.9	0.0	2153.0	2153.0	8.3	11.3	0	89.0	89.0	800	2000	1200	18.3	110
330	RI	34499.2	47° 44' 20.09" W	24° 23' 32.81" S	485.1	367.4	0.0	1972.0	1972.0	9.8	9.6	0	78.4	78.4	1100	3500	2400	19.0	110
346	IG	67547.7	51° 39' 33.38" W	25° 52' 37.57" S	796.7	240.5	105.0	1491.0	1386.0	4.8	3.9	0	42.9	42.9	1275	2250	975	17.5	68
331	SMA	38300.2	49° 8' 16.60" W	26° 57' 0.15" S	397.6	324.3	0.0	1740.0	1740.0	9.8	8.7	0	79.6	79.6	1334	2525	1191	18.0	97
333	UU	79546.8	51° 48' 13.73" W	27° 28' 13.70" S	767.3	266.4	161.0	1778.0	1617.0	6.1	4.6	0	44.7	44.7	1236	1425	189	16.0	153
332	LU	270059.8	56° 8' 1.62" W	30° 41' 14.18" S	144.7	101.4	0.0	616.0	616.0	1.7	1.7	0	26.2	26.2	823	1905	1082	18.5	230
334	LP	181520.0	52° 49' 56.74" W	31° 2' 21.70" S	222.7	245.4	0.0	1255.0	1255.0	3.4	4.5	0	51.9	51.9	1000	2100	1100	17.0	150
335	TM	8246.3	49° 47' 20.37" W	29° 7' 0.31" S	220.0	315.3	0.0	1452.0	1452.0	8.6	12.2	0	72.3	72.3	1300	2060	760	17.0	97

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Species	Freshwater ecoregions																								N	%
	315	323	314	316	325	326	322	321	324	320	327	328	319	343	344	329	352	330	346	331	333	332	334	335		
	AGS	AE	RN	AL	PR	NC	XI	MBS	TA	TJ	SF	NMA	GI	PA	UP	PS	FL	RI	IG	SMA	UU	LU	LP	TM		
Anodontites (A.) trapesialis (Lea, 1860)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	23	96
Corbicula fluminea (Müller, 1774)^IS^	1	1	1	1	0	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	20	83
Mycetopoda siliquosa (Spix, 1827)	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	17	71
Corbicula largillierti (Philippi, 1844) ^IS^	0	0	0	0	1	1	0	0	1	0	1	1	0	1	0	1	1	0	0	1	1	1	1	1	13	54
Anodontites (A.) elongatus (Swainson, 1823)	0	1	0	1	1	0	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	1	0	0	12	50
Anodontites (A.) trapezeus (Spix, 1827)	0	0	0	1	0	1	1	0	1	0	1	1	0	1	1	0	0	0	0	0	1	1	1	1	12	50
Castalia ambigua Orbigny, 1835	1	1	1	1	1	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	12	50
Anodontites (L.) ensiformis	0	1	1	1	1	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	11	46
Pisidium dorbignyi Clessin, 1897	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	1	1	1	0	11	46
Anodontites (A.) tenebricosus (Lea, 1834)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	10	42
Eupera simoni (Jousseaume, 1889)	1	1	1	1	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	10	42
Diplodon (D.) suavidicus (Lea, 1856)	1	1	0	1	0	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	9	38
Prisodon obliquus Schumacher, 1817	1	1	1	1	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	9	38
Anodontites (A.) crispatus Bruguière,1792	1	1	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	8	33
Diplodon (D.) multistratus (Lea, 1834)	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	1	0	8	33
Diplodon (D.) obsolescens (Baker, 1913)	1	1	0	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	33
Triplodon corrugatus (Lamarck, 1819)	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	33
Eupera bahiensis (Spix & Wagner, 1827)	0	0	0	1	1	1	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	8	33
Limnoperna fortunei (Dunker, 1857) ^IS^	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	1	1	7	29
Anodontites (*A.*) *patagonicus* (Lamarck, 1819)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	1	7	29
Anodontites (*A.*) *schomburgianus* (Sowerby, 1870)	1	1	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	7	29
Leila esula (Orbigny, 1835)	0	1	1	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	7	29
Diplodon (D.) rhombeus (Spix, 1827)	0	0	0	1	0	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	7	29
Eupera tumida (Clessin, 1879)	0	1	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	7	29
Anodontites (*A.*) *soleniformis* (Lamarck, 1819)	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	6	25
Monocondylaea corrientesensis Orbigny, 1834	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	0	6	25
Tamsiella schroeteriana (Lea, 1852)	0	1	1	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	6	25
Diplodon fontainianus (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	0	0	0	0	0	0	6	25

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	AGS	AE	RN	AL	PR	NC	XI	MBS	TA	TJ	SF	NMA	GI	PA	UP	PS	FL	RI	IG	SMA	UU	LU	LP	TM		
Paxyodon syrmathophorus (Meuschen, 1781)	1	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	25
Pisidium sterkianum Pilsbry, 1897	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	6	25
Fossula fossiculifera (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	5	21
Diplodon (D.) aethiops (Lea, 1860)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	5	21
Diplodon (D.) besckeanus (Dunker, 1848)	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	5	21
Diplodon (D.) ellipticus (Wagner, 1827)	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	5	21
Diplodon (D.) martensi (Ihering, 1893)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	5	21
Diplodon (R.) hylaeus (Orbigny, 1835)	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	5	21
Castalia quadrata (Sowerby, 1869)	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	21
Leila blainvilliana (Lea, 1834)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	4	17
Diplodon (D.) expansus (Küster, 1856)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	4	17
Diplodon (D.) granosus (Bruguière, 1792)	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	17
Diplodon (R.) charruanus Orbigny, 1835	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	4	17
Castalia duprei (Récluz, 1842)	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	17
Castalia inflata Orbigny, 1835	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	4	17
Triplodon chodo Mansur & Pimpão, 2008	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	17
Cyanocyclas limosa (Maton, 1809)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	4	17
Eupera guaraniana Ituarte, 1994	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	4	17
Eupera klappenbachi Mansur & Veitenheimer, 1975	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	4	17
Pisidium vile Pilsbry, 1897	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	4	17
Anodontites (A.) *obtusus* (Lamarck, 1819)	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3	13
Mycetopoda legumen (Martens, 1888)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	3	13
Mycetopoda soleniformis Orbigny, 1835	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	3	13
Monocondylaea franciscana (Moricand, 1837)	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3	13
Monocondylaea jaspidea Hupé, 1857	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	13
Monocondylaea minuana Orbigny, 1835	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	3	13
Monocondylaea paraguayana Orbigny, 1835	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	3	13
Diplodon (D.) berthae Ortman, 1921	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	3	13

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	AGS	AE	RN	AL	PR	NC	XI	MBS	TA	TJ	SF	NMA	GI	PA	UP	PS	FL	RI	IG	SMA	UU	LU	LP	TM		
Diplodon (D.) delodontus (Lamarck, 1919)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	3	13
Diplodon (D.) parallelopipedon (Lea, 1834)	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	3	13
Diplodon paranensis (Lea, 1834)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	3	13
Castalia orbignyi (Deville & Hupé, 1850)	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	13
Castalia psamoica	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	3	13
Musculium argentinum (D'Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	3	13
Pisidium taraguyense Ituarte, 2000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	3	13
Sphaerium cambaraense Mansur, Meier-Brook & Ituarte, 2008	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	3	13
Anodontites (A.) ferrarisi (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	8
Anodontites (A.) lucidus (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	8
Mycetopodella falcata (Higgins, 1868)	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	8
Monocondylaea costulata Moricand, 1858	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	8
Monocondylaea guarayana Orbigny, 1835	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	8
Bartlettia stefanensis Moricand, 1856	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	8
Diplodon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	8
Diplodon (D.) dunkerianus (Lea, 1956)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	8
Diplodon (D.) paulista (Ihering, 1893)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2	8
Diplodon (D.) rhuacoicus (Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	8
Diplodon (D.) vicarius Ortmann, 1821	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	8
Diplodon (D.) wymanii (Lea, 1860)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	8
Diplodon (R.) deceptus Simpson, 1914	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	8
Diplodon rotundus Wagner, 1827	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2	8
Castalia martensi (Ihering, 1891)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	8
Mytilopsis lopesi Alvarenga & Ricci,1989	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	8
Cyanocyclas paranensis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	2	8
Corbicula fluminalis (Müller, 1774)^{IS}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	8
Eupera iguazuensis Ituarte, 1989	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	2	8
Eupera platensis Doello-Jurado, 1921	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	8

Table 3. Bivalves species in the freshwater ecoregions in Brazil and bordering countries, ordered from north to south and from west to east. Occurence frequency (N and %) of bivalve species in ecoregions: <25% (□), 25 to 50% (░), 51 to 75% (▒), >75% (■). Invasive species^{IS}, Endemic species^{ES} (continuation).

Species	Freshwater ecoregions																								N	%
	315	323	314	316	325	326	322	321	324	320	327	328	319	343	344	329	352	330	346	331	333	332	334	335		
	AGS	AE	RN	AL	PR	NC	XI	MBS	TA	TJ	SF	NMA	GI	PA	UP	PS	FL	RI	IG	SMA	UU	LU	LP	TM		
Pisidium bejumae H.B. Baker, 1930	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	8
Pisidium boliviense Sturany, 1900	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	8
Pisidium forense Meier Brook, 1967	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	2	8
Pisidium globulus (Clessin, 1888)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	8
Anodontites (A.) iheringi (Clessin, 1882) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	4
Anodontites (A.) moricandi (Lea, 1860) ^{ES}	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
Monocondylaea parchappi Orbigny, 1835 ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	4
Tamsiella amazonica Bonetto, 1972 ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	4
Haasica balzani (Ihering, 1893) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	4
Diplodon (D.) caipira (Ihering1893) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	4
Diplodon (D.) imitator Ortman, 1921 ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	4
Diplodon (D.) piceus (Lea, 1860) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	4
Diplodon (R.) burroughianus (Lea, 1834) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	4
Diplodon (R.) koseritzi (Clessin, 1882) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	4
Diplodon (R.) hildae Ortman, 1921 ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	4
Diplodon (R.) iheringi (Simpson, 1900) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	4
Diplodon greeffeanus Ihering, 1893 ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	4
Diplodon pfeifferi (Dunker, 1848) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	4
Diplodon (R.) variabilis (Maton, 1811) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	4
Diplodon solisianus (d´Orbigny, 1835) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	4
Diplodon (R.) peraeformis (Lea, 1860) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	4
Diplodon decipiens^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	4
Diplodon (D.) parodizi Bonetto, 1960ES	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	4
Diplodon uruguayensis (Lea, 1860) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	4
Castalia nehringi (Ihering, 1893) ^{ES}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	4
Castalia sulcata (Krauss, 1849) ^{ES}	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
Castalia undosa Martens, 1885ES	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	4
Cyanocyclas amazonica (Prime, 1870) ^{ES}	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
Cyanocyclas brasiliana (Deshayes, 1854) ^{ES}	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4

Table 3. Bivalves species in the freshwater ecoregions in Brazil and bordering countries, ordered from north to south and from west to east. Occurence frequency (N and %) of bivalve species in ecoregions: <25% (□), 25 to 50% (░), 51 to 75% (▒), >75% (▓). Invasive species^{IS}, Endemic species^{ES} (continuation).

Species	Freshwater ecoregions																								N	%
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	AGS	AE	RN	AL	PR	NC	XI	MBS	TA	TJ	SF	NMA	GI	PA	UP	PS	FL	RI	IG	SMA	UU	LU	LP	TM		
Corbicula sp. ^{IS}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	4
*Polymesoda solida (*Phillipi, 1846)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
Polymesoda aequilatera (Deshayes, 1854)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
Eupera elliptica Ituarte & Mansur, 1993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	4
Eupera doellojuradoi Klappenbach, 1962ES	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	4
Pisidium iquito Ituarte, 2004ES	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
Anticorbula fluviatilis H.Adams,1860ES	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4

Table 4. Equations obtained by multiple regression based on all dataset freshwater ecoregions in Brazil and bordering countries, ordered from north to south and from west to east. Bivalve richness (BR) and average annual air temperature (AT). *Standardized values of slope and altitude: Log (x+1). ** $P < 0.0001$, ** P =.0.02

Equation*	F	R^2	R^2 (Adj)	*P*
BR = 4.56 - 0.98 Slope** - 1.95 Alt***	8.73	0.45	0.40	0.02

Capítulo 3

Can limnological variables influence the recruitment and survival of the invasive bivalve *Limnoperna fortunei* (Dunker, 1857)?

Can limnological variables influence the recruitment and survival of the invasive bivalve *Limnoperna fortunei* (Dunker, 1857)?

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Abstract

The environmental and economic impacts of invasive bivalve *Limnoperna fortunei* (Dunker, 1857) in South America are widely known. However, little is known about the factors that influence its recruitment and survival. In order to evaluate the influence of limnological variables on recruitment, during the period between October 2006 and September 2007 artificial substrates were exposed in two sampling stations located in an inner delta in the South of Brazil. The first design presented the monthly exposure of three replicates of the artificial substrate. After 30 days, during the period of twelve months, the substrate was removed from the water in order to have the attached mussels (recruits and adults) removed, and replaced with a new substrate. The recruits and adults were quantified, thereby obtaining the monthly abundance for these two development phases. The second design included the submersion of twelve sets of three replicas of artificial substrates in October 2006. A set of triplicates was removed every month for 12 months, and consequently obtained colonization records for different exposure times (2 to 12 months), or cumulative abundance values. The variance and multivariate analyses of monthly [larval (ind.m^{-3}) and recruits density (ind.m^{-2})] and cumulative [recruits and adults density (ind.m^{-2})] population descriptors and limnological variables showed definite seasonality. The release of larvae and recruitment began in the spring. The variation of the descriptors was associated with water temperature, conductivity, total alkalinity, total sulfates and total solids. The survival of the golden mussel in the pH range 4-11 after 120 hours of exposure can enable the survival of populations under adverse and intermittent conditions in the aquatic environment. It is worth noting the potential of golden mussel for colonization of acidic waters.

Key words: golden mussel, limiting limnological variables, forecast, population density, recruitment.

Introduction

The Asian clam *Limnoperna fortunei* (Dunker, 1857), introduced in South America in the early 1990s (Darrigran & Pastorino, 1995) is an invasive engineer species which causes significant environmental and economic impacts on both natural and built systems (Darrigran & Damborenea, 2011). The golden mussel was first recorded in mid-1998 in the inner delta of Jacuí River (Mansur et al., 1999 and 2003), Southern Brazil, and in the same year near Corumbá, in the Paraguay River (Oliveira, 2003), in the Central-West region of Brazil. Currently, the golden mussel is present in water bodies of five South American countries and chances are that it will disperse itself among other hydrographic basins of the continent (Pereira et al., 2013). According to Oliveira et al. (2010), predictive distribution scenarios using modeling tools showed that this invasive species also can disperse and establish itself in the North American watersheds.

The elimination of *L. fortunei* becomes impractical after the consolidation of populations in the invaded environment, thus only measures to prevent and control its spread along the continental watersheds (Darrigran et al., 2012a) are possible. The reproductive patterns of *L. fortunei* are slightly different in the original and invaded areas according to climatic regions (Damborenea & Penchaszadeh, 2009). Therefore, the recognition of dispersal patterns, of tolerance levels to extreme conditions, and environmental variables related to population fluctuations, are key factors to establishing management measures of invasive species in each invaded area.

The distribution of golden mussels along the South American watersheds and their relationship with environmental variables has been investigated, based on prediction models of dispersion scenarios (Oliveira et al. 2010a, 2010b; Barbosa & Melo, 2009; Darrigran et al., 2011, 2012b), and risk assessment indexes of watersheds contamination and their vulnerability to bioinvasion (Belz et al., 2012). However, the relationship between *L. fortunei* and environmental variables is poorly understood, although several references to this subject are found in the literature (Capítoli et al., 2008; Santos et al., 2008; Oliveira et al. 2010c, 2011; Campos et al., 2012, Pereira et al., 2012b). There is still a gap in knowledge about which variables are related to the larval production and release as well as recruitment of substrates. The recognition of predictor variables of *L. fortunei* population densities in each climatic region invaded can provide essential information for their management.

Most studies on survival of *L. fortunei* were based on exploratory data analysis of the occurrence data of the golden mussel associated with environmental variables in environmental gradients (Oliveira et al. 2010c, 2011; Campos et al., 2012). A given environmental gradient analysis, extreme situations of a particular limnological variable that influences the survival of the invader species are not always found. On the other hand, the dataset obtained at field and laboratory studies, about the tolerance levels of invasive species exposed to extreme conditions of limnological variables is distinct, due to synergism of factors. Therefore, laboratory tests provide more effective information about cause and effect or dose and response between limnological variable and organism survival rate, under controlled experimental conditions.

The maintenance of ionic composition of the body fluid and pH are of fundamental importance to homeostasis (Clark et al., 2004). It is one of the most important factors limiting the distribution and survival of freshwater bivalves (McMahon, 1991; Haag, 2012). The range of pH that limits the dispersal and survival of the golden mussel has sparked a controversy (Villar et al. 1997; Boltovskoy et al., 2006; Oliveira et al. 2006, 2010a, 2011; Darrigran et al., 2011).

This study aims to evaluate the influence of limnological variables on the recruitment of golden mussels in a seasonal cycle in a continental delta system in the South of Brazil, and also to evaluate the tolerance and survival of this invasive species in a wide range of pH.

Methods

Study Area

The study area is located in the inner delta of the Jacuí River (Figure 1), in the physiographic unit of the Central Depression of Rio Grande do Sul State, south of Brazil. The waters of this delta flows into the Guaiba Lake, which is connected to Patos Lagoon, and the latter to Atlantic Ocean. The Patos Lagoon basin is part of the great basin of rivers that flow into the South Atlantic, in the south of Brazil. The inner delta of the Jacuí River includes a set of sixteen islands, marshes and distributary channels, among which we highlight the Jacuí Canal and Navegantes Canal. The Jacuí Canal receives water flow from Jacuí River and the Navegantes Canal from Gravataí River. The Jacuí River drains extensive agricultural areas and the Gravataí River drains urban areas densely populated. Consequently, the first river contributes to good water quality in the Jacuí Canal, while the Gravataí River contributes to poor water quality in the Canal dos Navegantes (Faria & Lersch, 1998, Bendati et al, 2003). The inner delta of the Jacuí River has altitude between 2 and 5 m (Hasenack & Menegat, 1998) and covers soil resulting from deltaic Quaternary deposits (Menegat et al. 1998). The type of climate is temperate Cfa, with a humid winter. Regarding the air temperature, the average annual absolute highest temperature is 37.8° C and the absolute lowest is 1.4° C (Liv, 1998). One of the two sampling stations is situated on the right bank of the Jacuí Canal (JC), near the Pintada Island (30° 00'48, 29" S, 51º 15'36, 46" W), and the other on the shore of the Navegantes Canel (NC), at the Cais do Porto, specifically on the dock of the Fire Department (30º 01'31, 08" S, 51º 13'38, 26" W), near the historical center of the Porto Alegre City. The study area was chosen because it presents one of the most ancient and consolidated populations of *L. fortunei* in Brazil.

Recruitment process monitoring

The influence of limnological variables on recruitment of *L. fortunei* was investigated through monitoring actions of the population every month. To this end, artificial substrates were exposed at both sampling stations, from October 2006 to September 2007. The three phases of development of the golden mussel described by Santos et al. (2005 and 2008) were evaluated: the planktonic larvae with length <0.15 mm, benthic recruits, with a length of 0.15-0.5 mm, and benthic adult, >0.5 mm.

Plankton samples were collected every month in the same locations for the quantification of monthly larval density. Water samples were filtered and concentrated using plankton net with mesh 30μm and a motor pump as described in Santos et al. (2012). The suction of water (1000L) was made on the surface about 50 cm deep, with three replicas of filtered water at each collection station. The samples were fixed in 70% alcohol. The determination and quantification of larvae followed the method of Santos et al. (2005 and 2012) respectively.

Adults and recruit individuals were sampled with artificial substrates, thus standardizing the sampling and reducing the variability (Gibbons et al. 1993), which is common in natural substrates with different patterns of texture, surface roughness and porosity. Also, it enables quantification of individuals per area, which becomes unfeasible or inaccurate in natural substrates with irregular surface (Pereira et al., 2012a). X-shaped artificial substrate manufactured using wood (total sampling area: 0.072 m^2), adapted from Morton (1977) by Mansur et al. (2009) was used. The substrates were fixed in a pier situated on the shore of the Pintada Island, in the Jacuí Canal (JC), and suspended below a floating platform in the dock harbor, in the Navegantes Canal (NC).

Two sample designs described in Pereira et al (2012a) were used. The first design presented the monthly exposure of three replicates of the artificial substrate. After 30 days, during the period of twelve months, the substrate was removed from the water in order to have the attached mussels (recruits and adults) removed, and replaced with a new substrate. The recruits and adults were quantified, thereby obtaining the monthly abundance for these two development phases. The second design included the submersion of twelve sets of three replicas of artificial substrates in October 2006. A set of triplicates was removed every month for 12 months, and consequently obtained colonization records for different exposure times (2 to 12 months), or cumulative abundance values.

All sampling procedures and quantification of larvae and adults on the substrate are described in detail in Pereira et al. (2012a). Abundance figures were transformed into density in view of the sampling area of the substrate (0,0722m^{-2}). The following population descriptors of *L. fortunei* recruitment were considered: the values of monthly larval density ($ind.m^{-3}$), monthly density of recruits, cumulative density of recruits and cumulative density of adults ($ind.m^{-2}$). The processing of biological material was performed at the Laboratory of Malacology, Museum of Science and Technology of the Pontifical Catholic University of Rio Grande do Sul (PUCRS).

In monitoring period, water samples were collected for physical, chemical and microbiological analyses at both sampling stations every month. All analyses and sample collections were conducted with methods described in APHA (2001). The analyses were performed at the Laboratory of Environmental Processes (LAPA) of the Pontifical Catholic University of Rio Grande do Sul (PUCRS). Limnological variables analyzed were water temperature (mercury thermometer), dissolved oxygen (titration), chemical oxygen demand (open reflux and titration), pH (potentiometry), conductivity (conductivimetry), alkalinity (titration), the total hardness (titration), sulfate (turbidimetry), total phosphorus (colorimetric with ascorbic acid), nitrates (colorimetric with salicylate), ammoniacal nitrogen (nesslerization), total and fecal coliforms (chromogenic substrate).

In order to assess the seasonal variation of *L. fortunei* recruitment, population descriptors values were logarithmized (log (x +1)) and then compared through analysis of variance (ANOVA, *Duncan a posteriori test*, α=0.05). In order to assess the spatial variation, the records were compared to logarithmized values of population descriptors of *L. fortunei* recruitment verified in study sites by *Tukey* (α=0.05). The same procedure was used for the evaluation of seasonal and spatial variation of logarithmized values of limnological variables, with the exception of nitrate variable, which showed normal distribution through the *Kolmogorov-Smirnov* test for one sample (H0: data follow the normal distribution), with a significance level of 95%. The correlation coefficients (*Spearman's rho*) were obtained between population descriptors and limnological variables using the SPSS 13.0 software. All dataset collected in both samplings stations in the delta of the Jacuí River were taking into consideration for this analysis. The temporal and spatial relation between population descriptors and limnological variables were evaluated by means of canonical correspondence analysis (CCA), then the correlation of matrices by means *Monte Carlo* test ($\alpha \leq 0.01$) using the PC-ORD software, considering all dataset collected in both samplings stations. Predictive equations of population descriptors of *L. fortunei* recruitment (response variables) depending on limnological variables (predictors) were obtained through models generated by multiple regressions, considering all dataset collected in both samplings stations. Standardized data through the same procedures described above, adopted in the others statistical analyses, and were used in multiple regression analysis using SPSS 13.0 software (stepwise method). Models were generated considering the assumptions of normality, homoscedasticity, errors independence, multicollinearity, and linearity.

pH Tolerance

Experimental Design. The evaluation of the survival of golden mussels was based on stand experiments. Clusters of golden mussel were collected at Jacuí Canal (JC), disaggregated and washed in running water, brushed to remove algae, dipped in sterile distilled water three times consecutively, separated by size from 0.6 to 10 mm and then placed in becker glasses with 300 mL of test solution (10 individuals / bottle). The stones and aeration hoses were sanitized with 70% ethanol and then washed with distilled water three times in order to have the alcohol removed. The aeration stones and hoses were connected to aerators and then this kit was inserted into a becker glass (500mL) with 250 mL of reconstituted water. Ten organisms were introduced into each recipient, and then acclimated for 72 hours.

The following pH values were considered in the exposure tests golden mussel: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12 and 13. The solutions were obtained by adjusting the pH of the reconstituted water with salts, whose formulation is stated in Pereira et al. (2012c). To adjust the pH solutions hydrocloric acid (acid pH) and potassium hydroxide (basic pH) were used. The cultivation medium was renewed every 24 hours due to change in pH by virtue of the release of pseudofeces. Each treatment and control was assayed in triplicate and the experiment as a whole was repeated three times. Both experiments were carried out in a climatic chamber with an average air temperature of 21±1° C in the dark.

The organisms were fed with a mixture of *Monoraphidium* sp. culture (algae) and mashed fish feed. Every 24 hours, 2.5 mL of mixture was added in each flask containing mussels. The design of both trials followed procedures described in Pereira et al. (2012c). For the assessment of mortality the criteria established by Soares et al. (2009) were considered. All experiments were carried out at the Ecotoxicology Laboratory, Federal University of Rio Grande do Sul (UFRGS). The Letal pH to cause the mortality of 50% (LpH_{50}) of *L. fortunei* individuals and lethal time to cause the mortality of 50% (LT_{50}) of *L. fortunei* individuals at different pH values were calculated using the BioStat software.

Results

Population Descriptors of *L. fortunei* Recruitment.

No significant spatial differences were verified using analysis of variance (t test, $\alpha = 0.05$), on the values of monthly larval density ($P = 0.39$) and of monthly density of recruits ($P = 0.97$) (Figure 2A), as well as of cumulative density of recruits and adults ($P = 0.96$ and $P = 0.97$) respectively (Figure 2C). The monthly larval density, monthly density of recruits and cumulative density of recruits showed a peak in the spring, while the cumulative density of adults was verified in the winter. Adult individuals were observed in the fifth month of exposure to the substrates (Figure 2). Significant seasonal differences were verified using analysis of variance (ANOVA, *Duncan* retrospectively, $\alpha = 0.05$), population descriptors: as the monthly larval density (Figure 2C), two different seasonal groups (G1, spring and summer, G2, autumn and winter); monthly density of recruits (Figure 2C), three seasonal groups (G1, spring and summer G2, autumn, G3, winter), cumulative density of recruits (Figure 2D), four seasonal groups (G1, spring, G2, summer, G3, autumn, and, G4, winter), and cumulative density of adults (Figure 2D), three seasonal groups (G1, spring, G2, summer, G3, autumn and winter). The following correlation coefficients of *Spearman's rho* among population descriptors were observed: monthly larval density *versus* monthly density of recruits (r = 0.66, *P* <0.001), monthly larval density *versus* cumulative density of recruits (r = 0.71, *P* <0.001), monthly larval density *versus* accumulative density of adults (r = -0.55, *P* = 0.005), monthly density of recruits *versus* cumulative density of recruits (r = 0.91, *P* <0.001), monthly density of recruits *versus* cumulative density of adult (r = -0.70, *P* <0.001); cumulative density of recruits *versus* cumulative density of adults (r = -0.70, *P* <0.001).

Limnological Variables

Significant spatial differences were verified using analysis of variance (t test, α = 0.05), on the following limnological variables: conductivity (*P* <0.0001), total alkalinity (*P* <0.0001); total hardness (*P* = 0.01), ammoniacal nitrogen (*P* = 0.03), total coliforms (*P* <0.0001) and fecal coliforms (*P* <0.0001). All these limnological variables showed highest values in the NC sampling station. No significant spatial differences were observed on water temperature values (*P* = 0.97), pH (*P* = 0.71), dissolved oxygen (*P* = 0.07), chemical oxygen demand (*P* = 0.71), solids (*P* = 0.105), sulfates (*P* = 0.916), total phosphorus (*P* = 0.11) and nitrate (*P* = 0.53). The seasonal and spatial variation of limnological variables are shown in Figures 3, 4 and 5. The significant seasonal differences were verified using analysis of variance (ANOVA, *Duncan* retrospectively, α = 0.05) regarding the following limnological variables. Three distinct groups of water temperature values (G1 in winter, G2 in the autumn and spring, and G3 in the summer) were observed, while the others variables presented only two of the groups, as follows: dissolved oxygen (G1, spring, summer and winter, G2, summer, autumn and winter), pH (G1, summer, winter and spring, G2, autumn and winter), the total alkalinity (G1, summer, autumn and winter, G2, spring, summer and autumn), total sulphates (G1, summer, autumn and winter, G2, autumn, spring), ammoniacal nitrogen, (G1, spring, G2, summer, autumn, and winter), the total coliforms (G1, autumn, winter and spring, G2, spring, summer, and autumn). No significant seasonal differences were found regarding the values of chemical oxygen demand (*P* = 0.20), conductivity (*P* = 0.17), total hardness (*P* = 0.25), total solids (*P* = 0.06), total phosphorus (*P* = 0.27), nitrates (*P* = 0.1) and fecal coliforms (*P* = 0.1).

Population descriptors *versus* limnological variables

Correlations. The following *Spearman's rho* correlation coefficients between population descriptors and limnological variables were observed: monthly larval density *versus* water temperature (r = 0.79, *P* <0.001), *versus* conductivity (r = 0.48, *P* <0.018) *versus* total alkalinity (r = 0.46, *P* <0.024); monthly density of recruits *versus* water temperature (r = 0.64, *P* = 0.001), conductivity (r = 0.42, *P* <0.043) *versus* total solids (r = 0.46, *P* <0.025), ammoniacal nitrogen (r = -0.64, *P* = 0.001); cumulative density of recruits *versus* water temperature (r = 0.69, *P* <0.001), versus total solids (r = 0.46, *P* <0.025) *versus* sulfate (r = 0.45, *P* <0.027), ammoniacal nitrogen (r = -0.65, *P* = 0.001), cumulative density of adults *versus* dissolved oxygen (r = 0.64, *P* <0.001), ammoniacal nitrogen (r = 0.70, *P* <0.001).

Prediction of Population Descriptors. Significant predictor variables were selected by multiple regression analysis, thereby obtaining the equations which determine the population descriptors of golden mussels (Table 1). The water temperature and total alkalinity accounted and for 72% of the variation of monthly larval density according to the obtained model. When it comes to the monthly density of recruits, the water temperature and total solids accounted for 77% of the data variation. For the cumulative density of recruits, the predictor variables are water temperature and ammoniacal nitrogen, accounting for 65% of the data variance. On the other hand, 83% of the data variance of cumulative density of adults was explained by the ammoniacal nitrogen and condutivity.

Spatial Variation. Axis 1 (70.4.7%) and 2 (3.3%) accounted for 73.7% of the variance of the population descriptors in the sampling stations through canonical correspondence analysis (CCA) (Figure 6a). The monthly larval density, monthly density of recruits (0.55) and cumulative density of recruits had a positive relation to Axis 1. Moreover, the cumulative density of adults had a negative relation to Axis 1. The following *Pearson* correlation coefficients between CCA Axis 1 and limnological variables were observed: water temperature (r = 0.78), dissolved oxygen (r = -0.35), conductivity (r = 0.32), total alkalinity (r = 0.38), total sulfates (r = 0.33), total solids (r = 0.40), ammoniacal nitrogen (r = -0.54), and total alkalinity (r = 0.37). On Axis 2, though, the following population descriptors had a positive relation to this Axis: monthly density of recruits, cumulative density of recruits and cumulative density of adults. The following values of *Pearson* correlation coefficients between CCA Axis 2 and limnological variables were observed: water temperature (r = 0.17), dissolved oxygen (r = 0.47), conductivity (r = -0.58), total sulfates (r = 0.18), total solids (r = -0.32), ammoniacal nitrogen (r = -0.27), and total alkalinity (r = -0.64). The monthly larval density showed a negative relation to this Axis. The Monte Carlo test showed high positive and significant correlation (Axis 1, r = 0.89 and p = 0.001; Axis 2, r = 0.84 and p=0.001) among the axes and the matrix of limnological variables.

Temporal Variation. The Axis 1 (68.4 %) and Axis 2 (8.2 %) accounted for 76.6 % of the variance of population descriptors of golden mussel throughout the four seasons, through canonical correspondence analysis (CCA) (Figure 6b). The cumulative density of adults had a negative relation to Axis 1, showing characteristics of both autumn and winter. The monthly larval density, monthly density of recruits and cumulative density of recruits had a positive relation to Axis 1, showing characteristics of both spring and summer. The following *Pearson* correlation coefficients between CCA Axis 1 and limnological variables were observed: water temperature (r = 0.80), dissolved oxygen (r = -0.37), conductivity (r = 0.32), total alkalinity (r = 0.36), total sulfates (r = 0.30), total solids (r = 0.40) and ammoniacal nitrogen (r = -0.3). On Axis 2, though, all descriptors had a negative relation to it: monthly larval density, monthly density of recruits, cumulative density of recruits and cumulative density of adults. The following *Pearson* correlation coefficients between CCA Axis 1 and limnological variables were observed: water temperature (r = 0.54), conductivity (r = -0.19), total alkalinity (r = 0.07), total sulfates (r = 0.52), total solids (r = 0.26), and ammoniacal nitrogen (r = -0.36). The Monte Carlo test showed high positive and significant correlation (Axis 1, r = 0.92 and p = 0.001, Axis 2, r = 0.84 and p = 0.003) among the axes and the matrix of limnological variables.

pH Survival

Immediately after exposure to pH 1, 2, 3, 12 and 13 the shell of bivalve had closed. At pH values between 5 and 11, the median survival ranged between 90% and 100% for all experiments (Figure 7). Within 48 hours of exposure over 90% of mussels survived in extremes pH values 2 and 12 (Figure 7a and 7b). Within 96 hours of exposure over 90% of mussels survived in extremes pH values 3 and 12 (Figure 7a, 7b, and 7c). After 96 hours, increased mortality was observed in pH 2, 3, 4, and 12 treatments (Figure 7d-7g)). After 144 hours of exposure, the molluscs had a mean survival rate greater than 70% at pH 4 and greater than 50% at pH 12 (Figure 7f and 7g). The lethal pH (LpH_{50}) to cause 50% mortality of the mussels ranged from 2.08 (72 hours of exposure) and 3.54 (168) at pH<7, and between 12.96 (96) and 12.16 (168) at pH>7 (Table 2). The lethal time to cause 50% mortality of the mussels ranged from <24 hours (pH 1) and 203.8 hours (pH 4) for pH values <7, and between 20.1 hours (pH 13) and 169.77 (pH 12) at pH>7 (Table 3).

Discussion

Recruitment

All statistical analyses have shown seasonal variation with early release of larvae and recruitment in the spring, with the emergence of adults in summer. Santos et al. (2008) evaluated a population *L. fortunei* on a beach at Guaiba Lake, that borders the city of Porto Alegre, State of Rio Grande do Sul, Brazil. The Guaiba Lake is situated in the Temperate Cfa climatic region of South America, according to CIESIN (2012). The authors found higher abundance of larvae in the plankton in the spring (October, November and December), and the recruitment of ceramic substrate in the spring and summer. Boltovskoy and Cataldo (1999) also found a similar pattern of temporal variation in the density of larvae and recruits (<2 mm) on artificial substrates in water system located in Argentina. This location is also situated in the Temperate Cfa climatic region of South America, according to CIESIN (2012), where this study was conducted. Pestana et al. (2008) found a high density of larvae in the rivers Paraná and Iguazu (Brazil), where the climate is Tropical Aw, with dry winters (CIESIN, 2012), between the months of October and December. The Paraguay River, near the Miranda River (South Pantanal, Brazil) lies within the same climatic region mentioned above, the highest density of larvae was observed in the months of January, February and March, when the water temperature had the highest values (30-31° C). The same climate zone, in the São Simão Reservoir in the Upper Rio Paraná (Brazil), Fields et al. (2012) found maximum larval densities values between the months of March and May, while the recruits are reported in June. The seasonal pattern in climate zone Tropical Aw is a distinct seasonal pattern found in temperate zone Cfa. In the Tropical Aw climate zone there are not four different seasons as the Temperate Cfa climate zone. The larval release and recruitment was reported in warmer times in the summer, in the Tropical Aw climate zone.

The presence of few adult individuals was reported in cumulative substrates after the fifth month of exposure in the sampling stations, in the summer. On the other hand, the highest values of cumulative density of adults were reported in the winter. Adults were found in different artificial substrates after three months of exposure in the delta of Jacuí in the summer of 2005/2006: ceramic substrate (Bergonci et al, 2009.), wood (Mansur et al, 2009), and PET bottle filling nylon screen (Pereira et al., 2010). After three months of exposure to artificial substrates, recruits grow and reach adulthood (Bergonci et al., 2012) with 5 mm, becoming sexually mature (Damborenea & Penchaszadeh 2012). Darrigran et al. (1999) and Boltoskoy et al. (2009) found that reproduction of *L. fortunei* is continuous, but the release of larvae is inhibited during the coldest months of the year and stimulated with increasing water temperature in spring.

No significant differences were found regarding the amounts of monthly larval density and recruits in study sites, as well as the cumulative density of recruits and adults. The NC sampling station presents water quality inferior to JC sampling station (Bergonci et al., 2009) due to its receiving high loads of domestic sewage from the city of Porto Alegre, and neighboring cities situated in the Gravataí River basin (Faria and Lersch, 1998). Pereira et al. (2010) also found no significant differences between these two sites regarding the density of *L. fortunei* and many other components of the benthic fauna on artificial substrate type PET bottle, filled with nylon screen.

Limnological Variables

Despite the significant differences reported regarding values of total alkalinity and total hardness verified in study sites, the concentration values recorded for both variables are very low. Alkalinity is a measure of the ability of water to resist a drop in pH (Mackie and Claudi, 2010), or its buffering capacity. It is the sum of the quantity of carbonates, bicarbonates and hydroxides.

The buffer capacity of the aquatic environment is essential for the maintenance of aquatic life. Values below 10 $mg.L^{-1}$ show high sensitivity to pH drop, while values between 10 and 20 $mg.L^{-1}$, show moderate sensitivity and greater than 20 $mg.L^{-1}$, low sensitivity (Nagpal, 2006). The total hardness values are lower than 60 $mg.L^{-1}$, framing water from both stations in soft water category according to Hem (1985), which indicates low calcium and magnesium cations in water. Faria and Lersch (1998) also pointed out the high levels of ammoniacal nitrogen and conductivity in the Navegantes Canal, whereas other limnological variables showed no significant differences when compared with the values reported there. Bergonci et al. (2009) found significant differences between the two sampling stations (JC and NC) regarding the variables nitrate and fecal coliforms, with higher values in the Navegantes Canal (NC).

Recruitment versus limnological variables

In addition to water temperature, other variables such as sulfates, total alkalinity and ammoniacal nitrogen influenced the temporal patterns of the invading population. The rise in water temperature has been regarded as a determining factor for the early release of larvae in the plankton by several authors (Boltoskoy and Cataldo, 1999; Boltoskoy and Cataldo, 2000; Darrigran 2002; Santos et al, 2008, Boltoskoy et al, 2009; Eilers et al, 2011). In contrast, the same authors have reported low incidence of larvae on very low water temperature. Pereira et al. (2012b) found negative correlations between density of planktonic larvae and turbidity and ammoniacal nitrogen, a spatial gradient in the middle of the Tietê River basin. The same authors have found positive correlations between the mussels collected in sediments (recruits + adults) and the following limnological variables: water temperature, conductivity and pH. They have also found a negative correlation with turbidity. No temporal series of population descriptors and environmental variables were assessed in the Tietê River. Spaccesi (2013) observed high and significant correlations between the abundance of recruits on natural hard substrates and the following limnological variables in the intermediate area of the La Plata River Estuary: positive correlation with water temperature and negative correlations with oxygen and conductivity.

The multiple regression analysis allowed us to identify the predictor variables of population descriptors of golden mussels. The monthly larval density (Table 1) had a major positive relation to water temperature, and total alkalinity. Nakano et al. (2010) found that in deep zones of Japanese lakes at low water temperature and oxygen level, it is not suitable for the survival and reproduction of the mussels. The regression equation obtained reflects the temporal patterns of population descriptors and water temperature variations.

According to Mackie and Claudi (2010), the calcium content, alkalinity, pH, and total hardness have been used as a criterion to determine the distribution and abundance of *Dreissena polymorpha* Pallas potential, 1771, in the U.S.A. and Canada. The alkalinity is the significant second variable, which is generally higher after the rainy season due to rock dissolution and washing of the soil (Esteves, 1988). The increase in alkalinity after the rainy season coincided with the release of larvae. The increase of this variable indicates a greater water buffering and its resistance to pH drop. This may be a sign of environmental conditions favorable to the beginning of the recruitment cycle since the release of the larvae to the settlement of recruits. Equation 2 and Equation 3 (Table 2) explain the monthly density of recruits and cumulative density of recruits, which is enhanced along time. Again the water temperature is the first variable contributing to the equation. The recruits verified on the substrate resulting from the development and growth of larvae in plankton, which are released in the spring when the water temperature rises gradually until the summer, when it begins to reach adulthood. On a reservoir in temperate climate in Japan, Nakano et al. (2011) found a positive correlation between the water temperature and the growth rate of *L. fortunei* under conditions in which there was a sufficient availability of calcium. In Equations 2 and 3, in addition to the variables in the prediction equations larvae, also contributed the variables total solids and ammoniacal nitrogen respectively. Total solids, conductivity and ammoniacal nitrogen probably indicate food resources for the filter feeding *L. fortunei*. According to Callil et al. (2012), in addition to abiotic factors, the quality and availability of food resources are related to the reproductive process. As soon as the recruits grow up and become adults, they can reproduce. These hypotheses are reinforced based on the results obtained through temporal analysis using CCA method

The spatial analysis by means of ordination (CCA) also reflected the results obtained in the of variance analysis of population descriptors and limnological variables. Population descriptors are more closely related to the temporal variation of limnological variables rather than the spatial variation. Despite significant differences between values of limnological variables in the sampling stations JC and NC, these variables do not limit the densities of the golden mussel in its different stages of development. However, when considering other population descriptors such as weight and length ratios, Bergonci et al. (2012) found significant differences for the same sampling stations. Mansur et al. (2008) also found clear differences between length and weight ratios in different environments of the lower Jacuí River basin and Guaiba Lake. The authors attributed this pattern to different levels of food availability and water currents.

The temporal analyses by means of ordination (CCA) corroborated the results verified in the variance and multiple regressions analyses of population descriptors and limnological variables. In the spring, when it started to release larvae into the waters of the delta and intense recruitment is reported, the influence of the following variables can be verified: sulfates, total solids, alkalinity and conductivity. This period occurs after intense rainfall in August and September, which may be a standard pattern for freshwater fish. According to Ribeiro and Moreira (2012), the spawning of tropical fish such as *Eigenmannia virescens* is associated with a combination of rain, rising water level and conductivity decrease, which induces a complete gametogenesis and spawning, and does not occur if the parameters are tested individually. The same can be attributed to the golden mussel. However, the positive correlation with the conductivity may indicate feed in the form of particulate matter or the presence of ions necessary for the development of the mussel. The total solids and electrical conductivity are closely related (Pinto, 2007), the latter depending on the ionic concentrations and the water temperature, and indicating the amount of existing salts in water. On the other hand, sulfates are very common in surface waters as a result of the dissolution of rocks, from rainfall and the oxidation of sulfides, which may originate from the dissolution of soil after heavy rains and, sewage (Tundisi el al., 2008). The sulfate ion is one of the most common forms of sulfur in aquatic environment, available to primary producers (Esteves, 1988). The content of sulfates can be related to the presence of phytoplankton, which is used in feeding by the mussel.

The gradual rise in the water temperatures had been gradually reported since early in the spring until its peak in the summer. Water temperatures above 20° C, or each increasing water degree, serve as a stimulus for larval release, thus allowing for the beginning of the recruitment cycle (Cataldo et al., 2005). In the autumn, when the production of larvae and recruitment decreased and the densities of adults increased, the levels of oxygen increased due to lower water temperatures. In the same period there was an increase in the amount of ammoniacal nitrogen. This phase is considered to be the final stage for recruitment, when establishing the adult population in the substrate. The relation of recruits and adults individuals with ammoniacal nitrogen can be attributed to the fact that these animals are filter feeders and feed on particulate organic material suspended in the water. This unreduced form of nitrogen is an indicator of recent organic material which did not undergo oxidation (Person & Jordan, 2005). Furthermore, the high levels of ammoniacal nitrogen were associated with the high densities of adult mussels, possibly due to the increased production of pseudofeces resulting from the filtration process. In experiments with mesocosms, Cataldo et al. (2012) verified that *L. fortunei* removed 84% of the particulate nitrogen of the aquatic system, and also released ammonia form of nitrogen at the rate of 3 μM NH_3g DW^{-1} h^{-1}.

Until now, the golden mussel has not been reproduced in the laboratory, and this can be attributed to the difficulty in replicating the environmental conditions found in nature. Probably the synergism between the gradual rise in water temperatures, conductivity, pH, alkalinity, food availability and water currents, should induce the release of larvae in the water column, as well as to signal conditions suitable to the recruitment and colonization of substrates available in the aquatic environment.

pH Survival

The laboratory experiments in which this study was conducted, *L. fortunei* showed tolerance to extreme pH values between 2 and 12 after 24 hours. Rolla and Mota (2010) claim that the golden mussel survives a pH range from 2.7 to 9.0. However, the authors did not describe the experimental conditions under which this result was achieved. Freshwater bivalves are usually found in a pH range between 5.6 and 8.3 (McMahon, 1991; Haag, 2012). Kat (1982) found that the major cause of mortality of *Corbicula fluminea* (Müller, 1774) in Mosquito Creek (Florida, USA) was the low water pH (5.6), causing erosion of the shell. In experiments with *Anodonta anatina* (Linnaues, 1758), Oikari & Mäkelä, 1992 verified the dissolution of periostracum below pH 3.9, causing mortality of clam. The wide range of pH tolerated by *L. fortunei* after 120 hours is the same at which the invasive diptera and dengue vector *Aedes aegypti* can survive and even develop itself (Clark et al. 2004). Different authors have considered the extremes of pH as factors limiting the dispersal and establishment of populations of *L. fortunei* in environmental gradients of South American river basins: pH <5.8 (Mansur et al, 2004.); pH <6.2 and> 7.4 (Darrigran, 2002), pH<5.5 (Boltovskoy et al. , 2006); pH>7.8 (Oliveira et al 2010b);. pH>8.3 (Villar et al 1997); and pH> 8.8 (Darrigran et al, 2012b). Within the range of pH values in which the survival of *L. fortunei* in the present study was observed, different pH ranges in Brazilian surface waters are verified: 6.1 to 8.7 in Upper Paraná River basin (Campos et al, 2012.), 5.0 to 7.2 in Pantanal rivers (Oliveira et al, 2011, 2013.), 4.4 to 6.2 in Northeastern Amazon River tributaries (Horbe and Oliveira, 2008), 7.5 to 10.2 in reservoirs of the Tietê River (Suriani et al, 2007), 6.7 to 7.4 and of the Tietê River and Jacaré River (Pereira et al, 2012b), 6.6 to 8.6 in dams of Tietê River (France et al, 2007), 7.1 to 7.8 in mountainous streams in South Atlantic Basin (Pereira & De Luca, 2003), and 6.2 to 9.0 in the delta of Jacuí River (Faria and Lersch, 1998). Mackie and Claudi (2010) compiled bibliographic data of occurrence of golden mussel in several ecosystems and then they defined criteria based on pH ranges, to assess the infestation levels of invasive bivalve, as follows: no potential for adult survival (pH <3.0,>10), little potential for planktonic larvae stage D (3.0-5.0), moderate potential for nuisance infestations (5.0-7.0), and high potential for massive infestations (7.0-9.0). Massive infestations have developed in the Jacuí and Tietê in water pH <7.0, which shows the fragility of this criteria for assessing the potential infestation of this invasive species. Probably this variable does not act as a limiting factor for dispersal of golden mussel along most of the river basins in Brazil. The high values of lethal time to cause 50% mortality rate of the golden mussel population can favorer the organisms survival after acidification of surface water for a short period.

The extreme acid range in which the survival of golden mussel was verified is close to the pH range of the stomach of some fish, which would enable the mussels to survive after passing through the digestive tract and release of live mollusks via the feces of fish. In this way the fish can act as a vector of the dispersion of this invasive species. According to Rotta (2003) stomach pH of channel catfish, *Ictalurus punctatus* (Rafinesque, 1818) and of robalo *Centropomus* sp. present ranges of values 2 to 4 and 2 to 6 respectively. The golden mussel has been found in the stomach of many fish (Oliveira, 2003; Vermulm Junior & Giamas, 2008; Darrigran & Damborenea, 2011; Lopes and Vieira, 2012), which are an important means of spread of the invasive bivalve. The golden mussel can survive after passing through the digestive tract of fish, where the fish evacuation time is less than the lethal time checked at each pH range, under conditions similar to stomach pH.

Final Considerations

Recruitment in the tested substrates, showed a seasonal variation defined for this climate zone (Cfa Tempered). The early release of larvae in the water column and the recruitment of substrates occurred in the spring continuing in lesser density until the autumn. Recruits grew and reached adult life in the summer, and these adults reached larger population in the winter. The release of larvae and its recruitment was suspended in the winter when the water temperature dropped.

The recruitment cycle, from larval release, settlement and macrofouling of adult individuals was influenced by the variation of water temperature, total alkalinity, total solids, ammoniacal nitrogen and condutivity. The most significant predictors of population descriptors of the golden mussel verified in this case study were the same used for the prediction and risk analysis of colonization Dreissenidae in inland waters of North America.

The survival of the golden mussel in the pH range 4-11 after five days of exposure can permit the survival of populations under adverse and intermittent conditions in the aquatic environment. It is worth noting the potential of golden mussel for colonization of acidic waters. The golden mussel populations may also have high resilience to pollution like as acidification of waters, when being exposed to it on a temporary basis. Furthermore, the risk of accelerated dispersion should also be considered because the golden mussel can survive in the stomach of migratory fish. This higher tolerance to pH is comparable to that of the *A. aegypti*. It is possible that in the future both invasive species will reach the similar geographical distribution.

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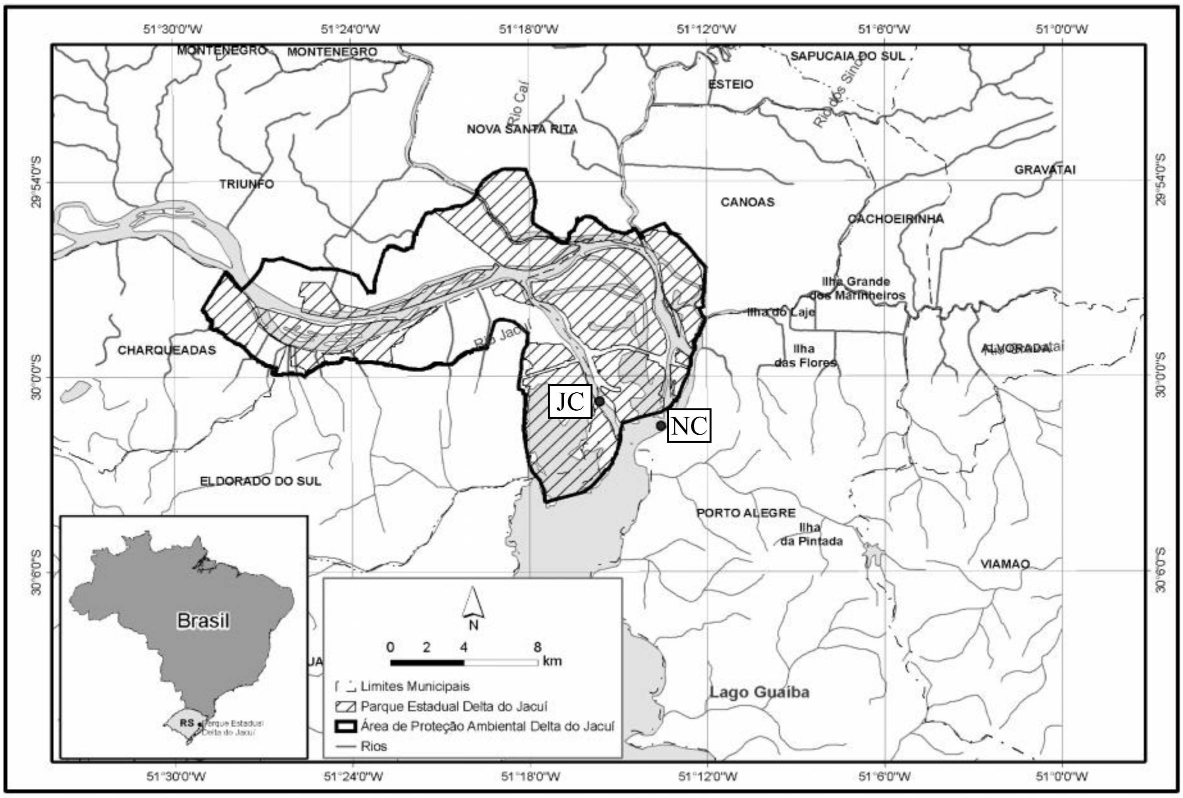

Figure 1. Sampling stations in the inner delta of the Jacuí River, Rio Grande do Sul State, Brazil: Jacuí Canal (JC) and Navegantes Canal (NC). Map lifted from Pereira et al. (2010).

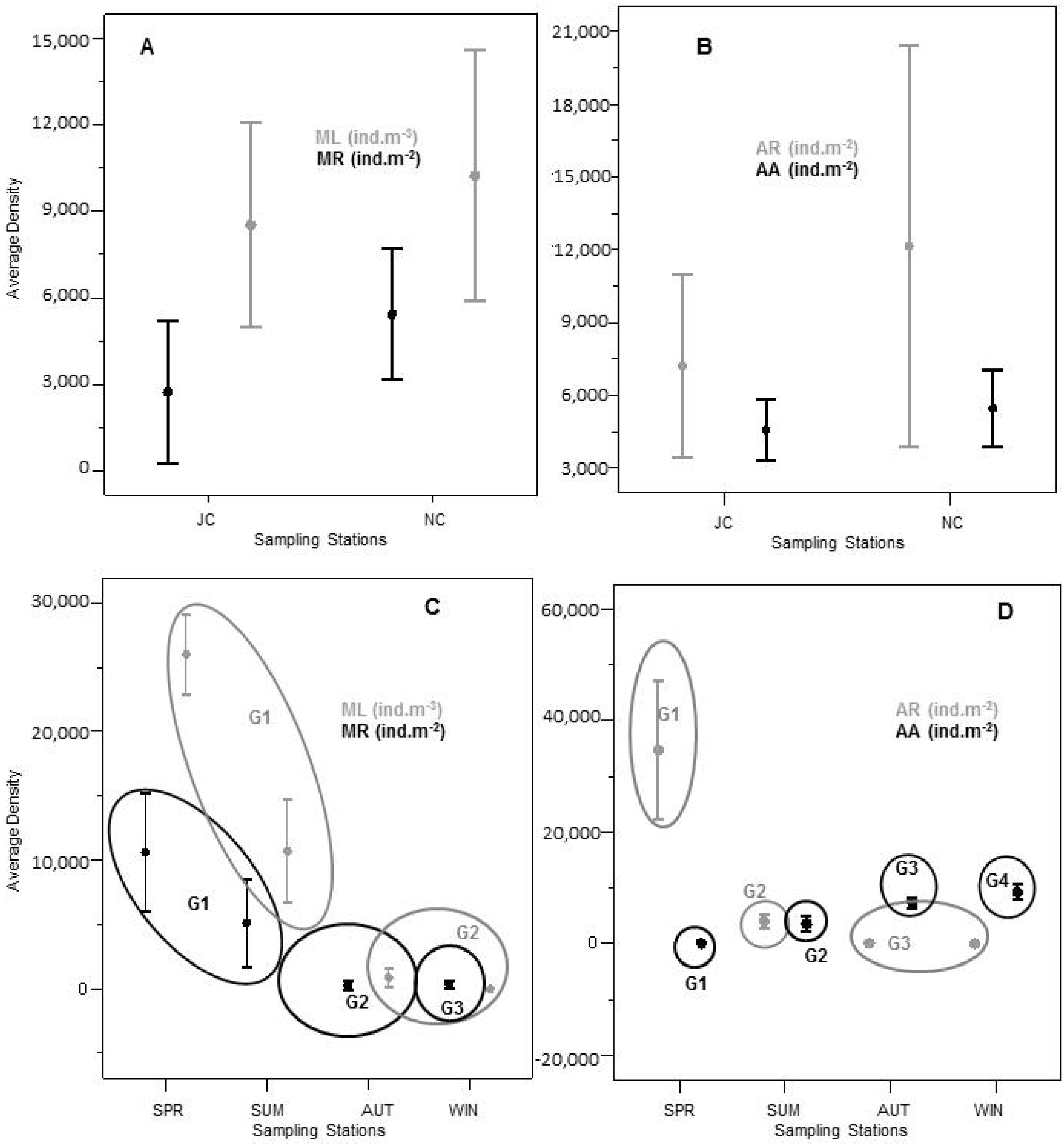

Figure 2. Spatial (A, B) and temporal variation (C, D) of *L. fortunei* (Dunker, 1857) population descriptors (mean values and standard error) in the delta of the Jacuí River, Rio Grande do Sul State, Brazil, from October 2006 to September 2007. Jacuí Canal (JC), Navegantes Canal (NC), Monthly larval density (ML), monthly density of recruitment (MR), cumulative density of recruits (AR), cumulative density of adult (AA), Spring (SPR), Summer (SUM), Autumn (AUT) and winter (WIN). Groups (G_n) differentiated by ANOVA (Duncan *a posteriori*, $\alpha = 0.005$).

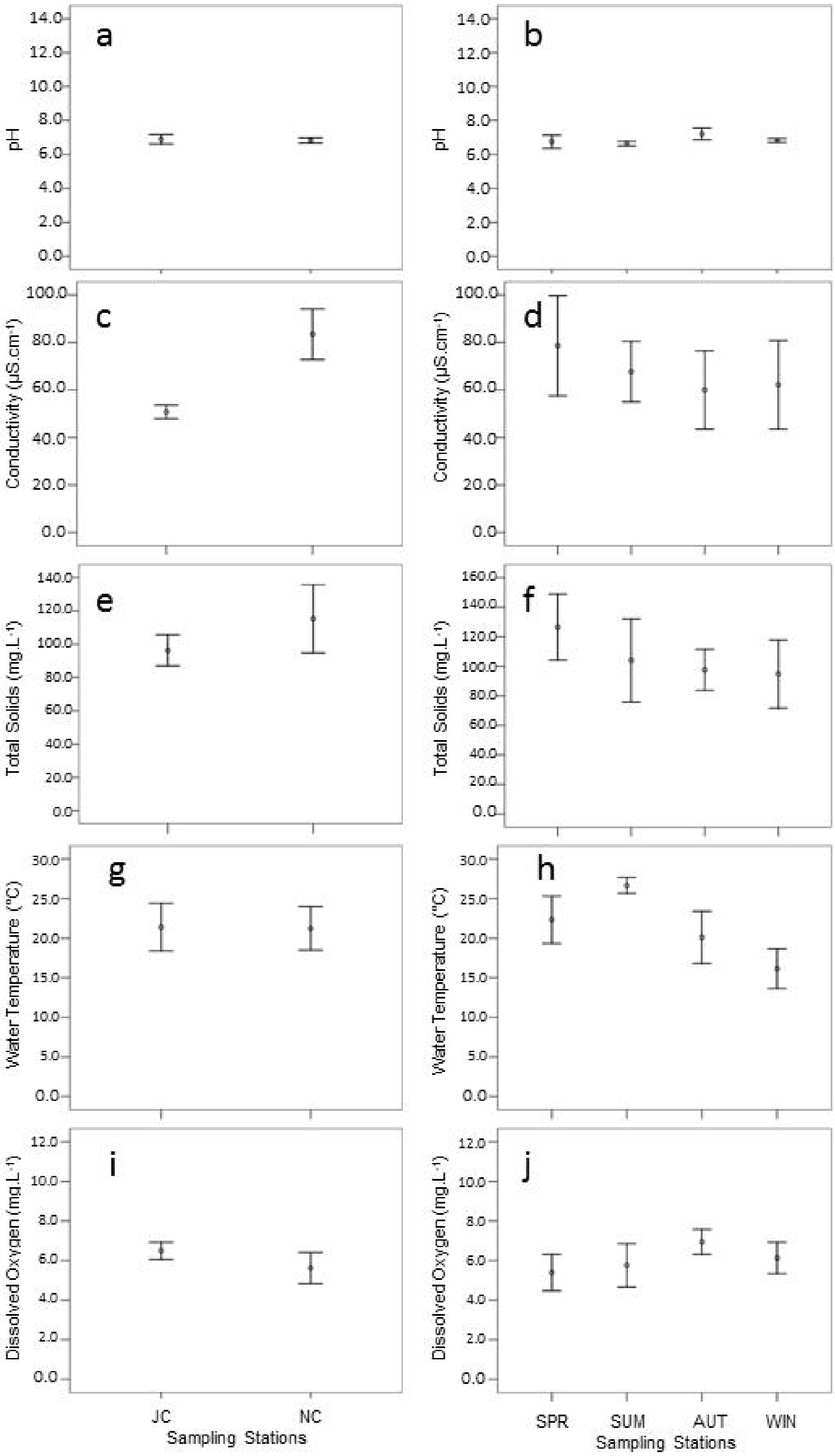

Figure 3. Spatial and temporal variation of limnological variables in the delta of the Jacuí River, Rio Grande do Sul State, Brazil, from October 2006 to September 2007: Spatial (a) and temporal (b) pH, spatial (c) and temporal (d) conductivity, spatial (e) and temporal (f) total

solids, spatial (g) and temporal (h) water temperature, and spatial (i) and temporal (j) dissolved oxygen. Spring (SPR), Summer (SUM), Autumn (AUT) and winter (WIN).

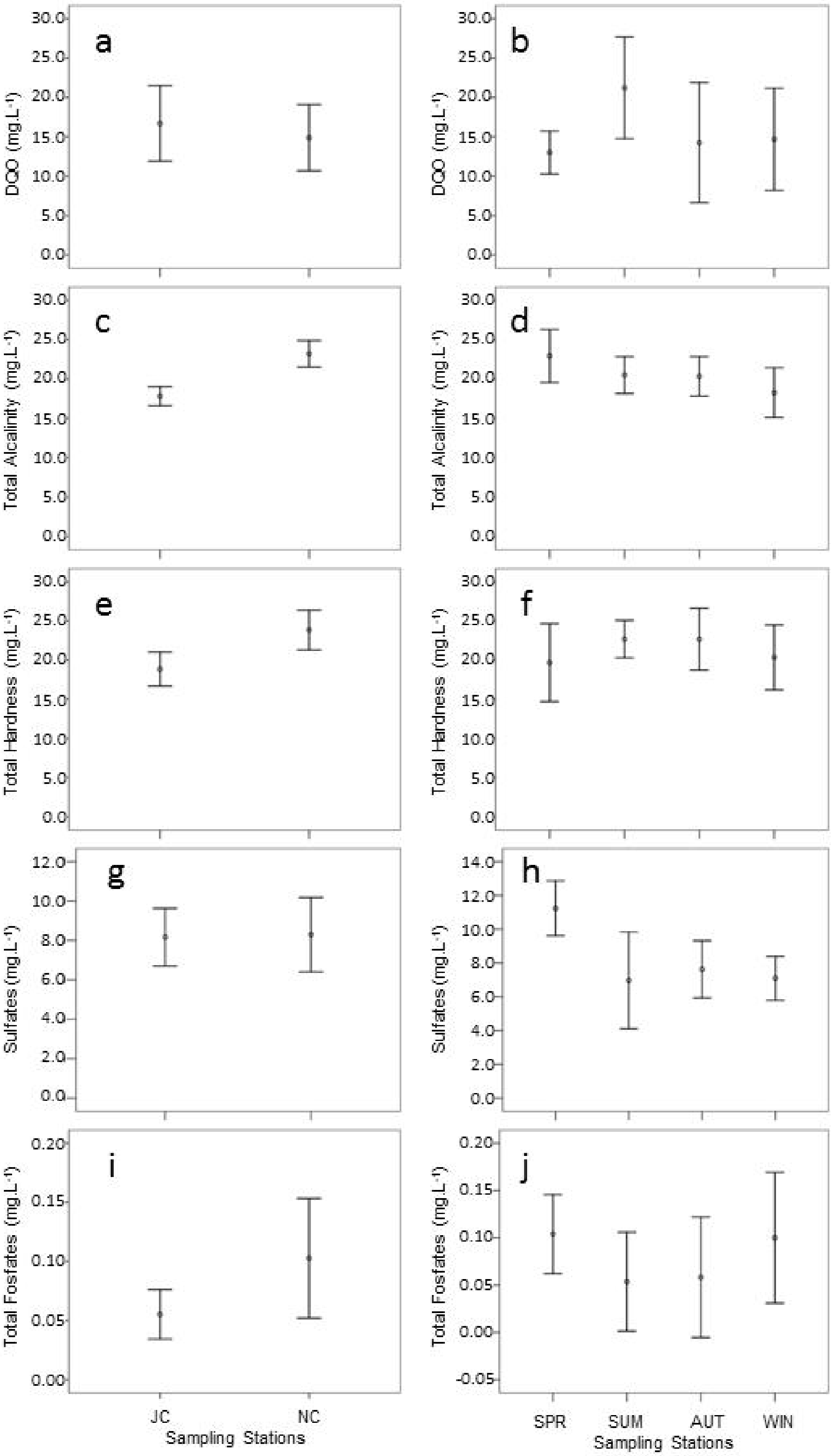

Figure 4. Spatial and temporal variation of limnological variables in the delta of the Jacuí River, Rio Grande do Sul State, Brazil, from October 2006 to September 2007: Spatial (a) and

temporal (b) chemical oxygen demand (COD), spatial (c) and temporal (d) total alkalinity, spatial (e) and temporal (f) total hardness, spatial (g) and temporal (h) sulfates, and spatial (i) and temporal (j) total phosphates. Spring (SPR), Summer (SUM), Autumn (AUT) and winter (WIN).

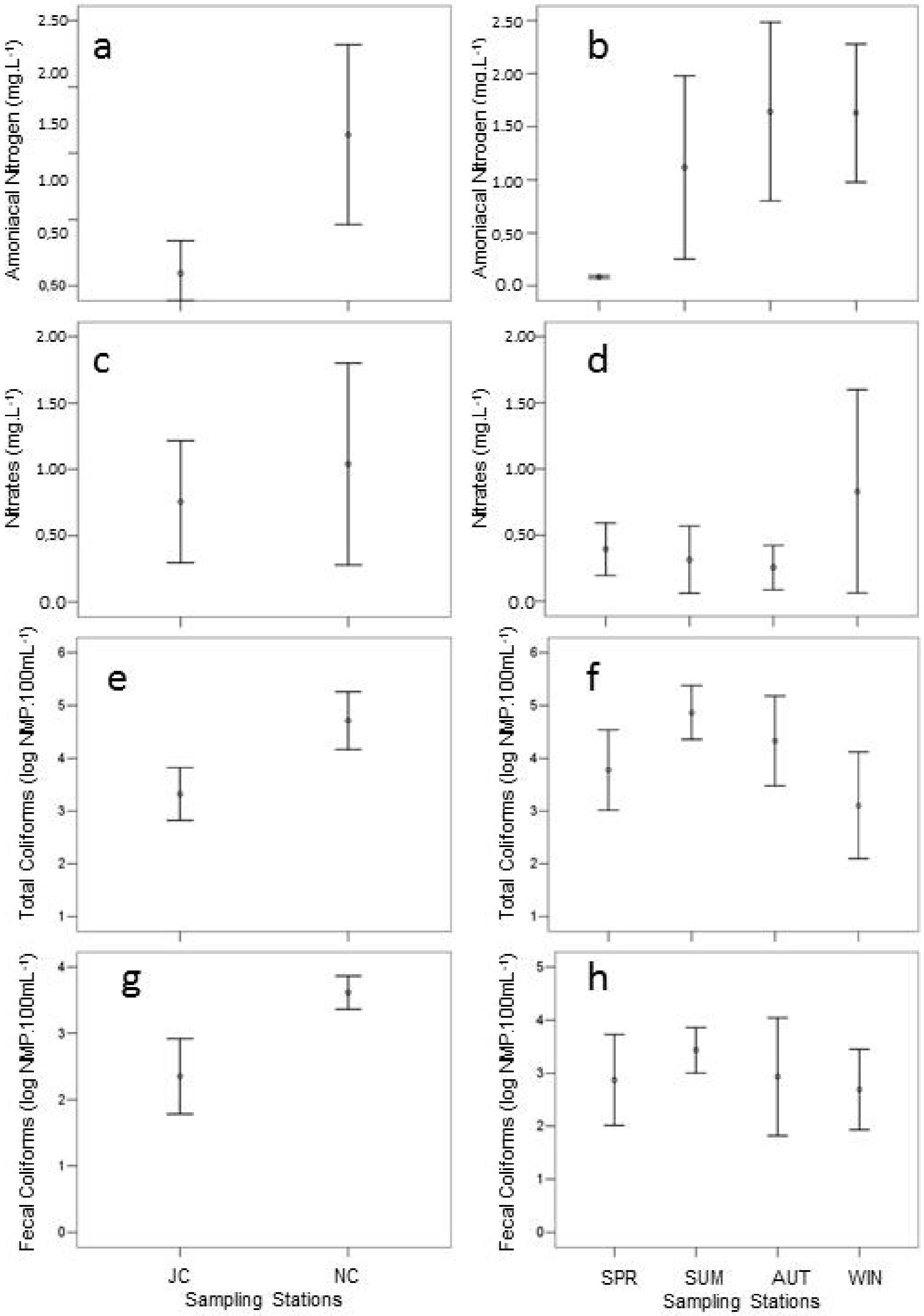

Figure 5. Spatial and temporal variation of limnological variables in the delta of the Jacuí River, Rio Grande do Sul State, Brazil, from October 2006 to September 2007: Spatial (a) and temporal (b) ammoniacal nitrogen, spatial (c) and temporal (d) nitrates, spatial (e) and temporal (f) total coliforms, and spatial (g) and temporal (h) fecal coliforms. Spring (SPR), Summer (SUM), Autumn (AUT) and winter (WIN).

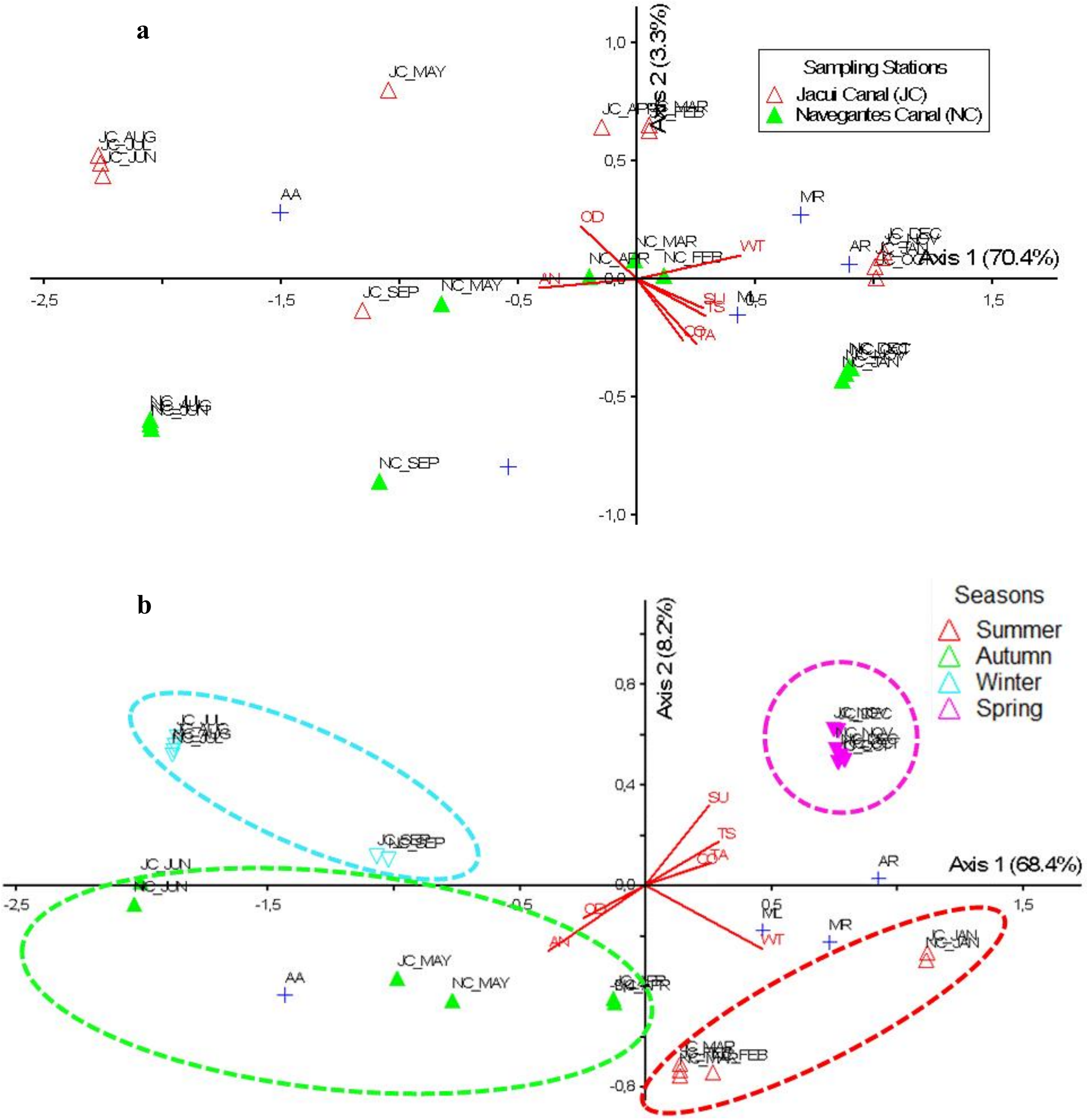

Figure 6. Ordination of sampling units based on population descriptors of *L. fortunei* (Dunker, 1857), considering all dataset collected in both sampling stations in the delta of the Jacuí River, Rio Grande do Sul State, Brazil, from October 2006 to September 2007, and their relation to the limnological variables by means of Canonical Correspondence Analysis (CCA). A) spatial and B) temporal variation. Monthly larval density (ML), monthly density of recruits (MR), cumulative density of recruits (AR), cumulative density of adults (AA), dissolved oxygen (DO), water temperature (WT), conductivity (CO), sulfates (SU), total alkalinity (TA), ammoniacal nitrogen (AN), total solids (TS), Jacuí Canal (CJ), Navegantes Canal (NC), January (JAN), February (FEB), March (MAR), April (APR), May (MAY), June (JUN), July (JUL), August (AUG), September (SEP), October (OCT), November (NOV), December (DEC).
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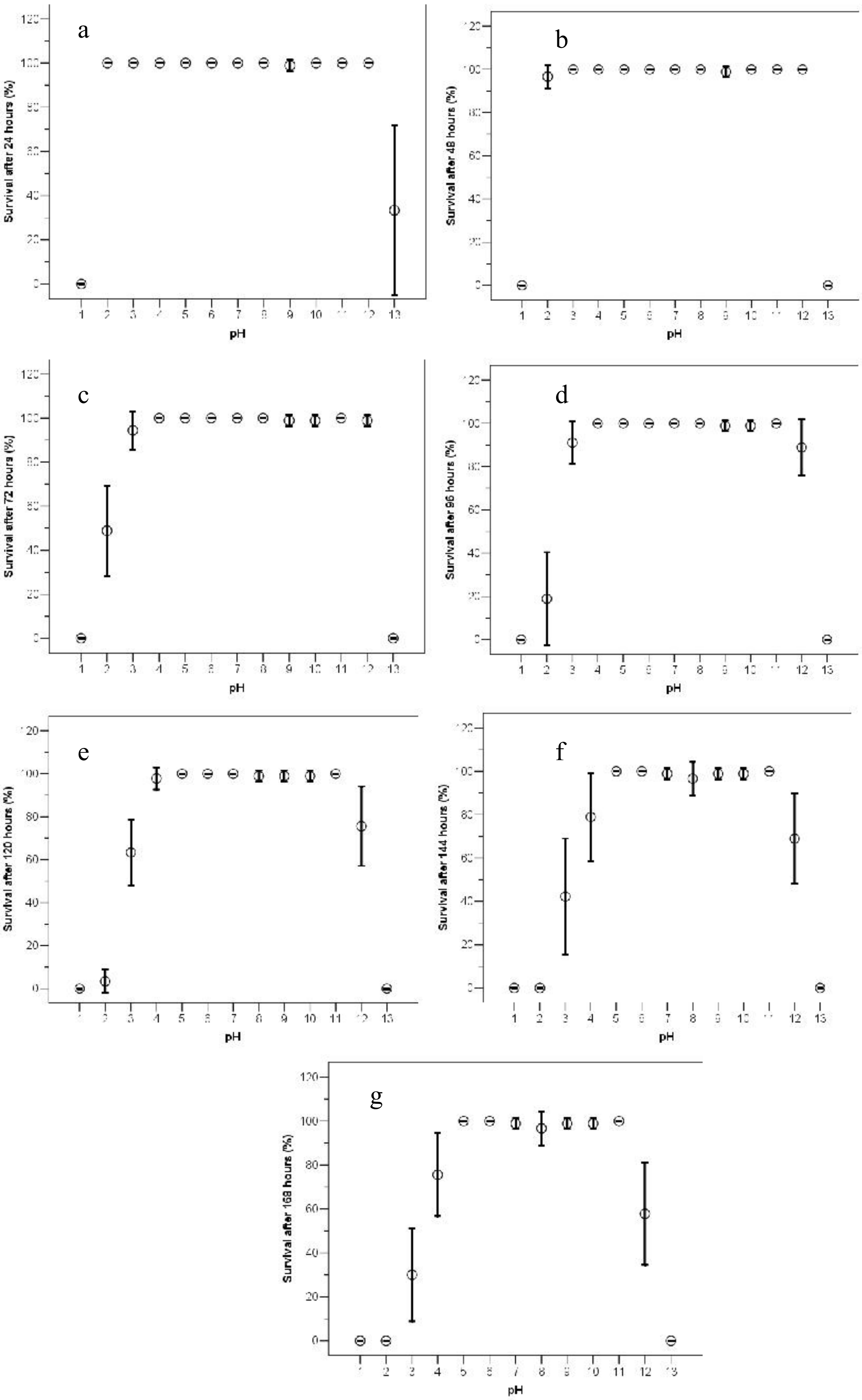

Figure 7. Survival (%) of *L. fortunei* at different pH values (1 to 13) and different times of esposure: 24 hours (a), 48 hours (b), 72 hours (c), 96 hours (d), 120 hours (e), 144 hours (f) e 168 hours (g).

Table 1. Equations obtained by multiple regressions based on all dataset of population descriptors of *L. fortunei* (Dunker, 1857) and limnological variables collected in both sampling stations in the delta of the Jacuí River, Rio Grande do Sul State, Brazil, from October 2006 to September 2007. Monthly larval density (ML), monthly density of recruitment (MR), cumulative density of recruits (AR), cumulative density of adult (AA), water temperature (WT), total alkalinity (TA), conductivity (CO), ammoniacal nitrogen (AN) sample size (N), F statistic (F), freedom degree (DF), multiple (M), adjusted (a), $p < 0.0001$**.

Equations (Eq.)		N	F	DF	R^2	
					M	A
ML = -21** + (11.6) WT** + (5.8) TA**	(Eq.1)**	24	7.9	1	0.77	0.72
MR = -24.8** + (15) WT ** + (34) ST**	(Eq.2)**	24	17.4	1	0.79	0.77
AR = -24.8** + (10.4) WT ** + (4.7) AN**	(Eq.3)**	24	15.0	1	0.68	0.65
AA = -24.8** + (7.7) AN ** + (5.6) CO **	(Eq.4)**	24	20.6	1	0.84	0.83

Table 2. Letal pH to cause the mortality of 50% (LpH50%) of *L. fortunei* individuals at different exposure time of the organisms. *not converged.

pH	Exposure Time (h)	Equation	LpH50%	LCL	UCL
<7	24	*	*	*	*
	48	*	*	*	*
	72	$y = 6.67 - 0.8x$ $p<0.0001$	2.08	2.45	1.71
	96	$y = 7.38 - 0.92x$ $p<0.0001$	2.60	2.80	2.35
	120	$y = 7.95 - 0.98x$ $p<0.0001$	2.98	3.30	2.70
	144	$y = 8{,}45 - 1.01x$ $p<0.0001$	3.40	3.60	3.20
	168	$y = 8.72 - 1.04x$ $p<0.0001$	3.54	3.74	3.35
>7	24	*	*	*	*
	48	*	*	*	*
	72	*	*	*	*
	96	$y = - 2.83 + 0.60x$ $p<0.0001$	12.96	12.47	13.45
	120	$y = - 2.86 + 0.62x$ $p<0.0001$	12.60	12.13	13.08
	144	$y = - 1.91+ 0.55x$ $p<0.0001$	12.51	11.97	13.05
	168	$y = - 2.28 + 0.60x$ $p<0.0001$	12.16	11.66	12.65

Table 3. Letal Time to cause the mortality of 50% (LT50%) of *L. fortunei* individuals at different pH values.

pH	Equation	LT50% (hours)	LCL	UCL
1	All subjects died within 24 hours			
2	$y = 1.86 - 0.04x$ $p<0.0001$	78.08	72.91	83.25
3	$y = 1.47 - 0.025x$ $p<0.0001$	140.65	134.80	146.51
4	$y = 1.26 - 0.02$ $p<0.0001$	203.80	192.47	215.13
5	no mortality			
6	no mortality			
7	test not converged (mortality rate <1%)			
8	test not converged (mortality rate <1%)			
9	no mortality			
10	test not converged (mortality rate <1%)			
11	no mortality			
12	$y = 1.75 - 0.02x$ $p<0.001$	169.77	162.11	177.43
13	$y = 5.47 – 0.059x$ $p=1$	20.10	16.97	22.51

Capítulo 4

Toxicity of *Bacillus* strains and commercial formulations on *Limnoperna fortunei* (Dunker, 1857)

Toxicity of *Bacillus* strains and commercial formulations on *Limnoperna fortune* (Dunker, 1857)

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Abstract

Microbial agents for the population control of the golden mussel, as well as bacteria pathogenic to this species are not known yet. Aiming to select microbial agents to control the golden mussel, two strains and three commercial formulations available in the market and registered for the control of diptera were evaluated through bioassay. Cultures (109 cells) of strains *Bacillus thuringiensis* sv. *kurstaski* HD-1 and *Bacillus thuringiensis* sv. *israelensis* IIRAC22 were used in bioassays with golden mussels. The commercial formulations used in bioassays to select microbial agents for the control of golden mussel were VECTOBAC® water-dispersible Granules, composed of *Bacillus thuringiensis* sv *israelensis* serotype H-14, VECTOBAC® aqueous Solution (AS), composed of on *Bacillus thuringiensis* sv *israelensis* strain AM65-52, and VECTOLEX® water-dispersible Granules, composed of active constituent Bacillus sphaericus Strain 2362. Ecotoxicological assays were conducted to assess the toxicity on non-target organisms of the most efficient commercial formulation for the mussel control. *Bacillus thuringiensis* sv. *kurstaski* HD-1 showed high potential for the control of golden mussel and could be assessed for development of new commercial formulation. VECTOBAC AS was the most efficient commercial formulation for the golden mussel control. However, the lethal concentration of VECTOBAC AS for the mussel control is higher than effective concentration to kill diptera, and can be toxic to non-target organisms. New strains may be isolated from the golden mussel and used in new bioassays in order to find most efficient microbial agents for the control of this invasive species.

Introdution

The original distribution of golden mussel *Limnoperna fortunei* (Dunker, 1857) stretches through Southeast of Asia. However, this freshwater bivalve was introduced in South America in the early 1990s (Darrigran & Pastorino, 1995). This mussel is an invasive and engineer species which causes significant environmental and economic impacts on both natural and built systems (Darrigran & Damborenea, 2011), mainly due to the formation of macrofouling. Currently, the golden mussel is present in water bodies of five South American countries and chances are that it will disperse itself among other hydrographic basins (Pereira et al., 2013). According to Oliveira et al. (2010), predictive distribution scenarios using modeling tools showed that this invasive species can also disperse and establish itself in the North American watersheds. And then, being able to cause extinction of many benthonic and planktonic species and change the trophic net of aquatic ecosystems in both continents (Darrigran & Damborenea, 2011).

Population control of invasive mussels is usually carried out by chemical (Soares et al., 2009, Claudi and Mackie 1993, Campos et al, 2012, Campos and Fernandes, 2012, Fernandes et al 2012, Rodriguez 2012, Darrigran et al., 2007) and physical methods (Santos et al. 2012a, b, Zurita, 2012). There are few biological methods suggested for controlling mussels, and the majority of then was developed for the control of *Dreissena polymorpha* Pallas (1771) using bacteria in North America. So far, no commercial bacterial formulation was developed and registered for the control of *L. fortunei* in South America.

According to Molloy (1998), two groups of organisms have great potential for the biocontrol of invasive *D. polymorpha* in North America. These are microrganisms producers of selective toxins and natural enemies. According to the author, techniques used to control mosquitoes gnats using *Bacillus thuringiensis var. israelensis* (Bti) could be adapted to control the *D. polymorpha*.

Species of the *Bacillus* and *Pseudomonas* genus represent the majority of microbial agents tested for the control of mollusks (Paz et al, 2012.), as well as in the control of insect pests and plant pathogens (Lanna Filho et al, 2010). Microbial control of mollusks are mostly restricted to bench experiments using bacteria, mainly species of Paenibacillaceae, Bacillaceae, Pseudomonadaceae and Shewanellaceae in control assays of schistosomiasis vectors (Osmam & Mohamed, 1991, Osmam et al., 2011, Singer et al. 1997, Oliveira et al., 2004, Halina et al, 2006, Ali et al., 2010) and zebra mussel *D. polymorpha* (Singer et al. 1997, Genthner et al. 1997, Gu and Mitchell, 2001). Molloy & Mayer (2007) tested 700 bacterial strains isolated from soil, and selected *Pseudomonas fluorescens* Pf isolated-CL145A, which demonstrated effective control of zebra mussel and quaga mussel. According to Molloy et al. (2013a), *P. fluorescens* produces a protein which is toxic to *D. polymorpha* that causes vacuolization of gut tissues of the mussel, but is innocuous to non-target organisms at different trophic levels (Molloy et al., 2013b). In the next step, an aqueous solution commercial formulation (Zequanox®) based on this strain was developed, registered, and currently, is used in wide scale to control zebra mussels in the USA.

Bacillus strains can be toxic to a wide range of pest insects or disease vectors: Blattaria (Alles et al., 2010), Lepidoptera (Polanczyk et al., 2003a, 2004, Pinto & Fiuza, 2003, Fiuza et al., 2012), Coleoptera (Pinto & Fiuza, 2003), Isoptera (Castilhos-Fortes et al., 2002), Hymenoptera (Pinto et al., 2003), and Diptera (Rabinovitch et al., 1999, Cavados et al., 2001, 2004, Polanczyk et al. 2003b). Toxic effects also are observed in Mollusca (Osmam et al., 1991 and 2011, Genthner et al. 1997, Singer et al. 1997, Oliveira et al., 2004, Halima et al, 2006, Ali et al., 2010).

This is due to the wide range of different toxic proteins produced by these microbial agents (Paz et al. 2012). The mechanism of action of *Bacillus* on insects is well described in the scientific literature. This pathogen sporulates, which enables it to resist adverse environmental conditions, occupying different environmental compartments, such as water, soil, sediment and plant tissues. When the microorganism is ingested by insects, inhibits the feeding of host that dies very soon. The toxicity of *B. thuringiensis* is basically it related to crystal proteins called Cry (δ-endotoxins), during the sporulation phase (Bravo et al., 2007). Cry proteins are produced in bodies of parasporal inclusions commonly called crystals, which accumulate at the periphery of the spore (Bravo et al., 2007). When the Bti is ingested by an insect, the Cry proteins in form of prototoxin are solubilized in the gut, resulting in the release of toxic fragments of crystals. And then, these bind to specific receptors that are found on the membrane of the intestinal epithelium. Consequently pores are formed in the epithelium that causes osmotic lysis of cell carrying to death of target organism (Fiuza et al., 1996). According to Genthner et al. (1997), *Bacillus alvei* Strain 2771 causes similar effects on *D. polymorpha*. The authors observed digestive epithelial atrophy, disruption of apical cytoplasm, sloughing of cells with pycnotic nuclei into tubule lumens in exposed mollusks (after 36 hours), severe vacuolization and sloughing (after 48 hours).

Several commercial formulations based on *Bacillus* strains were assessed to control many Insecta species, especially Diptera (Andrade & Branco Jr, 1991, Scovmand & Bauduin, 1997, Mulla et al., 1997, Fillinger et al., 2003, Petry et al., 2004, Lima et al., 2005, Aldemir, 2007, Litaiff et al., 2008, Majambere et al., 2007, Lopes et al., 2010, Nartey et al., 2013). These are available as aqueous solution (Bactivec®, Teknar®, Skeetal®, Bactimos® and Vectobac® AS), water-dispersible granules (Spherimos®, Vectolex® WG and Vectobac® WG), and soluble direct tablet (Culinex Tab plus® and Vectobac® DT) (Andrade & Campos, 1995, World Health

Organization, 1999, Walker & Lynch, 2007) in order to control insects. Toxicological studies have attested no toxic effects of commercial formulations on several non-target organisms (Merritt et al., 2006, Lucho et al., 2009).

So far there is no product developed and registered for the control of golden mussel. The present study aims to evaluate the toxicity of two *Bacillus* strains and three commercial formulations based on *Bacillus*, as well evaluate the toxicity of the more efficient commercial formulations to non-target freshwater organisms.

Methods

Bacillus strains and commercial formulations

Two strains from Bacterial Collection of Laboratory of Microbial Genetics, School of Agriculture "Luiz de Queiroz" (ESALQ), University of São Paulo (USP) were used in bioassays: *Bacillus thuringiensis* sv. *kurstaski* HD-1 (Btk) and *Bacillus thuringiensis* sv. *israelensis* (Bti) IIRAC22. The commercial formulations used in bioassays were VECTOBAC® water-dispersible Granules (WG), composed of *Bacillus thuringiensis* sv *israelensis* serotype H-14 (3000 International Toxic Units, ITU/mg against *Aedes aegypti*, *Aedes albopictus*, *Culex quinquefasciatus* and *Anopheles* spp.), and VECTOBAC® aqueous Solution (AS), composed of on *Bacillus thuringiensis* sv *israelensis* strain AM65-52 (1200 ITU/mg against *Aedes aegypti*), and VECTOLEX® water-dispersible Granules (WG), composed of active constituent *Bacillus sphaericus* Strain 2362 (650 ITU/mg against *Aedes melanimon*, *Aedes nigromaculis*, *Aedes sollicitans*, *Aedes stimulans*, *Aedes triseriatus*, *Aedes vexans*, *Anopheles darlingi*, *Anopheles gambiae*, *Anopheles quadrimaculatus*, *Coquillettidia perturbans*, *Psorophora columbiae*, *Psorophora ferox*).

Target organism

Adult individuals (1.5 - 2.5 cm) of golden mussels were collected in the inner delta of the Jacuí River, in the physiographic unit of the Central Depression of Rio Grande do Sul State, south of Brazil. Macroclusters of mussels attached to the bedrock in the right bank of the Jacuí Canal (JC), in the Pintada Island (30°00'48.3" S, 51º15'36.5" W) were manually removed and sent to the laboratory in plastic bags.

Non-target organism

Pimephales pomelas (Cope, 1858) (fish), *Ceriodaphnia dubia* Richard, 1894 (microcrustacean) and *Pseudokirchneriella subcaptata* (Korshikov) Hindak (algae) were obtained from laboratory cultures of the Laboratory of Ecotoxicology of Ecology Center of the Federal University of Rio Grande do Sul (UFRGS). The freshwater pea clam *Pisidium taraguyense* Ituarte, 2000, was sampled in the Capivara Creek (29°53'48.7" S, 51º28'58.5" W), tributary of Jacuí River, in the city of Triunfo, State of Rio Grande do Sul. The pea clams were sampled using strainer (mesh size: 0,5mm) in the marginal sediments of stream. All specimens were sent to the laboratory in a plastic box covered with wet cotton from the Capivara Creek, in a cooler with ice.

Strain Suspensions

Bioassays were conducted to evaluate the potential of two strains mentioned above in the control of the mussel, and the susceptibility of the target organism. Suspensions of *Bacillus* strains and dilutions of commercial formulations were prepared in the Laboratory of Microbiology of the Federal University of Rio Grande do Sul (UFRGS). The live bacterial suspension was obtained through the following procedures: Bti and Btk strains were grown and sporulated in CCY medium at 28 ± 1ºC under agitation for 3 days, spore-crystal complexes were harvested by centrifugation at 10,000 rpm for 10 min at 4ºC, the supernatant was removed aiming to eliminate of the extracellular components, the pellets were suspended in sterile-distilled water, and the final number of cells was monitored using the spectrophotometric method. Part of live bacterial suspension was autoclaved aiming to obtain dead bacterial suspensions.

Bioassays (target organism)

The bioassays were conducted at the Laboratory of Ecotoxicology, at the Federal University of Rio Grande do Sul (UFRGS). The golden mussels were disaggregated and washed in running water. The periphyton adhered to the shells was removed using a toothbrush. The mollusks were immersed in sterile distilled water for three times consecutively. 300 ml of water reconstituted with salts (total hardness, 20 mg/L) and sterilized were used in beaker cups previously sterilized. Hoses and aeration stones previously immersed in 70% alcohol for 24 hours were washed with sterile distilled water. They were then connected to each other and then connected to aerator. The aeration stones were put inside of each beaker cup with reconstituted water. The aerators were turned on and the air flow was adjusted so that all flasks received aeration at the same level. Ten mussels were placed inside each flask, where were acclimated for 72 hours at 21±2 °C. The feed consisted of adding 5 mL of culture *Monoraphidium* sp. every 48 hours. The flasks containing aerated water and mussels were covered in plastic film. Each experiment consisted of a set of five replicates for the control group and five replicates for each concentration of bacterial strain or commercial product assessed.

Part of the flasks previously prepared was used for the maintenance of mussels without addition of bacterial strains or commercial formulations. Inside the other flasks, different concentrations of *Bacillus* strains (live and dead suspensions) and commercial formulations were added according to the experimental design showed in Table 1. The assays were conducted at 21±2 °C in the darkness. The mortality of mussels was assessed daily (Table 1) following the criteria defined by Soares et al. (2009). All laboratory procedures are also described in Pereira et al. (2012).

Statistical Analysis

Only experiments with mortality rate lower than 10% in the control group were considered The corrected mortality was calculated using the Abbott formula according to Alves (1998). The mortality rate of treatments and the control group were compared trough analysis of variance (ANOVA, Tukey *a posteriori*), with a significance level of 5%. Lethal concentrations ($LC_{50,}$ LC_{70} and LC_{95}) and lethal time ($LT_{50,}$ LT_{70} and LT_{95}) were calculated trough regression analysis (Probit). All statistical procedures were conducted using SPSS software 13.0 for windows. To compare the doses needed to cause mortality of golden mussel with the appropriate doses to cause the mortality of target-dipteran, the lethal concentrations obtained through bioassay were also expressed in International Toxic Units, considering the potency of commercial formulations to control the target-dipteran according to manufacturer.

Ecotoxicological Assays

The commercial formulation that caused higher mortality rate than 80% of golden mussel was used in bioassays on non-target organisms, the pea clam *P. taraguyense* (Sphaeriidae), and through standard methods described by U.S. EPA (2002) using organisms of three trophic levels: the fish *P. pomelas*, microcrustacean *C. dubia* and algae *P. subcaptata*. Chronic assays using non-target pea clams (Sphaeriidae) to assess the toxicity of Bti formulations are recommended by Metropolitan Mosquito Control District (2013).

The toxicity on non-target organism was evaluated using the same concentrations described in Table 1.

Results

Descriptive statistics of mortality rate values observed in the control groups and treatments of all bioassays is shown in table 2.

Strains *versus* Target Organism

Bacillus thuringiensis sv. *israelensis* (Bti) strain IIRAC22

The corrected mortality values of golden mussels exposed at different concentrations (cells/mL) of live and dead bacterial suspension (Bti strain IIRAC22) are show in Figure 1A and B respectively. Significant statistical differences between mortality rate values of the control group and the following live bacterial suspensions were verified through analysis of variance (ANOVA, Tukey *a posteriori*, $\alpha=0.05$) (Table 2): 10^7 cells/mL ($P<0.0001$) and 10^8 cells/mL ($P<0.0001$). No statistically significant differences between the control group and the 10^6 cells/mL live bacterial suspension ($P=0.915$) were verified. Significant statistical differences between mortality rate values of the control group and the 10^8 cells/mL dead bacterial suspensions ($P=0.001$) were verified through analysis of variance. No statistically significant differences between the control group and the following dead bacterial suspensions were verified: 10^6 ($P=0.37$) and 10^7 cells/mL ($P=0.07$). The lethal time (LT) values to cause 50%, 70% and 95% of mortality rate of golden mussels at 10^7, and 10^8 cells/mL bacterial suspensions (live and dead) are show in Table 3. The lethal concentration (LC) values to cause 50%, 70% and 95% of mortality rate of golden mussels at 10^6, 10^7, and 10^8 cells/mL bacterial suspensions (live and dead) are show in Table 4.

Bacillus thuringiensis sv. *kurstaski* (Btk) strain HD-1

The corrected mortality values of golden mussels exposed at different concentrations of live bacterial suspension (Btk strain HD-1) are show in Figure 1C. Significant statistical differences (<0,0001) between the mortality values of control group and the treatment 10^8 cells/mL live bacterial suspension were found through analysis of variance (ANOVA, Tukey *a posteriori*, $\alpha=0.05$). No statistically significant differences between the control group and the following treatments were verified: 10^6 cells/mL ($P=0.91$) and 10^7 cells/mL ($P=0.99$). The lethal time (LT) values to cause 50%, 70% and 95% of mortality rate of golden mussels at 10^7, and 10^8 cells/mL bacterial suspensions (live and dead) are show in Table 3. The lethal concentration (LC) values to cause 50%, 70% and 95% of mortality rate of golden mussels at 10^6, 10^7, and 10^8 cells/mL bacterial suspensions (live and dead) are show in Table 4.

Commercial formulations *versus* Target Organism

Vectobac® AS

The corrected mortality values of golden mussels exposed at different dilutions of commercial formulation Vectobac® AS is showed in the Figure 2A. Higher mortality rate than 80% was observed at 6,666.7 mg/L of Vectobac® AS. Significant statistical differences between mortality rate values of the control group and the following treatments were verified through analysis of variance (ANOVA, Tukey *a posteriori*, $\alpha=0.05$): 1.7 x 10^3 mg/L ($P=0.002$), 3.3 x 10^3 mg/L ($P<0.0001$) and 6.7 x 10^3 mg/L ($P<0.0001$). The lethal time (LT) values to cause 50%, 70% and 95% of mortality rate of golden mussels at 3.3 x 10^3 mg/L and 6.7 x 10^3 mg/L of Vectobac® AS are show in Table 3. The lethal concentration (LC) values to cause 50%, 70% and 95% of mortality rate of golden mussels at 1.7 x 10^3 mg/L, 3.3 x 10^3 mg/L and 6.7 x 10^3 mg/L of Vectobac® AS are show in Table 4.

Vectobac® WG

The corrected mortality values of golden mussels exposed at different dilutions of commercial formulation Vectobac® WG is showed in the Figure 2B. Lower mortality rate than 40% was observed at all treatments. Significant statistical differences between mortality rate values observed in the control group and the following treatments were verified through analysis of variance (ANOVA, Tukey *a posteriori*, $\alpha=0.05$): 1 x 10^2 mg/L ($P<0.001$) and 2 x 10^2 mg/L ($P=0.005$). No statistically significant differences between the control group and the concentration 5 x 10 mg/L ($P=0.065$) were observed. The lethal time (LT) values to cause 50%, 70% and 95% of mortality rate of golden mussels at 1 x 10^2 mg/L and 2 x 10^2 mg/L of Vectobac® WG are show in Table 3. The lethal concentration (LC) values to cause 50%, 70% and 95% of mortality rate of golden mussels at 5 x 10 mg/L, 1 x 10^2 mg/L and 2 x 10^2 mg/L of Vectobac® WG are show in Table 4.

Vectolex® WG

The corrected mortality values of golden mussels exposed at different dilutions of commercial formulation Vectolex® WG is showed in the Figure 2B. Lower mortality rate than 40% was observed at all treatments. Significant statistical differences between mortality rate values of control group and the following treatments were verified through analysis of variance (ANOVA, Tukey *a posteriori*, α=0.05): 1 x 10^2 mg/L (P=0.003) and 2 x 10^2 mg/L (P=0.008). No statistically significant differences between the control group and the concentration 5 x 10 mg/L (P=0.087) were observed. The lethal time (LT) values to cause 50%, 70% and 95% of mortality rate of golden mussels at 1 x 10^2 mg/L and 2 x 10^2 mg/L of Vectobac® WG are show in Table 3. The lethal concentration (LC) values to cause 50%, 70% and 95% of mortality rate of golden mussels at 5 x 10 mg/L, 1 x 10^2 mg/L and 2 x 10^2 mg/L of Vectobac® WG are show in Table 4.

Vectobac® AS *versus* Non-Target Organisms

The concentrations 3.3 x 10^3 mg/L and 6.7 x 10^3 mg/L of Vectobac® AS showed toxicity to all non-target organisms evaluated using standard method described by U.S. EPA (2002) (Table 5).

Regarding the bioassays to evaluate the toxicity of Vectobac on native freshwater pea clam (*P. taraguyense*), significant statistical differences between mortality rate values of the control group and the following Vectobac® AS suspensions were verified through analysis of variance (ANOVA, Tukey *a posteriori*, α=0.05): 3.3 x 10^3 mg/L (P=0.001) and 6.7 x 10^3 mg/L (P<0.0001). No statistically significant differences between the control group and the 1.7 x 10^3 mg/L (P=0.20) were verified. The lethal time (LT) values to cause 50%, 70% and 95% of mortality rate of native pea clams at 3.3 x 10^3 mg/L and 6.7 x 10^3 mg/L of Vectobac® WG, and the lethal concentration (LC) values to cause 50%, 70% and 95% of mortality rate of native pea clam at 1.7 x 10^3 mg/L, 3.3 x 10^3 mg/L and 6.7 x 10^3 mg/L of Vectobac® WG are show in Table 6.

Discussion

The lethal concentration 5.3 x 10^8 cells/mL (1.0 x 10^8 - 4.8 x 10^{11}) of live bacterial suspension (Btk strain HD-1) to cause 95% mortality of the golden mussel is lower than the lethal concentration of Bti strain IIRAC22. Several bioinsecticides have been developed based on Btk strain HD-1, which may point to a broad spectrum of action on target species. This strain HD-1 should be investigated by new bioassays with live and dead bacterial suspensions in order to understand the pathogenicity and virulence of golden mussels in face of bacterial metabolites. Furthermore it is necessary to evaluate the toxic proteins that are more effective to the control of the target species. Gu et al. (1994) conducted bioassays using 10^7 cells/L suspensions of bacterial isolates to select microbial agents for the control of zebra mussel and observed a mortality rate of 100% after 3 days. Genthner et al. (1997) observed $LC_{50} = 0.81\%$ v/v (dilutions of the bacterial culture, 6.3 x 10^8 CFU/mL) suspension of *Bacillus alvei* to kill *Dreissena polymorpha* after 3 days. High mortality rates of *Biomphalaria pfeifferi* (100% after 6 hours) and *Bulimus truncatulus* (100% after 24 hours) was observed by Ofori, (2000) using 7 x 10^4 spores/L suspensions of *Bacillus brevis* strain isolated from soil. Despite the high concentrations and lethal time to kill golden mussels using the strains assessed, the results encourage the selection of new strains, mainly isolated from the target organism itself. Several authors obtained high mortality rates for Leptodeptera (Polanczyc et al., 2003 and 2004), Blattaria (Alles et al., 2009), and Hymenoptera (Pinto et al., 2003) using suspensions of Bt strains in the same order of magnitude (1 x 10^6 - 1 x 10^{10} cells/L).

Despite the high mortality of mussels in response to Vectobac® AS treatments (>80% at 6.7 x 10^3 mg/L), all lethal concentrations (LC_{50}, LC_{70} and $LC9_5$) to cause mussel mortality are very high. The LC_{95} (1.2 x 10^4 mg/L equivalent to 1.4 x 10^8 ITU/L against target-diptera) value to kill golden mussels is 48,000 times higher than LC_{95} (0.25 mg/L equivalent to 300 ITU/L) of Vectobac® AS to kill *Culex saltanensis* Dyar, 1928 observed by Zequi & Lopes (2007), under laboratory conditions. Similar results were observed by Osman & Mohamed (1991) regarding the effects of another aqueous formulation, Thuricide® insecticide (potency: 16,000 UTI/mg against target-caterpillars, active constituent *Bacillus thuringiensis* sv. *kurstaski* strain HD-1), on adult snails *Biomphalaria alexandrina* at different concentrations. The authors observed 100% of mortality rates for *B. alexandrina* after 6 days at 1000 mg/L (equivalent to 1.6 x 10^7 target-caterpillars). Osman et al. (2011) also assessed the effects of the Dipel-2x® (potency: 32,000 UTI/mg against target-caterpillars, active constituent *B. thuringiensis* sv. *kurstaski*) on adult snails *B. alexandrina* and observed LC_{90} (392.3 mg/L) equivalent to 1.2 x 10^7 ITU/L against target-caterpillars. According to the label of Dipel®, the recommended dosage is 600 to 1000mg/L (2.7 x 10^7 to 3.7 x 10^7 ITU/L against target-caterpillars) against several species of Lepdoptera, which would be sprayed on the soil and vegetation. This dose is very similar to the concentration used for killing Planorbidae observed by Osman et al. (2011).

The LC_{95} values (after 168 hours) of Vectobac® WG to kill golden mussels obtained in bioassays (6.7 x 10^2 mg/L equivalent to 2 x 10^6 ITU/L against target-dipteran) is 5,050 times higher than LC_{95} values (396 ITU/L) observed by Majambere et al. (2007) to kill third instar larvae of *Anopheles gambiae* after 24 hours, and also 33,333 times higher than dose (0.02 mg/L = 60 ITU/L) observed by Nartey et al. (2013) to cause higher mortality rate (100%) of the third instar larvae of *A. gambiae* after 24 hours.

Similar occurrences were observed on Vectolex® WG bioassays, the LC_{95} values (6.7 x 10^2 mg/L) to kill golden mussels (after 168 hours) equivalent to 4.3 x 10^5 ITU/L against target-dipteran, which is 28,859 times higher than LC_{95} values (14.9 ITU/L) to kill *A. gambiae* larvae after 24 hours, also observed by Majambere et al. (2007). The authors also found higher mortality rate (100%) of mosquitoes in inferior lethal time (24 h). The higher mortality rates of mussels exposed to Vectobac® WG (30%) and Vectolex® WG (28%) were observed only after 168 hours.

The difference between mortalities values of mussels observed in bioassays using aqueous formulation (Vectobac® AS) and those using formulations using water-dispersible granules (Vectobac® WG and Vectolex®) may be attributed to quick dissolution of the aqueous formulation in the water. In contrast, the granular formulation is quickly settled at the bottom of the flasks. Thus, the active ingredient of granulate formulation is probably not available in the water for the mussels which are filter feeders. It is possible that the aqueous formulation can more easily provide the active ingredient. Despite the constant aeration of bottles used inthe bioassays, no resuspension of the granules were observed.

Bioassays using chemical agents such as various formulations of chlorine (Fernandes et al., 2012), copper sulfate (Soares et al., 2009, Pereira & Soares, 2012), potassium chloride (Campos & Fernandes, 2012) and their respective encapsulated formulation for control of golden mussel adults demonstrated that their survival is affected only at high concentrations, often becoming economically unviable besides offering toxicity to the aquatic environment. Our results support the premise that the mussel is resistant to wide range of control agents. High concentrations of Vectobac to cause mortality rates for satisfactory control of adult mussels become economically unviable and offers damage to the ecosystem.

The high mortality observed in the treatments with higher concentrations of strains and commercial formulations may also be attributed to starvation, since some mussels close shells during the experiment. According to Fernandes et al. (2012), the control of adult mussels using forms of chlorine requires higher dosages those use for control in the larval stage. The adult individual feels the presence of the chemical agent and closes the valves and is therefore often impossible to attribute the death of the organism to by starvation (Soares et al., 2009, Fernandes et al., 2012). On the other hand, higher concentrations of cultivated strains resulted in higher levels of visible suspended solids and turbidity in the flasks, which may have affected the mussel gill and filtration process, causing their death. For better understanding of the effect of doses of bacterial suspensions and formulations, histological analyses of the tissues of the digestive apparatus could elucidate the mode of action and the effectiveness of treatments (Genthner et al., 1996, Molloy et al., 2013a).

In order to obtain adequate commercial formulations in order to control golden mussels, it is necessary to prospect the bacterial strains from several environment compartments occupied by this invasive species. Moreover, the resident microflora of this target species should have their strains bioprospected. Several microrganisms were isolated from freshwater snail *Biomphalaria glabrata*, such as species of *Citrobacter*, *Aeromonas*, *Pseudomonas*, *Enterobacter*, and *Flavobacterium*, among others (Cheng, 1986). Just as mentioned snail, different bacterial strains can be isolated from the mussel and subsequently tested in bioassays using adult specimens, especially larvae.

The size of the target organism has a positive relationship with the lethal dose. Oliveira et al., 2004 observed differences between the mortality rates of young snails of two ages (0 to 3 and 12 to 15 days after eclosion) in bioassays using *Brevibacillus laterosporus*. Similar results were also observed in bioassays using Bti formulations to control Simulidae (Andrade & Branco Jr., 1991). Bioassays using *Bacillus* strains and commercial formulations to control larvae could get more promising results for the control of the golden mussel, since less time and lethal concentration could be obtained. According to Singer et al (1997), in bioassays using different strains of *Bacillus*, the lethal time to kill 50% of adult individuals of *D. polymorpha* was higher than the lethal time to kill 50% of larvae (stage D).

The filtration rate of the mussel varies with temperature (Sylvester et al., 2005), thus this factor may interfere in the absorption of strains and commercial formulations. Molloy & Mayer (2007) observed that mortality rates of Zebra mussel exposed to bacterial suspensions (*Pseudomonas fluorescens)* increases with temperature. This could be better explained by the analysis of bioassay experiments at different temperatures.

The lowest concentration of Vectobac® AS (2.0 x 10^6 ITU/L against target-dipteran) evaluated in ecotoxicological assays is 6,711 times higher than lethal concentration (298 ITU/L) observed by Zequi & Lopes (2007), to kill 95% of the target-organism *Culex saltanensis* under laboratory conditions. Therefore, the toxicity of Vectobac AS on non-target organisms of three trophic levels (*P. pomelas*, *C. dubia* and *P. subcaptata*) was already expected at the concentrations tested. This result reinforces the need to use the recommended dosage by the manufacturer for controlling target organisms without negative effects on non-target organisms. The use of a commercial formulation for the control of target organisms not mentioned in product registration requires new assays and new registration. Hurst et al. (2007) assessed the action of commercial formulations (Vectobac® AS and Vectolex® WG) on *Melanotaenia duboulayi*, a native fish from Australia, and no toxic effects were observed in the following treatments: 12,230 ITU/L (Vectobac® AS) and 1,110 ITU/L against target-dipteran (Vectolex® WG). The lowest Vectobac® AS concentration (2.0 x 10^6 ITU/L against target-dipteran) used in our ecotoxicological assay is 163.5 times higher than the concentration use by Hurst et al. (2007), and the latter is 10 times higher than effective field concentration, according to the same author. Lagadic et al. (2014) assessed an aquatic invertebrate community in French Atlantic coastal wetlands after long period of submission to Bti treatment for controlling dipteran and no effects on non-target aquatic invertebrates were observed. Similar results were verified by Hershey et al. (1995) through the assessment of Vectobac® G on biomass and density of macroinvertebrates in temporary ponds (USA), and by Merrit e al. (2005) through the assessment of Vectolex® CG on richness, diversity and abundance of non-target macroinvertebrates in streams (USA).

The lethal concentration (4.3 x 10^3 mg/L equivalent to 5 x 10^6 ITU/L against dipteran-target) of Vectobac® AS to kill 95% of pea clam *Pisidium taraguyense* is 409 times higher than the Vectobac® AS dose used by Hurst et al. (2007) to assess toxicity on fish. According to literature review by Glare & Maureen O'Callaghan (1998), several studies conducted in order to assess adverse effects of Bti formulations on non-target organism showed no reported effects to different freshwater invertebrate species, including the pea clams *Pisidium* sp. No difference between abundance of pea clams (Sphaeriidae) was reported in two sampling sites, both treated and untreated, using Bti commercial formulations in a stream in North American agricultural lands (Chambers et al., 2010).

Besides the high lethal dose of Vectobac® AS to cause 95% of mortality of golden mussels and their toxic effects on non-target organisms, the high lethal time to cause a mortality rate of 95% of the golden mussels (194.5 hours (182.9-210.6) at 6.7 x 10^3 mg/L), would be a problem to control mussel populations in areas of high flow which would require continued application of high concentrations, resulting in high economic costs. On the other hand, treatment with Vectobac® AS can be effective in the treatment of macrofouling in equipment of power plants, where there is no water flow.

Final considerations

The strains *Bacillus thuringiensis* sv. *kurstaski* HD-1 is more effective than *Bacillus thuringiensis* sv. *israelensis* IIRAC22. This result indicates possibilities for the future of biological control using Bt strains.

New formulations should be appropriate for the mechanism of filtration of target mussels in order to optimize the intake and the effect of microbial agents.

The prospect of more effective strains to control the golden mussel especially in the larval stage should be a future priority. However, it is essential to assess the effects of new formulations on non-target organisms especially native species of freshwater bivalves.

Besides mortality, other factors such as loss of fertility of organisms exposed to bacterial agents could be investigated in future bioassays using strains of Bti and Btk, and other microorganisms.

Vectobac® AS cause high mortality of golden mussels at extreme concentrations resulting in toxic effects to non-target organisms and high economic costs.

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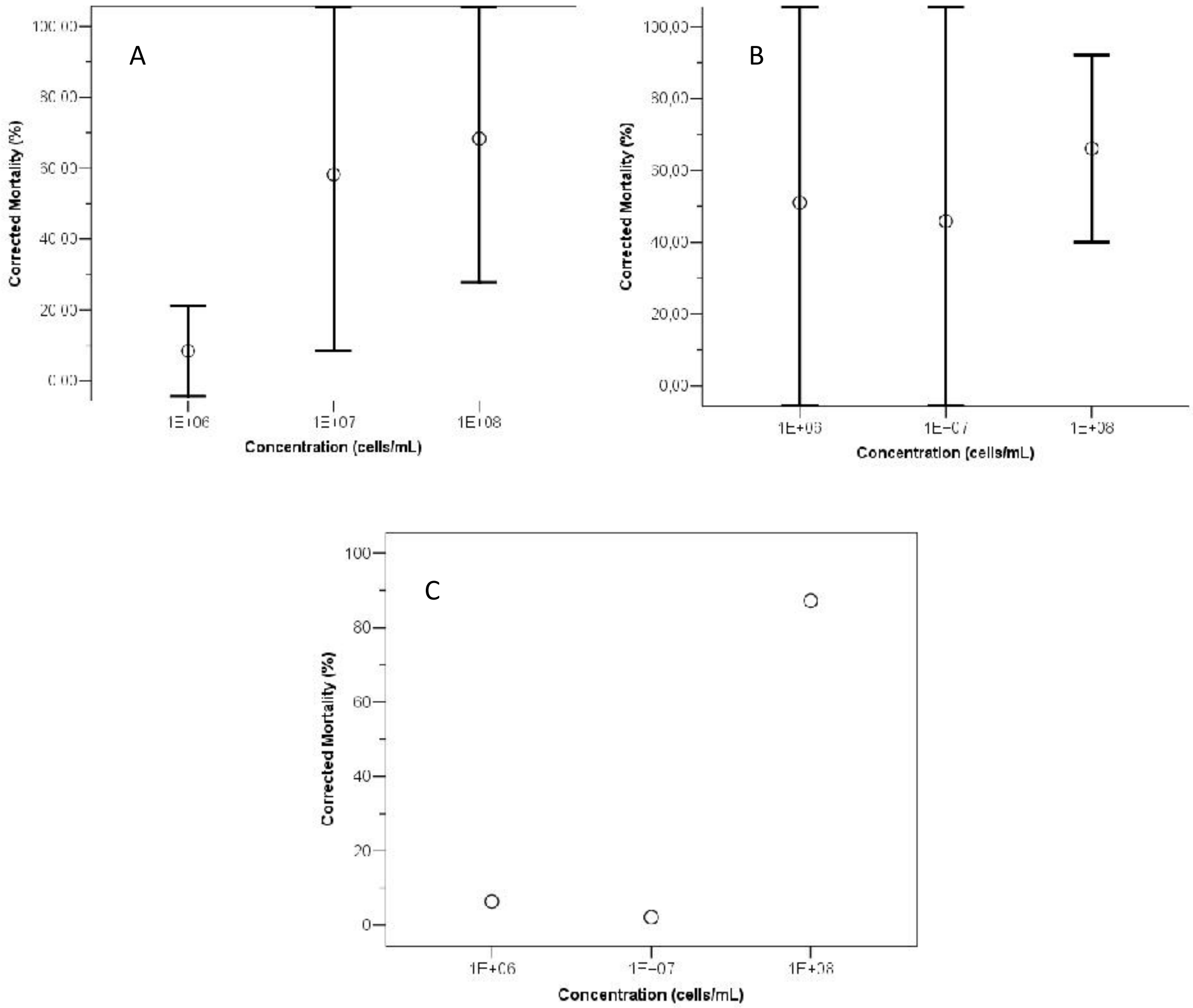

Figure 1. Corrected mortality (%) of golden mussels exposed to different concentrations of two *Bacillus* strains at 21±2°C: A) live bacteria suspension and B) dead bacteria suspension of *Bacillus thuringiensis* sv. *israelensis* strain IIRAC22, and C) live bacteria suspension of *Bacillus thuringiensis* sv. *kurstaski* strain HD-1.

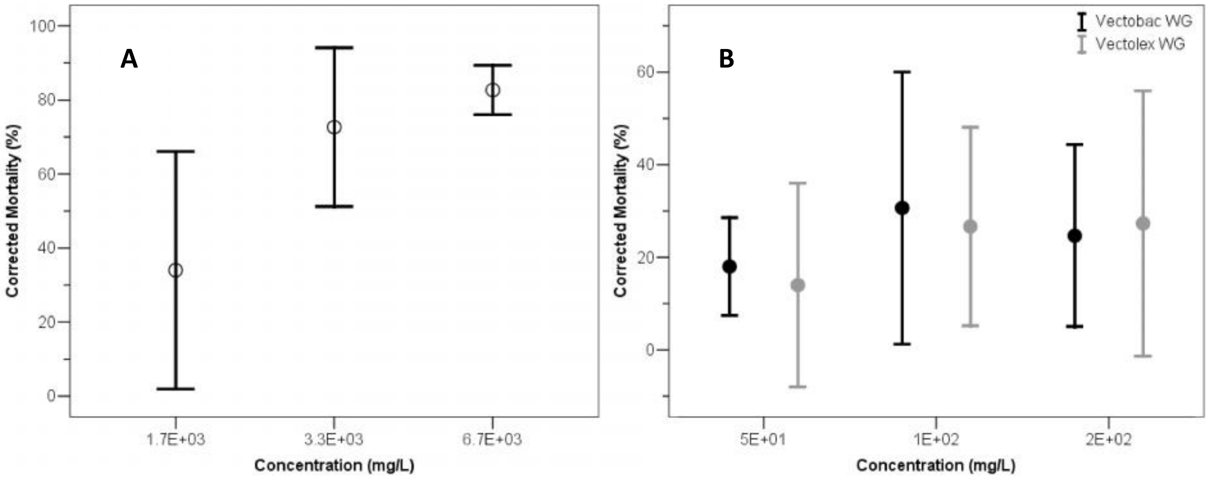

Figure 2. Corrected mortality (%) of golden mussels exposed to different concentrations of three commercial formulations based on *Bacillus* strains 21±2°C: A) *Bacillus thuringiensis* sv. *israelensis* strain AM65-52 (aqueous suspension), B) *Bacillus thuringiensis* sv. *israelensis* Serotype H-14 (water-dispersible granules), and *Bacillus sphaericus* strain 2362 (water-dispersible granules).

Table 1. Experimental design of the bioassay using *Bacillus* strains and commercial formulations for golden mussels control at 21±2°C. Bti - *Bacillus thuringiensis* sv. *israelensis*, Btk - *Bacillus thuringiensis* sv. *kurstaski*, Bs - *Bacillus sphaericus*, LS - live bacteria suspension, DS - dead bacteria suspension, AS - aqueous suspension, WG - water-dispersible granules, ATD – concentration equivalent to Internation Toxic Units estimated - ITU/L Against Target-Dipteran.

		Strain Cultures			Commercial Formulations		
Treatments	Replicas (N)	Bti Strain IIRAC22		Btk Strain HD-1	Vectobac® Bti Strain AM65-52 (1,200 ITU/mg)	Vectobac® Bti Serotype H-14 (3,000 ITU/mg)	Vectolex® Bs Strain 2362 (650 ITU/mg)
		LS	DS	LS	AS	WG	WG
Control	5	0	0	0	0	0	0
Concentration 1	5	10^6 cells/mL	10^6 cells/mL	10^6 cells/mL	1.7 x 10^3 mg/L 2.0 x 10^6 ITU/L ATD	5 x 10 mg/L 1.5 x 10^5 ITU/L ATD	5 x 10 mg/L 3.2 x 10^4 ITU/L ATD
Concentration 2	5	10^7 cells/mL	10^7 cells/mL	10^7 cells/mL	3.3 x 10^3 mg/L 4.0 x 10^6 ITU/L ATD	10^2 mg/L 3.0 x 10^5 ITU/L ATD	10^2 mg/L 6.5 x 10^4 ITU/L ATD
Concentration 3	5	10^8 cells/mL	10^8 cells/mL	10^8 cells/mL	6.7 x 10^3 mg/L 8.0 x 10^6 ITU/L ATD	2 x 10^2 mg/L 6.0 x 10^5 ITU/L ATD	2 x 10^2 mg/L 1.3 x 10^5 ITU/L ATD
Total of Assays (N)		3	2	1	3	3	3
Time of Exposure		216 hours (9 days)	216 hours (9 days)	216 hours (9 days)	168 hours (7 days)	168 hours (7 days)	168 hours (7 days)

Table 2. Descriptive statistics of mortality values of mussels exposed to different concentrations of *Bacillus* strains and commercial formulations at 21±2°C.

Treatments			N	Mean	Standard Deviation	Standard Error	Minimum	Maximum
Strain Cultures	Btk Strain HD-1 (live suspension)	Control	5	0.33	0.82	0.21	0	3
		10^6 cells/mL	5	1.07	2.58	0.67	0	10
		10^7 cells/mL	5	5.93	4.20	1.08	0	10
		10^8 cells/mL	5	6.93	3.63	0.94	0	10
	Bti Strain IIRAC22 (live suspension)	Control	15	0.20	0.42	0.13	0	1
		10^6 cells/mL	15	5.20	4.94	1.56	0	10
		10^7 cells/mL	15	4.70	4.79	1.51	0	10
		10^8 cells/mL	15	7.70	3.89	1.23	0	10
	Bti Strain IIRAC22 (dead suspension)	Control	10	0.60	0.89	0.40	0	2
		10^6 cells/mL	10	1.20	1.30	0.58	0	3
		10^7 cells/mL	10	0.40	0.89	0.40	0	2
		10^8 cells/mL	10	8.80	2.17	0.97	5	10
Commercial Formulations	Vectobac® AS Bti Strain AM65-52	Control	15	0.00	0.00	0.00	0	0
		1.7×10^3 mg/L	15	3.40	3.36	0.87	0	10
		3.3×10^3 mg/L	15	7.27	3.08	0.80	0	10
		6.7×10^3 mg/L	15	8.27	1.75	0.45	4	10
	Vectobac® WG Bti Serotype H-14	Control	15	0.00	0.00	0.00	0	0
		5 x 10 mg/L	15	1.80	1.78	0.46	0	6
		1×10^2 mg/L	15	3.07	2.74	0.71	0	8
		2×10^2 mg/L	15	2.47	2.10	0.54	0	7
	Vectolex® WG Bs Strain 2362	Control	15	0.00	0.00	0.00	0	0
		5 x 10 mg/L	15	1.73	1.91	0.49	0	6
		1×10^2 mg/L	15	2.67	2.06	0.53	0	6
		2×10^2 mg/L	15	2.40	2.77	0.72	0	9

Table 3. Lethal time (hours) to cause 50 (LT_{50}), 70 (LT_{70}) and 95% (LT_{95}) of mortality rate to golden mussels exposed to different concentrations of *Bacillus* strains and commercial formulations at 21±2°C. Lower (LCL) and upper (UCL) confidence limits (95%).

Treatments			Equation	Lethal Time (hours) (LCL - UCL)	
Strain Cultures	Bti Strain IIRAC22 (live suspension)	10^7 cells/mL	y = -1.58 + 0.01x *P*<0.0001	LT_{50}	175.4 (153.9-208.3)
				LT_{70}	233.5 (202.3-291.8)
				LT_{95}	357.6 (297.5-478.3)
		10^8 cells/mL	y = -1.68 + 0.01x *P*<0.0001	LT_{50}	151.9 (129.2-180.0)
				LT_{70}	199.4 (172.8- 247.7)
				LT_{95}	300.8 (251.3-406.8)
	Bti Strain IIRAC22 (dead suspension)	10^7 cells/mL	y = -3.16 + 0.02x *P*<0.0001	LT_{50}	178.1 (165.0-195.0)
				LT_{70}	207.7 (191.4-232.2)
				LT_{95}	270.8 (243.7-315.9)
		10^8 cells/mL	y = -1.54 + 0.12x *P*<0.0001	LT_{50}	128.6 (106.5-150.7)
				LT_{70}	172.1 (150.1-206.5)
				LT_{95}	265.2 (225.3-343.9)
	Btk Strain HD-1 (live suspension)	10^8 cells/mL	y = -3.25 + 0.25x *P*<0.0001	LT_{50}	129.4 (118.8-140.3)
				LT_{70}	150.3 (139.4-164.5)
				LT_{95}	194.9 (178.0-221.7)
Commercial Formulations	Vectobac® AS Bti Strain AM65-52	3.3 x 10^3 mg/L	y = -2.69 + 0.02x *P*<0.0001	LT_{50}	141.0 (132.3-151.5)
				LT_{70}	168.8 (157.3-184.7)
				LT_{95}	228.4 (208.2-258.1)
		6.7 x 10^3 mg/L	y = -3.61 + 0.03x *P*<0.0001	LT_{50}	133.7 (128.0-140.0)
				LT_{70}	153.1 (146.2-161.7)
				LT_{95}	194.5 (182.9-210.6)
	Vectobac® WG Bti Serotype H-14	1 x 10^2 mg/L	y = -4.38 + 0.22x *P*<0.0001	LT_{50}	117.4 (181.3-228.0)
				LT_{70}	221.0 (199.3-265.2)
				LT_{95}	271.5 (237.1-343.3)
		2 x 10^2 mg/L	y = -5.21 + 0.02x *P*=0.207	LT_{50}	195.1 (184.6-214.6)
				LT_{70}	215.5 (200.4-241.6)
				LT_{95}	257.6 (233.6-299.8)
	Vectolex® WG Bs Strain 2362	1 x 10^2 mg/L	y = -5.33 + 0.02x *P*<0.0001	LT_{50}	194.1 (177.3-231.7)
				LT_{70}	213.2 (190.8-277.4)
				LT_{95}	254.0 (218.6-358.9)
		2 x 10^2 mg/L	y = -5.08 + 0.25x *P*=0.207	LT_{50}	198.5 (181.0-242.6)
				LT_{70}	219.0 (195.6-280.3)
				LT_{95}	262.6 (226.0-361.7)

Table 4. Lethal Concentration of *Bacillus* strains and commercial formulations to cause 50 (LC_{50}), 70 (LC_{70}) and 95% (LC_{95}) of mortality rate to golden mussels at 21±2°C. Lower (LCL) and upper (UCL) confidence limits (95%).*No possible to calculate.

	Treatments	Exposure Time (h)	Equation		Lethal Concentration (LCL - UCL)
Strain Cultures	Bti Strain IIRAC22 (live suspension)	216	$y = -5.93 + 0.83x$ $P < 0.0001$	LC_{50}	1.4×10^{7} cells/mL ($5.0 \times 10^{6} - 4.5 \times 10^{7}$)
				LC_{70}	6.0×10^{7} cells/mL ($2.2 \times 10^{7} - 5.4 \times 10^{8}$)
				LC_{95}	1.3×10^{9} cells/mL ($2.2 \times 10^{8} - 2.7 \times 10^{11}$)
	Bti Strain IIRAC22 (dead suspension)	216	$y = -2.1 + 0.33x$ $P < 0.0001$	LC_{50}	2.0×10^{6} cells/mL (*)
				LC_{70}	7.5×10^{7} cells/mL (*)
				LC_{95}	2.0×10^{11} cells/mL (*)
	Btk Strain HD-1 (live suspension)	216	$y = -9.5 + 1.27x$ $P < 0.0001$	LC_{50}	2.8×10^{7} cells/mL ($8.5 \times 10^{6} - 2.0 \times 10^{8}$)
				LC_{70}	7.2×10^{7} cells/mL ($2.3 \times 10^{7} - 2.0 \times 10^{9}$)
				LC_{95}	5.3×10^{8} cells/mL ($1.0 \times 10^{8} - 4.8 \times 10^{11}$)
Commercial Formulations	Vectobac® AS Bti Strain AM65-52	168	$y = -7.75 + 2.31x$ $P < 0.0001$	LC_{50}	2.3×10^{3} mg/L ($1.5 \times 10^{3} - 2.3 \times 10^{3}$)
				LC_{70}	3.8×10^{3} mg/L ($3 \times 10^{3} - 5.5 \times 10^{3}$)
				LC_{95}	1.2×10^{4} mg/L ($7.3 \times 10^{3} - 3.9 \times 10^{4}$)
	Vectobac® WG Bti Serotype H-14	168	$y = -1.41 + 0.36x$ $P < 0.0001$	LC_{50}	3×10^{2} mg/L ($2.1 \times 10^{2} - 6.7 \times 10^{2}$)
				LC_{70}	4.2×10^{2} mg/L ($2.9 \times 10^{2} - 1 \times 10^{3}$)
				LC_{95}	6.7×10^{2} mg/L ($4.4 \times 10^{2} - 1.7 \times 10^{3}$)
	Vectolex® WG Bs Strain 2362	168	$y = -1.34 + 0.004x$ $P < 0.0001$	LC_{50}	3×10^{2} mg/L ($2.1 \times 10^{2} - 6.7 \times 10^{2}$)
				LC_{70}	4×10^{2} mg/L ($2.9 \times 10^{2} - 1 \times 10^{3}$)
				LC_{95}	6.7×10^{2} mg/L ($4.4 \times 10^{2} - 1.7 \times 10^{3}$)

Table 5. Toxicity of Vectobac® AS on non-target organisms of three trophic levels using standard methods described by U.S. EPA (2002).

Non-target standard organisms	Concentration (mg/L)		
	1.7 x 10^3	3.3 x 10^3	6.7 x 10^3
Fish *Pimephales pomelas*	Acute	Acute	Acute
Microcrustacean *Ceriodaphnia dubia*	Acute	Acute	Acute
Algae *Pseudokirchneriella subcaptata*	Chronic	Chronic	Chronic

Table 6. Toxicity Vectobac® AS on non-target pea clam *Pisidium taraguyense* Ituarte, 2000 at 21±2°C: lethal time (LT) values to cause 50%, 70% and 95% of mortality rate of native pea clams at different concentrations, and lethal concentration (LC) values to cause 50%, 70% and 95% of mortality rate of native pea clam. Lower (LCL) and upper (UCL) confidence limits (95%).

Non-Target Species	Equation	Lethal Time and Lethal Concentration (LCL - UCL)	
Pisidium taraguyense Ituarte, 2000	$y = -0.91 + 0.012x$ $P = 0.026$	LT$_{50}$ at 3.3 x 10^3 mg/L	65.4 hours (46.6 - 80.5)
		LT$_{70}$ at 3.3 x 10^3 mg/L	104.9 hours (89.3 - 128.3)
		LT$_{95}$ at 3.3 x 10^3 mg/L	189.1 hours (157.4 - 252.5)
	$y = -0.87 + 0.013x$ $P = 0.931$	LT$_{50}$ at 6.7 x 10^3 mg/L	76.9 hours (45.6 - 102.2)
		LT$_{70}$ at 6.7 x 10^3 mg/L	121.1 hours (96.5 – 168.7)
		LT$_{95}$ at 6.7 x 10^3 mg/L	215.5 hours (168.1 – 347.9)
	$y = -18.41 + 5.51x$ $P = 0.126$	LC$_{50}$	2.2 x 10^3 mg/L (1.6 x 10^3 - 2.8 x 10^3)
		LC$_{70}$	2.7 x 10^3 mg/L (2.1 x 10^3 – 4 x 10^3)
		LC$_{95}$	4.3 x 10^3 mg/L (3.2 x 10^3 - 1 x 10^4)

Capítulo 5

Diretrizes para a conservação de bivalves nativos de água doce e o controle da bioinvasão no Brasil: desafios e conflitos

Diretrizes para a conservação de bivalves nativos de água doce e o controle da bioinvasão no Brasil: desafios e conflitos.

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O Brasil é o país que apresenta a maior diversidade de bivalves límnicos na América do Sul (Figura 1), sendo que as regiões hidrográficas do Rio Amazonas, Rio Paraguai, Rio Uruguai e Rios do Sul e Sudeste que correm para o Atlântico apresentam a maior riqueza de espécies (Pereira et al. 2012).

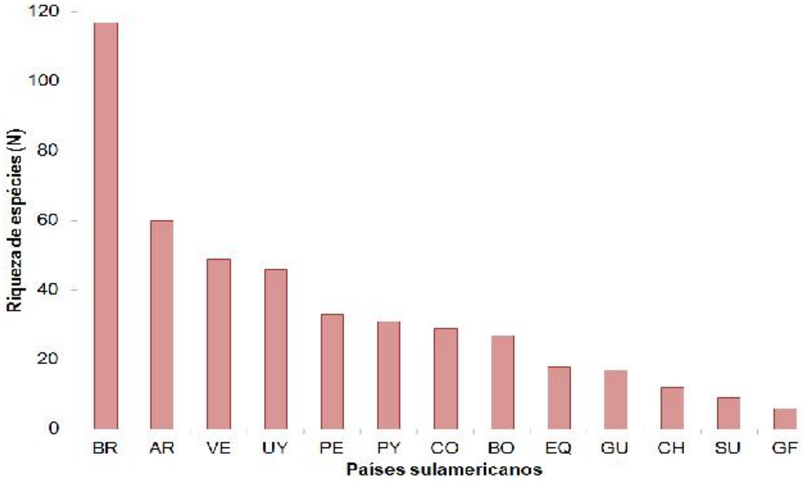

Figura 1. Riqueza de espécies de bivalves nos países da América do Sul de acordo com Pereira et al. (2013). Brasil (BR), Argentina (AR), Venezuela (VE), Uruguai (UY), Peru (PE), Paraguai (PY), Colômbia (CO), Bolívia (BO), Equador (EQ), Guiana (GU), Chile (CH), Suriname (SU), Guiana Francesa (GF).

Dentre estas regiões hidrográficas, existem várias ecorregiões que constituem unidades biogeográficas menores, delimitadas por Abell et al. (2008), com base na ictiofauna. Estas ecorregiões apresentam níveis de riqueza distintos, como por exemplo, na região hidrográfica do rio Amazonas, a ecorregião das Terras Baixas do Amazonas apresenta 36 espécies, enquanto a ecorregião do Rio Negro apenas 11. De acordo com Pereira et al (capítulo 2), na região hidrográfica do rio Uruguai, as ecorregiões do Alto Rio Uruguai e do Baixo Rio Uruguai diferem consideravelmente quanto à riqueza de espécies, que são respectivamente 19 e 48 espécies. Os mesmos autores verificaram que na região hidrográfica dos Rios do Sul e Sudeste que correm para o Atlântico, também se observam diferenças quanto as principais ecorregiões: Lagoa dos Patos (42), Tramandaí-Mampituba (14) e Mata Atlântica do Sudeste (8).

Estas considerações são importantes para o manejo das espécies de bivalves nativos e devem ser consideradas na priorização de áreas conservação e no processo e licenciamento de empreendimentos, sobretudo hidrelétricos que fragmentam rios, gerando uma série de lagos em cascatas e comprometem a migração de peixes potenciais vetores de dispersão de bivalves de água doce. Pereira et al (2012) fez uma avaliação histórica da perda de espécies em trechos poluídos e barrados por uma série de reservatórios em cascata no Rio Tietê e verificou um expressivo declínio na riqueza de espécies.

Os principais fatores ambientais que estão relacionados à composição de espécies de bivalves em macrohabitats de ecorregiões na América do Sul são a declividade, a área e a riqueza de espécies de peixes Pereira et al (capítulo 2) (Figura 2). O que mostra que a maior riqueza está em áreas baixas, muitas vezes impactadas pela irrigação, agricultura, pastagens, áreas urbanas e pelo maior número de espécies invasoras.

No entanto, pouco se sabe sobre fatores de microhabitat e mesohabitat. Investimentos devem ser direcionados para o mapeamento de espécies em cada ecorregião e a identificação dos seus habitats, o que poderá subsidiar medidas de restauração de áreas degradadas. Outra lacuna que deverá ser priorizada em investigações futuras é a realização de estudos populacionais e sobre as estratégias reprodutivas das espécies, que aparentemente são mais importantes para o sucesso da dispersão destes organismos que fatores de microhabitat.

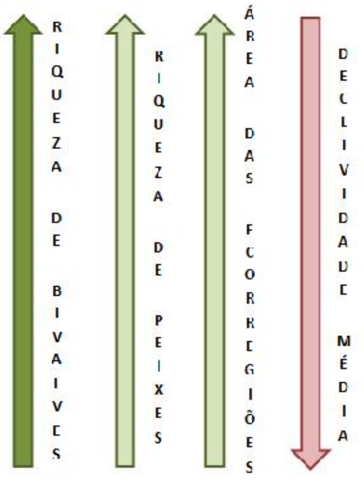

Figura 2. Fatores ambientais relacionados à riqueza de espécies em ecorregiões de água doce na América do Sul acordo com Pereira et al. (capítulo 2).

Uma série de ameaças à conservação dos bivalves límnicos nas ecorregiões de água doce no Brasil e parte de países limítrofes constam na tabela 1. Considerando estas ameaças, são feitas algumas considerações sobre estratégias de conservação a seguir. Quando a recuperação de microhabitats, especial atenção deve ser dada ao reflorestamento de áreas ribeirinhas aos cursos d´água, pois a erosão e o assoreamento estão entre as principais ameaças a conservação dos bivalves límnicos (Mansur et al., 2004, Amaral et al., 2008). A drenagem das áreas úmidas, bem como a deposição de resíduos e consequentemente a oficialização de aterros sanitários junto destes ambientes é uma prática devastadora e contribui para a diminuição de refúgios tanto para a malacofauna quanto para peixes, que são seus principais vetores.

A irrigação também exerce seus impactos, Pereira et al (2000 e 2001) observaram que a tomada de água para a irrigação de arroz na microbacia do arroio Capivara (RS, Brasil) acarretaram na intermitência do arroio e na consequente alteração da composição da fauna de moluscos. Muitas destas atividades passam pela tangência dos processos de licenciamento no Brasil e causam danos irreversíveis. Conflitos entre as atividades de irrigação e a conservação da biota aquática também são verificados em um grande sistema de áreas úmidas na Reserva Biológica do Taím, no Sul do Brasil, onde segundo Mansur et al (1991), a fauna de bivalves é expressivamente rica.

A extração de areia é outra atividade extremamente impactante que deve ser acompanhada de forma eficaz e tem comprometido inúmeros rios em todo país. Esta afeta diretamente os bivalves já que estes organismos dependem de áreas de deposição para viver, como barras laterais e transversais de areia e cascalho (Haag, 2012, Pereira et al, 2011). A extração de predatória de areia simplesmente remove estas feições morfológicas que definem a morfologia dos rios e simplificam a calha principal, ocorrendo expressiva perda de habitats.

As listas vermelhas devem ser atualizadas e novas espécies devem ser incluídas, segundo Pereira et al. (2012), 42 espécies deveriam ser avaliadas quanto a possível inclusão na revisão destas listas (Figura 3). No entanto, a lista de espécies de ameaçadas do RS foi revisada e devido ao curto espaço de tempo dado aos revisores, resultados de pesquisas recentes não puderam ser considerados, e assim, as espécies de bivalves que constavam na lista foram excluídas.

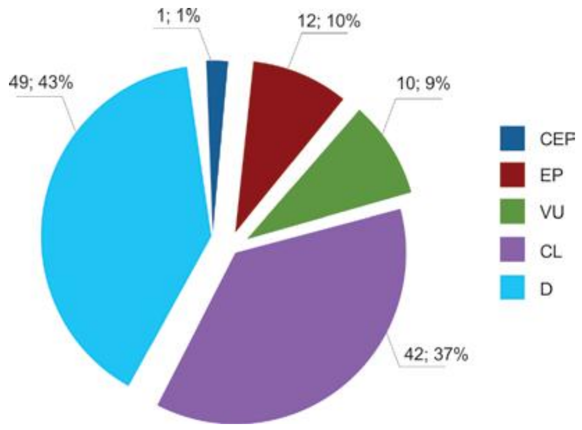

Figura 3. Bivalves límnicos (Número de Espécies – N, percentual - %) enquadrados em categorias de ameaça em listas vermelhas de espécies ameaçadas de extinção no Brasil, e espécies candidatas à inclusão nas listas: criticamente em perigo (CEP), em perigo (EP), vulnerável (VU). Espécies candidatas à lista de espécies ameaçadas de extinção do Brasil (CL) que deverão ser avaliadas por meio de critérios apropriados; espécies desconhecidas (D) quanto a quaisquer aspectos da sua conservação. Fonte: extraído de Pereira et al. (2012).

A criação e realocação tem sido uma prática de sucesso na América do Norte (Haag, 2012 e Streyer, 1993). No entanto, na América do Sul pouco se conhece sobre o ciclo reprodutivo das espécies. Os principais estudos realizados sobre o ciclo larval encontram-se compilados em Mansur et al. (2012), mas pouco se sabe sobre os hospedeiros e não se conhece na literatura científica, a documentação de casos com sucesso no estabelecimento de populações alocadas no Brasil. A espécie mais estudada e com sucessos em prática de realocação é *Diplodon chilensis* no Chile e deve ser utilizada como modelo para estudos no Brasil (Parada e Peredo, 2005, Peredo et al, 2005). Algumas experiências iniciais foram desenvolvidas no Uruguai (Clavijo et al, 2012). No Brasil nada de concreto foi desenvolvido até agora, o que deve ser alvo emergencial de novas pesquisas e programas de financiamento governamental.

Quanto ao manejo de espécies invasoras, é extremamente urgente o estabelecimento de barreiras e postos de controle de barcos nos sistemas hidrográficos do Amazonas e São Francisco, pois o limite norte de ocorrência atual do mexilhão dourado é a o Alto Rio Paraguai, que está muito próximo destas bacias, principalmente na fronteira com a Bolívia, onde em épocas de cheia se conecta com a Bacia Amazônica. O Monitoramento da dispersão e das densidades populacionais deverá ser efetuado nas bacias que ainda não foram invadidas e nas bacias invadidas vizinhas.

O controle biológico tem potencial para ser aplicado em campo, mas esforços na indução de projetos emergenciais de prospecção de microrganismos malacopatógenos específicos ao mexilhão deverão estar entre as prioridades dos órgãos de fomento de instituições de pesquisa envolvidas com esta temática. Considerando que no Brasil o registro de Agentes de Controle Biológico é um processo muito lento, não devem ser medidos esforços na busca de caminhos para desenvolver esses produtos.

O manejo integrado, por meio do uso de diversos tipos de controle não deve ser descartado, mas o acompanhamento ecotoxicológico deve ser obrigatório. Controladores químicos podem ser utilizados em sistemas fechados ou abertos, quando a diluição em grandes vazões propiciar à ausência de efeitos tóxicos a biota aquática. O controle eficaz levará deverá considerar a ausência de efeitos em todos os compartimentos ambientais, com uma abordagem integrada da avaliação das comunidades afetadas, populações alvo e não alvo, fatores limitantes que poderão maximizar os efeitos de controladores e a seleção de agentes de controle adequados, com doses letais mínimas, sem toxicidade a biota e com baixo custo, já o controle eficiente não leva em consideração os efeitos sobre os demais compartimentos e apenas causa a mortalidade das espécies alvo, sendo somente usado em sistemas fechados. Até o momento, as pesquisas realizadas contribuíram apenas para controles eficientes e não eficazes. Deve-se dar esse passo a mais e manejar as espécies invasoras sem causar mais passivos ambientais.

Abaixo são listados alguns temas prioritários de pesquisa que poderão futuramente contribuir para o estabelecimento de estratégias de manejo, que minimizarão os efeitos das espécies invasoras sobre as espécies nativas e a conservação dos bivalves nativos:

- Avaliar o impacto das espécies de bivalves límnicos invasores sobre os bivalves nativos;
- Estudo morfológico das espécies nativas e invasoras visando à elaboração de chaves e catálogos;
- Mapeamento das espécies nativas de bivalves citadas para o Brasil, especialmente nas bacias subamostradas;
- Descrição do ciclo de desenvolvimento dos bivalves nativos e reconhecimento das espécies de peixes vetores e dispersores das larvas destes moluscos; relação das rotas migratórias de peixes vetores com a dispersão de bivalves límnicos;
- Criação de espécies de bivalves límnicos para repovoamento de áreas com declínio das populações das mesmas;
- Avaliação do impacto da construção de reservatórios em série (cascata) sobre a distribuição da malacofauna e a busca de estratégias alternativas para a conservação de espécies de bivalves típicos de água corrente, visando subsidiar o estabelecimento de medidas compensatórias e mitigadoras; reconstrução de habitats em represas e nos seus tributários para a conservação da malacofauna.
- Monitoramento populacional das espécies invasoras e nativas;
- Identificação de áreas para a implantação de unidades de conservação; estabelecimento de estratégias de conservação;
- Revisão das listas de espécies ameaçadas estaduais e a nacional, visando rever a categorização das espécies enquadradas e a categorização de espécies que não constam nas listas.
- Fomentar pesquisas sobre o controle biológico de invasoras, com base na prospecção de bactérias malacopatógenas.

Table 1. Ameaças à conservação dos bivalves límnicos nas ecorregiões de água doce no Brasil e parte de países limítrofes. Atividades humanas compiladas de Youssef et al (2002) e Tundisi et al (2006).

Code	Ecorregiões de Água Doce	Major Habitats	Ameaças	NEE	NEI
314	Rio Negro	Planícies de Inundação de Rios Tropicais e Substropicais e Complexos de Terras Úmidas	Desmatamento, mineração		
315	Escudo Amazonas Guiana	Rios Tropicais e Substropicais de Terras Altas	Mineração de ouro e bauxita, desmatamento, Construção de barragens,		
316	Terras baixas do Amazonas	Planícies de Inundação de Rios Tropicais e Substropicais e Complexos de Terras Úmidas	Rejeitos de mercúrio de mineradoras de ouro, Desmatamento.		
319	Guapore - Itenez	Rios Tropicais e Substropicais de Terras Altas	Desmatamento.		
320	Tapajos - Juruena	Rios Tropicais e Substropicais de Terras Altas	Desmatamento, Usinas hidrelétricas, agricultura.		
321	Escudo Brasileiro do Madeira	Rios Tropicais e Substropicais de Terras Altas	Rejeitos de mercúrio de mineradoras de ouro, desmatamento,		
322	Xingu	Rios Tropicais e Substropicais de Terras Altas	Usinas hidrelétricas, desmatamento,		
323	Estuário do Amazonas e Drenagens Costeiras	Grande Deltas de Rios	Mineração de manganês, embarcações sem controle de incrustação, desmatamento, uso de agrotóxicos, desmatamento,		
324	Tocantins - Araguaia	Rios Tropicais e Substropicais de Terras Altas	Mineração de ferro, manganês, alumínio e cobre, usinas hidrelétricas,		
325	Parnaíba	Rios Tropicais e Substropicais de Terras Altas	Áreas portuárias de grande escala.		
326	Caatinga e Drenagens Costeiras	Tropical and subtropical coastal rivers	Salinização, lançamento de esgotos in natura,		
327	São Francisco	Rios Tropicais e Substropicais de Terras Altas	Transposição, drenagem, usinas hidrelétricas, salinização, lançamento de esgotos in natura,		
328	Mata Atlântica do Nordeste	Rios Tropicais e Substropicais Costeiros	lançamento de esgotos in natura, usinas hidrelétricas e termoelétricas, áreas portuárias de grande escala.		
329	Paraíba do Sul	Rios Tropicais e Substropicais Costeiros	Ocupação imobiliária, lançamento de esgotos in natura, áreas portuárias de grande escala.		
330	Ribeira de Iguape	Rios Tropicais e Substropicais Costeiros	Agricultura		

331	Mata Atlântica do Sudeste	Rios Tropicais e Substropicais Costeiros	Ocupação imobiliária, irrigação, drenagem de áreas úmidas, desmatamento, agrotóxicos, extração de areia, pesca, navegação como lazer, lançamento de esgotos in natura, assoreamento, erosão, poluição industrial (água e solo).
332	Baixo Uruguai	Rios Tropicais e Substropicais de Terras Altas	Irrigação, drenagem de áreas úmidas, desmatamento, agrotóxicos, extração de areia, pesca, navegação como lazer, lançamento de esgotos in natura, assoreamento, erosão, usinas hidrelétricas, presença de espécies invasoras, agricultura e pecuária intensiva.
333	Alto Uruguai	Rios Tropicais e Substropicais de Terras Altas	Desmatamento, agrotóxicos, pesca, lançamento de esgotos in natura, assoreamento, erosão, usinas hidrelétricas, presença de espécies invasoras.
334	Laguna dos Patos	Rios Temperados Costeiros	Ocupação imobiliária, irrigação, drenagem de áreas úmidas, desmatamento, agrotóxicos, extração de areia, pesca, navegação como lazer, lançamento de esgotos in natura, assoreamento, erosão, usinas hidrelétricas e termoelétricas, presença de espécies invasoras, poluição industrial (água e solo), áreas portuárias de grande escala, agricultura e pecuária intensiva.
335	Tramandai - Mampituba	Rios Tropicais e Substropicais Costeiros	Ocupação imobiliária, irrigação, drenagem de áreas úmidas, desmatamento, pesca, navegação como lazer, presença de espécies invasoras.
343	Paraguai	Planícies de Inundação de Rios Tropicais e Substropicais e Complexos de Terras Úmidas	Drenagem de áreas úmidas, desmatamento, agrotóxicos, extração de areia, pesca, navegação como lazer, lançamento de esgotos in natura, assoreamento, erosão, usinas hidrelétricas, presença de espécies invasoras, agricultura e pecuária intensiva.
344	Alto Paraná	Rios Tropicais e Substropicais de Terras Altas	Ocupação imobiliária, presença de espécies invasoras, usinas hidrelétricas, aquicultura, agrotóxicos, extração de areia, pesca, navegação como lazer, lançamento de esgotos in natura, assoreamento, erosão, poluição industrial (água e solo) , agricultura e pecuária intensiva.
346	Iguaçu	Rios Tropicais e Substropicais de Terras Altas	Drenagem de áreas úmidas, desmatamento, construção de barragens, presença de espécies invasoras.
352	Fluminense	Rios Tropicais e Substropicais Costeiros	Ocupação imobiliária, lançamento de esgotos in natura, poluição industrial (água e solo).

Tabela 2. Impactos ambientais, econômicos e estratégias de manejo das principais espécies de bivalves invasores de acordo com Mansur et al. (2012) e Darrigran e Damborenea (2009).

Espécies	Impactos		Estratégias Básicas de Prevenção e Controle
	Ambientais	Econômicos	
Corbicula fluminea	1. Alteração das comunidades bentônicas, do plâncton e da cadeia trófica, pois serve de alimento para vertebrados.	1. Entupimento de filtros e tubulações. 2. Potencialização de processos erosivos em estruturas de engenharia. 4. Diminuição do fluxo de água. 5. Alteração da qualidade água por meio da clarificação, remoção de sólidos suspensos, nutrientes e pela liberação de pseudofeses.	1. Diagnóstico e mapeamento das populações na área de influência de empreendimentos hidrelétricos (montante e jusante), em hidrovias, sistemas de irrigação, e áreas com colonização recente e avançada vizando estabelecer um banco de dados sobre fatores ambientais relacionados a bioinvasão. 2. Monitoramento permanente das larvas no plâncton, dos recrutas e adultos com substratos artificiais apropriados (montante e jusante), durante a operação da UHE. 3. Adequação da planta geradora de energia às tecnologias de controle e monitoramento da invasora. 4. Revestimento das estruturas de engenharia da UHE. 5. Controle, inspeção e adequação das embarcações que utilizam a hidrovia e circulam pelas eclusas 6. Adequação de tecnologias com base em métodos físicos, químicos e biológicos para controle populacional da invasora, por meio de práticas de manejo integrado, conforme as particularidades da planta geradora de energia. 7. Educação ambiental visando o controle da dispersão em bacias hidrográficas não afetadas. 8. Integração de pesquisadores e instituições por meio de ações estratégicas e unificadas permitindo a troca de informações e otimização de recursos de pesquisa e monitoramento. 9. Formação de câmaras técnica para discussão de legislações e açoes visando a normatização do controle populacional com o mínimo de efeitos deletérios ao ecossistema. 10. Prospecção de novos agentes de biocontrole e a padronização de métodos ecotoxicológicos com organismos nativos ou geneticamente relacionados a moluscos ameaçados.
Corbicula largillierti	1. Alteração das comunidades bentônicas, do plâncton e da cadeia trófica, pois serve de alimento para vertebrados.	1. Entupimento de filtros e tubulações. 2. Potencialização de processos erosivos em estruturas de engenharia. 4. Diminuição do fluxo de água. 5. Alteração da qualidade água por meio da clarificação, remoção de sólidos suspensos, nutrientes e pela liberação de pseudofeses.	
Limnoperna fortunei	1. Alteração das comunidades de macrófitas aquáticas marginais (formas emergentes). 2. Alteração das comunidades bentônicas.	1. Diminuição do fluxo de água . 2. Danificação de redes de pesca e barcos. 3. Obstrução de grades 4. Entupimento de tubulações e filtros. de resfriamento de hidrelétrica. Incrustação de superfícies (metais, concretos, rochas, etc.).	

	3. Destruição de habitats. 4. Modificação da estrutura do plâncton.	5. Potencialização de processos erosivos em estruturas de engenharia. 6. Alteração da qualidade água por meio da clarificação, remoção de sólidos suspensos, nutrientes e pela liberação de pseudofeses.	

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Conclusões

Conclusões

No que diz respeito às assembleias de bivalves límnicos sul-americanos, o número de 111 espécies de Unionoida na América do Sul confere ao continente o *status* de muito rico, mas não mais do que a América do Norte.

Foram reconhecidas regiões hidrográficas com maior riqueza de espécies:

1) Riqueza muito elevada: Rio Amazonas, Rio Paraguai, Rio Uruguai e rios do Sul e Sudeste do Atlântico, no Brasil;

2) Riqueza elevada: Rio Orinoco, na Venezuela; Sistema Paranoplatense na Argentina; rio Uruguai, Rio da Prata, e rio Negro, no Uruguai;

3) Riqueza média, rio Amazonas, no Peru, Alto rio Paraná no Brasil, e do Rio Paraguai no Paraguai.

As regiões hidrográficas sul-americanas apresentam composições filogenéticas distintas, independentemente do nível de riqueza. Portanto, a riqueza não deve ser considerada como um critério único para priorizar áreas de conservação, mas também a diversidade filogenética das comunidades, que prestam serviços relevantes à manutenção dos ecossistemas.

A ampla distribuição de algumas espécies nativas pode ser atribuída à sua alta tolerância aos fatores ambientais, à transposição de barreiras geográficas e à adaptação a condições ambientais adversas diante eventos geológicos no passado.

Espécies nativas com ampla distribuição no continente tanto em regiões hidrográficas como em ecorregiões, como por exemplo, *Anodontites trapesialis*, podem ter propriedades semelhantes às espécies invasoras, o que explicaria o padrão de distribuição atual e o sucesso na colonização de açudes de piscicultura. No entanto, são necessários mais estudos sobre a biologia desta espécie para a compreensão de seus mecanismos de dispersão e se os mesmos estão relacionados com certo grau de invasibilidade.

A invasão do mexilhão-dourado poderá resultar na redução da diversidade de moluscos bivalves nas diferentes áreas avaliadas que ainda não foram invadidas, alterando os padrões de riqueza e composição de espécies, bem como de composição filogenética das comunidades. Medidas emergenciais de controle e a contenção da dispersão das espécies invasoras deverão ser estabelecidas pelos governos dos países sul-americanos, em especial o Brasil, com áreas ricas em espécies e com endemismo expressivo.

O controle da dispersão de espécies invasoras depende principalmente de ações educativas destinadas à sensibilização dos diversos usuários dos recursos hídricos sul-americanos, bem como a padronização de procedimentos de vistoria e fiscalização de atividades com potencial de risco de contaminação em novas áreas.

A distribuição das espécies invasoras *L. fortunei*, *C. fluminea* e *C. fluminalis* não apresentou uma relação positiva com regiões hidrográficas pobres em espécies. *C. largillierti* apresesentou correlação positiva com a riqueza de espécies. Esta distribuição não corrobora a hipótese de que as comunidades mais pobres seriam mais suscetíveis à bioinvasão.

Os padrões de composição de espécies e linhagens filogenéticas verificados neste estudo fornecerão subsídios para a definição de ações e reconhecimento de áreas prioritárias para a conservação das espécies nativas e controle de invasoras, assim como a revisão de listas de espécies ameaçadas.

As ecorregiões mais ricas em espécies de bivalves estão situadas nas regiões hidrográficas que também são mais ricas em espécies bivalves. No entanto, dentro das áreas das grandes regiões hidrográficas, os níveis de riqueza são diferenciados, o que pode ser atribuído ao gradiente ambiental destas áreas, com diferentes feições fisiográficas e características da água distintas.

O gradiente ambiental de altitude, declividade média, conteúdo catiônico, assim como a dimensão das áreas, influenciam a composição e distribuição de espécies nas ecorregiões avaliadas. Valores elevados de riqueza de espécies estão relacionados às terras baixas com pouco declive, assim como a riqueza de peixes.

As ecorregiões aquáticas delineadas com base nas assembleias de peixes são congruentes com os padrões de composição das assembleias de bivalves de água doce.

Quanto à população do mexilhão-dourado avaliada, o recrutamento mostrou uma variação sazonal definida para a zona climática - Cfa temperado.

O ciclo de recrutamento, desde a liberação larval até o surgimento de indivíduos adultos sobre os substratos, foi influenciado pela variação da temperatura da água, alcalinidade total, condutividade, sólidos totais e sulfatos.

As variáveis ambientais preditoras significativas dos descritores populacionais do mexilhão-dourado, identificadas no presente estudo, são em grande parte as mesmas utilizadas para a previsão e a análise de risco de colonização de dreissenídeos em águas interiores da América do Norte.

A sobrevivência do mexilhão-dourado em ampla faixa de pH 4-11 após cinco dias de exposição, sugere que com a chegada da invasora em águas ácidas da Amazônia, estas não representarão barreiras ecofisiológicas para a dispersão desta invasora.

Além disso, o risco de dispersão é elevado em consequência da alta probabilidade do mexilhão-dourado sobreviver a passagem pelo trato digestivo de peixes migratórios e ser liberado em ambientes não colonizados.

A ampla tolerância ao pH é comparável à de *A. aegypti*, sendo possível que ambas espécies invasoras sobreponham áreas de distribuição num futuro próximo.

No que diz respeito aos ensaios de seleção de agentes microbianos e a avaliação de toxicidade de formulações comerciais, a cepa *Bacillus thuringiensis* sv. *kurstaski* HD-1 demonstrou ser promissora para a formulação de novos produtos comerciais destinados ao controle biológico do mexilhão-dourado. No entanto, estas formulações deverão ser desenvolvidas considerando o complexo mecanismo de filtração do mexilhão, distinto dos insetos e com isto, optimizar o consumo e o efeito destes agentes.

A formulação comercial Vectobac® AS, causou mortalidade elevada do mexilhão-dourado sob concentrações extremas, mas resultou em efeitos tóxicos para organismos não-alvo. Desta forma, não é adequada ao controle desta espécie, pois pode conferir toxicidade à biota aquática quando aplicada as dosagens efetivas para causar a mortalidade da mesma. Além disso, as dosagens letais tornariam o controle biológico inviável economicamente.

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Anexo 1 –
Publicações resultantes da tese:

Artigo resultante do capítulo 1. Pereira et al., 2013. Bivalve distribution in hydrographic regions in South America: historical overview and conservation. On line first. http://dx.doi.org/10.1007/s10750-013-1639-x

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FRESHWATER BIVALVES

Review Paper

Bivalve distribution in hydrographic regions in South America: historical overview and conservation

Daniel Pereira · Maria Cristina Dreher Mansur · Leandro D. S. Duarte · Arthur Schramm de Oliveira · Daniel Mansur Pimpão · Cláudia Tasso Callil · Cristián Ituarte · Esperanza Parada · Santiago Peredo · Gustavo Darrigran · Fabrizio Scarabino · Cristhian Clavijo · Gladys Lara · Igor Christo Miyahira · Maria Teresa Raya Rodriguez · Carlos Lasso

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Abstract Based on literature review and malacological collections, 168 native freshwater bivalve and five invasive species have been recorded for 52 hydrographic regions in South America. The higher species richness has been detected in the South Atlantic, Uruguay, Paraguay, and Amazon Brazilian hydrographic regions. Presence or absence data were analysed by Principal Coordinate for Phylogeny-Weighted. The lineage Veneroida was more representative in hydrographic regions that are poorer in species and located West of South America. The Mycetopodidae and Hyriidae lineages were predominant in regions that are richest in species toward the East of the continent. The distribution of invasive species *Limnoperna fortunei* is not related to species richness in different hydrographic regions there. The species richness and its distribution patterns are closely associated with the geological history of the continent. The hydrographic regions present distinct phylogenetic and species composition regardless of the level of richness. Therefore, not only should the richness be considered to be a criterion for prioritizing areas for conservation, but also the phylogenetic diversity of communities engaged in services and functional aspects relevant to ecosystem maintenance. A plan to the management of this fauna according to

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Guest editors: Manuel P. M. Lopes-Lima, Ronaldo G. Sousa, Simone G. P. Varandas, Elsa M. B. Froufe & Amílcar A. T. Teixeira / Biology and Conservation of Freshwater Bivalves

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Anexo 2 –
Publicações resultantes da tese:

Artigo resultante do capítulo 1. Pereira et al., 2014. Bivalve distribution in hydrographic regions in South America: historical overview and conservation. Hydrobiologia. 735: 15-44.

Bivalve distribution in hydrographic regions in South America: historical overview and conservation

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Bivalve distribution in hydrographic regions in South America: historical overview and conservation

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particular ecological characteristics and human uses of hydrographic regions is needed.

Keywords Bivalve · South America · Literature review · Scientific collections · Phylogenetic composition

Literature review

Earlier works on the freshwater bivalves of South America (from ~1800 to ~1890) are descriptive and consist of illustrated catalogs of species collected by naturalists during exploratory expeditions along river basins (Spix, 1827; Orbigny, 1835, 1846; Hupé, 1857). Shells acquired from travelers or merchants, or through exchange with colleagues or amateurs, have been described and cataloged by collectors and naturalists such as Maton (1811), Lamarck (1819), Lea (1834, 1838, 1852, 1857, 1860, 1863, 1869, 1874), Philippi (1847), Küster (1842), Sowerby (1864, 1867, 1868, 1869a, b), among others. Most scientific collections were private and would be eventually sold or donated to European museums (Dance, 1966; Olazarri, 1975; Haag, 2012). At that time, descriptions of new species were extremely poor, largely vague, and based on outdated concepts containing few illustrations and mostly from single specimens. Some of these catalogs were more iconographic than descriptive. In some cases, with the intent of showing the beauty shells, some conchological features were overlooked by designers. This fact led to misunderstandings and wrong identification at the genus or species levels. Very often, collecting localities were unknown or poorly documented, consisting of vague references such as the continent or country name where a species was collected. Sometimes, old local names of rivers and lakes are no longer used, making the collection site difficult to locate.

In a subsequent period (~1890–1960), special attention was given to the works of Simpson (1900, 1914) who published a summary and a catalog of World Unionoida, including South American species. This publication includes redescriptions, lists of synonyms, and significant taxonomic comments, with many species being labeled as *incertae sedis*. Hermann von Ihering emigrated from Germany to Brazil and lived there for many years, where he studied and collected bivalve mollusks, starting in the State of Rio Grande do Sul. Some years later, he moved to São Paulo to open the Museu de Zoologia da Universidade de São Paulo in 1895. Ihering organized the malacological collection and published over 35 articles on mollusks (Vaz, 1986), including checklists and identification keys of taxa from several drainages from Brazil and neighboring countries (Ihering, 1890, 1893, 1910). He also revisited the bivalve species described by Spix and Lamarck (Ihering, 1890, 1910) by examining the types. He was the first researcher to see and describe the lasidium (Ihering, 1891) larvae of Mycetopodidae, which is very similar to the haustorium of African species of the same Etherioidea superfamily (Wächtler et al., 2001). Unfortunately, due to political problems during WWI, Ihering was forced to leave both the museum and the country, and ended up selling his collection to European museums. In the early twentieth century, a pioneering initiative by local researchers attempted to catalog bivalves.

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Among them, we can mention Formica-Corsi (1900) who looked at Uruguayan bivalves, as well as Morretes (1949, 1953) who worked with the mollusks from Brazil. Ortmann (1921) was the first researcher to include anatomical traits of the soft parts of adults and the glochidia larvae in the descriptions of his species. He proposed the first studies on phylogenetic relationships among Unionoida. However, his studies were not given the right recognition by his future fellow scholars.

Many Unionoida and Veneroida species were described for hydrographic basins located in Patagonia, Venezuela, Colombia, and Uruguay by Marshall (1916, 1922, 1924, 1927a, b, 1928, 1930) and Pilsbry (1896, 1897). Many new species were described (Baker, 1914, 1930) after conducting North American expeditions in the Amazon region, Brazil, and Venezuela. The 433 species of Unionoida described from South America were reduced by Haas (1930, 1931a, b, 1969) to 124, based primarily on shell characteristics. He mentioned 70 species and subspecies of Hyriidae and 54 Mycetopodidae.

With Argentino Bonetto and his team from Argentina, a new period (from ~1960 to present) pioneered by South American morphologists and taxonomists began. A series of morphological and taxonomic studies were published including the description of many species of glochidia and lasidia of South American freshwater bivalves (Bonetto, 1961a, b, 1962, 1963, 1964, 1965, 1966, 1967a, b, 1972, 1997); Bonetto & Ezcurra-de-Drago, 1966; Bonetto et al., 1986).

At the end of the last century, malacology was consolidated in many South American universities, mainly Argentina, Brazil, Chile, Uruguay, and in other research institutions like: Instituto Miguel Lillo at Tucuman and Instituto Nacional de Limnología at Santa Fé (both in Argentina), Plataforma de Investigación en Ecohidrología y Ecohidraúlica at Santiago (Chile), Museo Nacional de Historia Natural de Montevideo (Uruguay), and Fundação Zoobotânica do Rio Grande do Sul at Porto Alegre (Brazil). From there, the study of freshwater bivalve became more consolidated resulting in several important scientific publications (Olazarri, 1963, 1966, 1975; Mansur, 1970, 1972, 1974, 1999; Veitenheimer, 1973a, b; Hebling & Penteado, 1974; Mansur & Veitenheimer, 1975; Hebling, 1976; Veitenheimer & Mansur, 1978a, b; Mansur & Veitenheimer-Mendes, 1979; Alvarenga & Ricci, 1979a, b, 1989; Mansur & Anflor, 1981; Mansur et al., 1987, 1988, 1991, 1994;; Mansur & Garces, 1988; Mansur & Campos-Velho, 1990, 2000; Mansur & Silva, 1990, 1999; Ricci et al., 1990; Mansur & Valer, 1992; Simone, 1994, 1997, 1999, 2006; Mansur & Olazarri, 1995; Avelar & Mendonça, 1998; Serrano et al., 1998; Pereira et al., 2000, 2011, 2012; Callil & Mansur, 2002, 2005, 2007; Mansur & Pereira, 2006; Scarabino & Mansur, 2007; Mansur & Pimpão, 2008; Pimpão et al., 2008, 2012; Lasso et al., 2009; Pimpão & Mansur, 2009). Chilean researchers carried out multiple studies on *Diplodon chilensis* documenting its ecology (Lara & Parada, 1991, 2009; Lara & Moreno, 1995; Lara et al., 2002a, b; Grandón et al., 2008), taxonomy (Parada & Peredo, 2002), morphology (Parada et al., 1989a; Valdovinos & Pedreros, 2007), reproduction (Peredo & Parada, 1984, 1986, Parada et al., 1987, 1990; Peredo et al., 1990), life history (Parada et al., 1989b, Parada & Peredo, 1994), genetics (Jara-Seguel et al., 2000; Peredo et al., 2003), distribution (Lara & Parada, 1988, 2008; Parada et al., 2007), and relocation (Parada & Peredo, 2005; Peredo et al., 2005). This intensive effort propelled *D. chilensis* as the best known species of Hyriidae in the continent.

Considering the order Veneroida, Spix (1827), Orbigny (1835, 1846), Anton (1837), Baker (1930), Clessin (1879, 1888), Josseaume (1889), Pilsbry (1897, 1911), described the first species of Sphaeriidae from South America. Later, South American researchers described and cataloged several species for that continent: Doello-Jurado (1921), Meier-Brook (1967), Ituarte (1989, 1994a, 1995, 1996, 1999, 2000, 2001, 2004, 2005, 2007), Ituarte & Mansur (1993), Ituarte & Korniushin (2006), Klappenbach (1962), Mansur & Meier-Brook, (2000), and Mansur et al. (2008).

Parodiz & Hennings (1965) reviewed the 30 species of Corbiculidae described for the Paraná/Paraguay and Uruguay basins. The authors concluded that only *Cyanocyclas* (= *Necorbicula*) *limosa* (Maton, 1811) and *Cyanocyclas paranensis* (Orbigny, 1835) would be valid species, whereas the others would be synonymized. Nevertheless, the species cited for the Amazon [*Cyanocyclas amazonica* (Prime, 1870) and *Cyanocyclas brasiliana* (Deshayes, 1854)], and more to the North of South America [*Cyanocyclas bavayi* (Ancey, 1880); *Cyanocyclas cuneata* (Jonas, 1844); *Cyanocyclas rotunda* (Prime, 1860) and *Cyanocyclas surinamica* (Clessin, 1879)] need revision. Later, Ituarte (1994b) presented important publications that provided diagnostic morphological and reproductive data of invasive species *Corbicula fluminea* (Müller,

1774) and *Corbicula largillierti* (Philippi, 1884) compared to native species *C. limosa.* Martins et al. (2004) reviewed the Corbiculidae invasive species in Southern Brazil looking at morphological and conchological characters. Two known Dreissenidae species and *Anticorbula fluviatilis* (Adams, 1860), the last placed with doubts inside Myoida, requires taxonomic revisions. Darrigran & Damborenea (2009) and Mansur et al. (2012c) compiled a series of studies on *Limnoperna fortunei* (Dunker, 1857) after the invasion in South America since 1991.

Recently, Simone (2006) has published an illustrated catalog of the continental mollusks of Brazil and neighboring countries, which cited 120 species of freshwater bivalves. Despite this massive effort, many genera and species were listed without the proper taxonomic revision. Furthermore, synonyms of different species were brought together without considering advances in the study of the larvae.

Biological characterization

In South America, there are three lineages of freshwaters Bivalvia: Mytiloida, Unionoida, and Veneroida. According to Simone (1999), the systematic definition of *A. fluviatilis* into Lyonsiidae and Myoida was used as a temporary suggestion.

Mytiloida is represented by the invasive species *L. fortunei* commonly known as golden mussel. *L. fortunei* is native from Asia, and was probably brought to South America via ballast water in 1991 (Darrigran & Pastorino, 1995; Mansur et al., 2003b, 2004a, b; Santos et al., 2012). With morphological characteristics similar to marine mussels (Mansur, 2012), it presents the complete larval cycle in the plankton (Mansur et al., 2012a) and after recruitment forms macroclusters. *L. fortunei* is very aggressive to the environment since it modifies the landscape, the flora, and benthic fauna as an “ecosystem engineer” (Darrigran & Damborenea, 2011). In built environments that use untreated water for cooling, the golden mussel causes clogging with considerable economic losses (Darrigran et al., 2007).

The Unionoida are commonly known as freshwater mussels or only mussels, without marine members. They can be found all over the world except for Antarctica. In South America, this order is represented by two families, Hyriidae and Mycetopodidae, comprising of only native species. They normally have from 2 to 10 cm in length though they can be longer, but according to Castellanos & Landoni (1990), *Mycetopoda soleniformis* (Orbigny, 1835) can reach up to 22 cm in length. They are considered to be good biological (Pereira et al., 2011) and paleoenvironment (Wesselingh, 2006) indicators. During geological time, these bivalves were the first to adapt to freshwater. Fossil record of freshwater bivalve *Anthraconauta* Pruvost, 1930, from the Carboniferous and Permian (late Paleozoic era) (Pellant, 1996), hold many similarities to the current species (Parodiz, personal communication). The unionids are very biodiverse. They have an amazing life cycle and strategies allowing survival in extreme situations, such as waterfalls, drought, and flood pulses. In the larval stage, most are temporary fish parasites. The larvae form cysts on the gills, scales, and fish fins. After 1 month, the larvae evolve to the juvenile stage breaking the cysts and falling to the substrate. This strategy helps the bivalves to overcome the problems of dispersion in upstream rivers. The South American unionoids show two basic larval types: the lasidium of Mycetopodidae, and glochidium of Hyriidae (Mansur et al., 2012a). Both the larval types are modified veligers and act as temporary ectoparasites on fish. As fish parasites, the lasidium triples in size and sends haustorium that penetrates the host tissues and remove its nutrients. The larval shell consists of a single helmet-shaped piece which involves the dorsal part of a body. This is formed by an anterior tongue-shaped ciliated lobe or a bilobated one, a central body with ventral lobes, a bilobated posterior tail with terminal hooks, and an anterior transparent adhesive organ. Depending on the species, this can be either strip-shaped (genus *Monocondylaea* Orbigny, 1835), scourge-shaped (*Leila blainvilliana* Lea, 1834), or flower-shaped with a micro hook at one end, as *Anodontites* Bruguière, 1792, *Mycetopoda* Orbigny, 1835 and *Acostea rivolii* Deshayes, 1827) (Bonetto, 1997). The lasidia of other species and genera of the family, as *Mycetopodella* Marshall, 1927, *Diplodontites* Marshall, 1922, *Fossula* Lea, 1870, *Haasica* Strand, 1932, *Bartlettia* A. Adams, 1866, and *Tamsiella* Haas, 1931 are unknown.

The larval body of glochidia is protected by two valves with an edge on the ventral border, a hook and a basal callus on the internal side of the ventral edge. Internally, there is an adhesive flagellum (absent in

Castalia Lamarck, 1819), sensory cilia, cirrus, a central adductor muscle, a very rudimentary velum, and phagocytic cells lining inside the valves. With the flagellum and hooks, the glochidium is enabled to get attached to the gills, fins, or scales of the fish that develop a cyst covering the larva. However, there are exceptions among species of the genus *Diplodon* Spix (1827). Hook and adhesive filament are absent on glochidia of the subgenus *Rhipidodonta* Morch, 1853. So the respective species are not fish parasites. Larval development until the juvenile stage is complete inside parental marsupium. In general, the glochidia of Hyriidae does not present spinules at the edges of the valves and on the base of the hook like other species of Unionoidea (Unionidae and Margaritiferidae) (Mansur et al., 2012a). Bonetto (1961b) described glochidia of several species of *Diplodon* genus. Based on morphological studies, Pimpão et al. (2012) reviewed and standardized the terminology of glochidia shells from South American Hyriidae, thus facilitating the differentiation between several species of Amazonian Basin.

The order Veneroida includes the following families: Corbiculidae, Sphaeriidae, and Dreissenidae. They are too considered to be good biological indicators (Lanzer & Schäfer, 1987; Pereira et al., 2011). The Corbiculidae native genera are represented by *Cyanocyclas* Blainville, 1818, and *Polymesoda* Rafinesque, 1828 with pallial sinus. The invasive Corbiculidade are represented by four species of the genus *Corbicula* Mergele von Muehlfeld, 1811. The incubation of larvae is complete in *Cyanocyclas* until it reaches an advanced stage inside the marsupium, a case of euvivipary. The number of embryos is small, ranging from 25 to 45 per gill, and the release is not synchronized. Two species of *Polymesoda* occur in brackish waters in the Northern part of the continent. The pallial sinus is absent in the invasive species of Corbiculidae. Only *C. fluminea* and *C. largillierti* have their larval and life cycles known; their embryos are incubated in marsupial gills until the end of stage veliger or pediveliger, and liberated synchronously (Mansur, 2012; Mansur et al., 2012a, b).

In Sphaeriidae, species of the genera *Sphaerium* Scopoli, 1777 and *Musculium* Link, 1807 show sequential development of broods into independent marsupial brood sacs. In *Pisidium* Pfeiffer, 1821 a synchronized development in a single marsupial brood sac occurs (Cooley & Ó Foighil, 2000). An exception was observed in *Pisidium punctiferum* (Guppy, 1867) which form one brood at a time, but with different sizes of embryos which suggest unsynchronized release (Anflor & Mansur, 2001). *Eupera* Bourguignat, 1854 has the most primitive system of reproduction. Embryos have synchronized development, but there is no brood sac inside the marsupium (Cooley & Ó Foighil, 2000). The species of this genus produce delicate byssus threads that facilitate adherence to pebbles, plants, or floating aquatic vegetation. The great expansion of its excretory sac may explain its adaptation and resistance to prolonged periods of drought. Among Dreissenidae, we only know of the biology of *Mytilopsis lopesi* Alvarenga & Ricci, 1989. In this species, the embryos grow attached to the mantle in the pallial cavity until the juvenile stage, with no synchronous release (Mansur et al., 2012a). *A. fluviatilis* is known from the Amazon River in Brazil and Peru (Simone, 1999). It is a nestling bivalve that lives attached to sandy grains and litter underneath (Beasley, pers. communication). Simone (1999) described its morphology for the first time including it with doubts in Lyonsiidae (Pandoroidea). According to him, this species has been reported by various authors also in Corbulidae (Myoida), sharing some similaritie with Myidae, Hiatelloidea, and Thraciidae as well.

The purpose of this paper is to survey freshwater bivalve species from South America, to classify and rank hydrographic regions based on species richness, composition, and phylogenetic lineages in order to facilitate the identification of region-specific conservation needs of this highly threatened fauna.

Compilation of species records and analysis

South America, with an area of 17,819.100 km^2, represents 12% of the world land area and is home to 6% of the world population. It has several major river systems such as the Amazon, Orinoco, Parana, and La Plata River basins, with a total drainage area of 9,583.000 km^2. Both these systems and other smaller ones show areas of endemism, diversity hotspots, and unique landscapes.

Data on the occurrence of bivalve species in hydrographic regions in South America (Fig. 1; Table 1) were compiled from the scientific literature and examinations of the following scientific collections: Academy of Natural Sciences of Philadelphia (ANSP; Philadelphia, USA); Carnegie Museum of

Fig. 1 Hydrographic regions in South American countries and territory. Respective codes shown in Table 1

Natural History (CM; Pittsburgh, USA); Coleção de Moluscos da Universidade do Estado do Rio do Janeiro (UERJ; Rio de Janeiro, Brazil); Coleção de Moluscos da Universidade Federal do Mato Grosso (UFMT; Cuiabá, Brazil); Fundación Miguel Lillo (FML; Tucumán, Argentina); Instituto Nacional de Pesquisas da Amazônia (INPA; Manaus, Brazil); Musée d'Histoire Naturelle Bâle (MHNB; Basel, Switzerland); Musée de Zoologie (ZML; Lausanne, Switzerland); Musée d'Histoire Naturelle de la Ville de Genève (MHNG; Geneva, Switzerland); Museo Argentino de Ciencias Naturales"Bernadino Rivadávia" (MACN; Buenos Aires, Argentina); Museo de La Plata (MLP; La Plata, Argentina); Museo Nacional de Historia Natural de Chile (MNHNC; Santiago, Chile); Museo Nacional de Historia Natural de Montevideo (MNHM; Montevideo, Uruguay); Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP; Porto Alegre, Brazil); Museu de Ciências Naturais Fundação Zoobotânica do Rio Grande do Sul (MCN; Porto Alegre, Brazil); Museu de Zoologia da UNISINOS (MZU; São Leopoldo, Brazil); Museu de Zoologia da Universidade de São Paulo (MZUSP; São Paulo, Brazil); Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ; Rio de Janeiro, Brazil); Museu Paraense

Table 1 Hydrographic regions in South America

Countries	Hydrographic regions	Codes
Argentina (AR)[a]	Patagonico System	APT
	Endorreico Central System	ACH
	Cuyano Subandino System	ACY
	Bonaerense	ABO
	Paranoplatense System	APP
	Misionero System	AMI
	Uruguay River System	AUR
	Salado del Sur System	ASS
	Noa System	ANO
Brazil (BR)[b]	Amazonas River	BAM
	Tocantins/Araguaia River	BTA
	Rivers of the North and Northeast Atlantic	BAN
	São Francisco River	BSF
	Rivers of the East Atlantic	BAL
	Upper Paraná River	BAP
	Paraguay River	BPG
	Uruguay River	BUR
	Rivers of the south and southeast Atlantic	BAS
Bolivia (BO)[c]	Madeira River	BoMA
	Titicaca Lake—endorheic basins	BoTT
	Paraguay River	BoPG
Chile (CH)[d]	Atlantic exorheic basins	CEAT
	Trans-Andean exorheic basins	CET
	Andean exorheic basins	CEA
	Pre-Andean exorheic basins	CEP
	Coastal exorheic basins	CEC
	Endorheic Basins of Alta Puna	CNE
	Endorheic basins of intermediate elevations	CNCI
Colombia (CO)[e]	Rivers that flow into the Caribbean Sea	CoCA
	Magdalena River	CoMA
	Orinoco River	CoOR
	Rivers that flow into the Pacific Ocean	CoPA
	Amazon River	CoAM
Guyana (GU)[f]	Rivers that flow into the Atlantic Ocean	GUA
French Guiana (GF)[g]	Rivers that flow into the Atlantic Ocean	GFA
Ecuador (EQ)[h]	Rivers that flow into the Pacific Ocean	EPA
	Amazon River	EAM
Paraguay (PY)[i]	Paraguay River	PPG
	Paraná River	PPR
Peru (PE)[j]	Rivers that flow into the Pacific Ocean	PPA
	Andine Lakes	PLA
	Amazon River	PAM
Suriname (SU)[k]	Rivers that flow into the Atlantic Ocean	SUA
Venezuela (VE)[l]	Rivers that flow into Caribbean Sea	VCA
	Maracaibo Lake	VMA
	Orinoco River	VOR
	Amazon River	VAM
Uruguay (UY)[m]	Uruguay River	UUR
	Negro River	UNE
	La Plata River	ULP
	Mirim Lake	UMI
	Coastal Lagoons	UCO

The hydrographic regions were delimited and adapted according to the following sources:

[a] IADIZA—Instituto Argentino de Investigaciones de las Zonas Áridas (www.cricyt.edu.ar/ladyot/lava_carto/mapas/argentina_cuencas/index.html)

[b] ANEEL—Agência Nacional de Energia Elétrica (www.aneel.gov.br/area.cfm?id_area=104)

[c] Mondaca (2011)

[d] IGM—Instituto Geografico Militar del Chile (www.igm.cl/)

[e] IGAC—Instituto Geográfico Agustín Codazzi (www.igac.gov.co)

[f,g,k] Each country is one Hydrographic region considering that all rivers flow into the Atlantic Ocean

[h] IGM—Instituto Geográfico Militar del Ecuador (www.igm.gob.ec)

[i] Paraguay Biodiversidad (www.pybio.org/)

[j] MINEM—Ministerio de Energia Y Minas del Peru (www.minem.gob.pe/minem/archivos/file/DGAAM/mapas/mapas_cuencas.htm)

[l] IGVSB—Instituto Geográfico de Venezuela Simon Bolívar (www.igvsb.gob.ve/#)

[m] IA—Instituto de Agrimensura Facultad de Ingeniería UdelaR (www.fing.edu.uy/ia/deptogeom/libro/capitulo8/hidrografia.htm)

Emilio Goeldi (MPEG; Belém, Brazil); Museum für Naturkunde (ZMB; Berlin, Germany); Museum National d'Histoire Naturelle (MNHN; Paris, France); National Museum of Natural History, Smithsonian Institution (USNM; Washington D.C., USA); Natural

History Museum of United Kingdom (NHMUK; London, United Kingdom); Naturhistorisches Museum (NMW; Wien, Austria); Senckenberg Forschungsinstitut und Naturmuseum (SMF; Frankfurt a.M., Germany); Staatliches Museum für Naturkunde (SMNS; Stuttgart, Germany); and Zoologische Staatssammlung München (ZSM; Munich, Germany). Part of the data on the occurrence of species in Peru, Ecuador, and Colombia were extracted from Mussel Project (mussel-project.uwsp.edu/). All records of species (presence or absence) were tabulated for each country according to the main hydrographic regions.

In order to recognize the phylogenetic composition of Bivalvia in the main hydrographic regions in South America (Fig. 1; Table 1), the following phylogenetic relationships were looked at (Mytilidae ((Hyriidae + Mycetopodidae) (((Sphaeriidae + Corbiculidae) Dreissenidae) *Anticorbula fluviatilis*))))) and supported by the molecular and morphological analyses according to Walker et al. (2006) and Giribet & Wheeler (2002).

A pairwise phylogenetic distance matrix (D_P) for the presence or absence of bivalve species in hydrographic regions included in the dataset was generated using Mesquite software (available at http://mesquiteproject.org/mesquite/mesquite.html). Hence, tree branch lengths were fixed to 1.0, as clade age estimates for bivalves were not available, and patristic distances between species were computed. The phylogenetic composition of each hydrographic regions was addressed using the phylogenetic fuzzy-weighting method developed by Pillar & Duarte (2010), and implemented in the software SYNCSA v. 2.5.22 (Debastiani & Pillar, 2012, available at http://www.cran.org). Pairwise phylogenetic distances in $\mathrm{D_P}$ were transformed into a phylogenetic similarity matrix ($S_P = 1 - D_P$). Then, phylogenetic similarities in $\mathrm{S_P}$ were used to weigh species composition in hydrographic regions, using a fuzzy set algorithm (see Pillar & Duarte, 2010 for details). This procedure generates a matrix describing the phylogeny-weighted species composition for each hydrographic region in South America in the dataset. That is, the presence of each species *i* in a given hydrographic region is shared with each species *j* occurring in the array of hydrographic regions, taking into account the phylogenetic similarity between *i* and *j*. Accordingly, those species *j* that are more phylogenetically related to *i* (e.g., from the same genus) will receive a proportionally higher fraction of the presence of *i* in those hydrographic regions than more phylogenetically distant species (e.g., from a different family), which will receive a proportionally lower fraction, and so on. Note that the sum of species presences (i.e., species richness) in each hydrographic region will remain exactly the same after phylogenetic fuzzy-weighting. After defining a multivariate matrix describing phylogenetic composition of hydrographic regions, we conducted a principal coordinates analysis (Gower, 1966; Legendre & Legendre, 1998) on that matrix to generate principal coordinates of phylogenetic structure (PCPS) for each hydrographic regions (Duarte, 2011; Duarte et al., 2012). This analysis was conducted on square-rooted Bray–Curtis dissimilarities between hydrographic regions. Then, we plotted the two first PCPS in a scatter plot to evaluate the association between the hydrographic regions and major bivalve lineages. PCPS analysis was conducted using the PCO statistical software (by M. Anderson, available at http://www.stat.auckland.ac.nz/~mja/Programs.htm). The Mantel test was used to assess the possible relationship of the distribution of invasive species with species richness in hydrographic regions. The test verified the possible correlation between two arrays: presence and absence of *L. fortunei* or *Corbicula* species (obtained from Jaccard index) and richness species of freshwater bivalves (chord distance).

Species richness and distribution

Based on the survey of presence and absence, 168 native limnic bivalves and 5 invasive species were recorded for the 52 hydrographic regions of 12 South American countries, and one territory (Table 2).

Hyriidae (36.42%) accounts for the highest percentage of species, followed by Mycetopodidae (27.75%) and Sphaeriidae (24.86%), Corbiculidae (8.09%), Dreissenidae (1.73%), and Mytilidae and Lyonsiidae (0.58%). The Unionoida represents 64.18% of the species richness of freshwater bivalves in South America while Veneroida 35.26% and Mytilioida 0.58%.

The country that has the highest species richness is Brazil (117 species), followed by Argentina (60), Venezuela (49), and Uruguay (46) (Table 2). Hydrographic regions with the greatest species richness (Fig. 2) are in Brazil followed by Argentina and Uruguay, Venezuela and Peru. In Brazil, the richest hydrographic regions are in the South and Southeast

Table 2 Freshwater bivalves species of South American countries and territory

Species	South American countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Mytiloida													
Mytilidae													
Limnoperna fortunei (Dunker, 1857)	1	1	1	1	1	0	0	0	0	0	0	0	0
Unionoida													
Mycetopodidae													
Anodontites (*Anodontites*) *aroanus* H.B. Baker, 1930	0	0	0	0	0	0	0	0	0	0	0	0	1
Anodontites (*A.*) *carinatus* (Dunker, 1858)	0	0	0	0	0	0	1	1	1	0	0	0	1
Anodontites (*A.*) *colombiensis* Marshall, 1922	0	0	0	0	0	0	1	0	0	0	0	0	0
Anodontites (*A.*) *crispatus* Bruguière, 1792	0	1	0	0	1	0	1	1	1	1	1	1	1
Anodontites (*A.*) *elongatus* (Swainson, 1823)	1	1	1	1	1	0	1	1	1	0	0	0	1
Anodontites (*A.*) *ferrarisii* (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *guanarensis* Marshall, 1927	0	0	0	0	0	0	0	0	0	0	0	0	1
Anodontites (*A.*) *iheringi* (Clessin, 1882)	0	1	0	0	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *infossus* H.B. Baker, 1930	0	0	0	0	0	0	0	0	0	0	0	0	1
Anodontites (*A.*) *irisans* Marshall, 1926	0	0	0	0	0	0	0	0	0	0	0	0	1
Anodontites (*A.*) *lucidus* (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *moricandii* (Lea, 1860)	0	1	0	0	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *obtusus* (Spix 1827)	0	1	0	0	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *patagonicus* (Lamarck, 1819)	1	1	1	1	0	0	0	0	0	0	0	0	0
Anodontites (*A.*) *puelchanus* (Orbigny, 1835)	1	0	0	0	0	0	0	0	0	0	0	0	0
Anodontites (*A. pittieri*) Marshall, 1922	0	0	0	0	0	0	0	0	0	0	0	0	1
Anodontites (*A.*) *schomburgianus* (Sowerby, 1870)	0	1	0	0	0	0	0	0	1	1	0	0	1
Anodontites (*A.*) *soleniformis* (Orbigny, 1835)	1	1	0	1	1	0	0	0	1	0	0	0	0
Anodontites (*A.*) *tenebricosus* (Lea, 1834)	1	1	1	1	1	0	0	0	1	0	0	0	1
Anodontites (*A.*) *tortilis* (Lea, 1852)	0	0	0	0	0	0	1	1	1	0	0	0	1
Anodontites (*A.*) *trapesialis* (Lamarck, 1819)	1	1	1	1	1	0	1	1	1	0	0	0	1
Anodontites (*A.*) *trapezeus* (Spix, 1827)	1	1	1	1	1	0	0	0	0	0	0	0	1
Anodontites (*Lamproscapha*) *ensiformis* (Spix, 1827)	1	1	1	1	1	0	0	1	1	1	0	0	1
Anodontites (*L.*) *falsus* (Simpson, 1900)	0	0	0	0	0	0	0	0	0	0	0	0	1
Mycetopoda legumen (Martens, 1888)	1	1	1	1	0	0	0	0	0	0	0	0	0
Mycetopoda siliquosa (Spix, 1827)	1	1	1	1	1	0	1	1	1	0	1	0	1
Mycetopoda soleniformis Orbigny, 1835	1	1	1	1	1	0	1	0	1	0	0	0	1
Mycetopodella falcata (Higgins, 1868)	0	1	0	0	0	0	1	0	1	0	0	0	0
Monocondylaea corrientesensis (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
Monocondylaea costulata (Moricand, 1858)	0	1	0	0	1	0	0	0	1	0	0	0	0
Monocondylaea franciscana (Moricand, 1837)	0	1	0	0	0	0	0	0	0	0	0	0	0
Monocondylaea guarayana (Orbigny, 1835)	0	0	0	1	1	0	0	0	0	0	0	0	0
Monocondylaea jaspidea (Hupé, 1857)	0	1	0	0	0	0	0	0	0	1	0	0	1
Monocondylaea minuana (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
Monocondylaea paraguayana (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
Monocondylaea parchappii (Orbigny, 1835)	1	1	0	0	0	0	0	0	0	0	0	0	0
Fossula fossiculifera (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
Tamsiella amazonica Bonetto, 1972	0	1	0	0	1	0	0	0	1	0	0	0	0

Table 2 continued

Species	South American countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Tamsiella schroeteriana (Lea, 1852)	0	1	0	0	0	0	0	0	1	0	0	0	0
Tamsiella tamsiana (Dunker, 1858)	0	0	0	0	0	0	1	0	0	0	0	0	1
Diplodontites cookei Marshall, 1922	0	0	0	0	0	0	1	1	1	0	0	0	0
Diplodontites olssoni Pilsbry, 1933	0	0	0	0	0	0	1	0	0	0	0	0	0
Diplodontites pilsbryana Olsson & Wurtz, 1951	0	0	0	0	0	0	1	0	0	0	0	0	0
Haasica balzani (Ihering, 1893)	0	1	0	0	0	0	0	0	0	0	0	0	0
Leila blainvilliana (Lea, 1834)	1	1	1	1	0	0	0	0	0	0	0	0	0
Leila esula (Orbigny, 1835)	0	1	0	1	1	0	1	0	1	1	0	0	1
Acostaea rivolii (Deshayes, 1827)	0	0	0	0	0	0	1	0	0	0	0	0	0
Bartlettia stefanensis (Moricand, 1856)	0	1	0	1	1	0	0	1	1	0	0	0	0
Hyriidae													
Diplodon (*Australis*) *solidulus* (Philippi, 1869)	0	0	0	0	0	1	0	0	0	0	0	0	0
Diplodon (*Diplodon*) *aethiops* (Lea, 1860)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *berthae* Ortmann, 1921	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *besckeanus* (Dunker, 1848)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *caipira* (Ihering, 1893)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *chilensis* (Gray, 1828)	1	0	0	0	0	1	0	0	1	0	0	0	0
Diplodon (*D.*) *delodontus* (Lamarck, 1819)	1	1	1	1	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *dunkerianus* (Lea, 1856)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *ellipticus* Spix, 1827	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *expansus* (Küster, 1856)	0	1	0	1	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *granosus* (Bruguière, 1792)	0	1	0	0	0	0	0	0	0	1	1	1	1
Diplodon (*D.*) *guaranianus* (Orbigny, 1835)	0	0	0	1	1	0	0	0	0	0	0	0	0
Diplodon (*D.*) *imitator* Ortmann, 1921	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *martensi* (Ihering, 1893)	0	1	0	1	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *multistriatus* (Lea, 1831)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *obsolescens* Baker, 1913	0	1	0	0	0	0	0	0	0	1	0	0	1
Diplodon (*D.*) *parallelopipedon* (Lea, 1834)	1	1	1	1	1	0	0	0	0	0	0	0	0
Diplodon (*D.*) *parodizi* Bonetto, 1960	1	1	0	1	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *paulista* (Ihering, 1893)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *piceus* (Lea, 1860)	0	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *rhombeus* Spix, 1827	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *rhuacoicus* (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *suavidicus* (Lea, 1856)	0	1	0	0	0	0	1	0	0	1	0	0	1
Diplodon (*D.*) *vicarius* Ortmann, 1821	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*D.*) *wymanii* (Lea, 1860)	1	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*Rhipidodonta*) *burroughianus* (Lea, 1834)	1	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *charruanus* (Orbigny, 1835)	1	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *deceptus* Simpson, 1914 sensu Ortmann, 1921	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *funebralis* (Lea, 1860)	0	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *koseritzi* (Clessin, 1888)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *hildae* Ortmann, 1921	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *hylaeus* (Orbigny, 1835)	1	1	1	0	1	0	0	1	1	0	0	0	0

Table 2 continued

Species	South American countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Diplodon (*R.*) *iheringi* Simpson, 1914	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *peraeformis* (Lea, 1860)	1	0	1	0	0	0	0	0	0	0	0	0	0
Diplodon (*R.*) *variabilis* (Maton, 1811)	1	0	1	0	0	0	0	0	0	0	0	0	0
Diplodon fontainianus (Orbigny, 1835)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon greeffeanus (Ihering, 1893)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon paranensis (Lea, 1834)	1	1	1	1	0	0	0	0	0	0	0	0	0
Diplodon pfeifferi (Dunker, 1848)	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon rotundus Spix, 1827	0	1	0	0	0	0	0	0	0	0	0	0	0
Diplodon solisianus (Orbigny, 1835)	0	0	1	0	0	0	0	0	0	0	0	0	0
Diplodon uruguayensis (Lea, 1860)	0	1	1	0	0	0	0	0	0	0	0	0	0
Diplodon voltzi Vernhout, 1914	0	0	0	0	0	0	0	0	0	0	1	1	1
Castalia ambigua Lamarck, 1819	0	1	0	0	1	0	1	1	1	1	1	0	1
Castalia cordata Swainson, 1840	0	1	0	0	0	0	0	0	0	0	0	0	0
Castalia crosseana Hidalgo, 1865	0	0	0	0	0	0	0	1	0	0	0	0	0
Castalia duprei (Récluz, 1842)	0	1	0	0	0	0	0	0	0	0	0	0	0
Castalia ecarinata Mousson, 1869	0	0	0	0	0	0	1	1	0	0	0	0	0
Castalia inflata Orbigny, 1835	1	1	1	1	1	0	0	0	0	0	0	0	0
Castalia martensi (Ihering, 1891)	0	1	1	0	0	0	0	0	0	0	0	0	0
Castalia multisulcata Hupé, 1857	0	0	0	0	0	0	1	0	0	0	0	0	1
Castalia nehringi (Ihering, 1893)	0	1	0	1	0	0	0	0	0	0	0	0	0
Castalia orbignyi (Deville & Hupé, 1850)	0	1	0	0	0	0	0	0	0	0	0	0	0
Castalia orinocensis Morrison, 1943	0	0	0	0	0	0	1	0	0	0	0	0	1
Castalia psammoica (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
Castalia quadrata (Sowerby, 1869)	0	1	0	0	0	0	0	0	0	1	0	0	1
Castalia schombergiana Sowerby, 1869	0	1	0	0	0	0	0	0	0	0	0	0	1
Castalia stevensi (Baker, 1930)	0	0	0	0	0	0	1	0	0	1	0	0	1
Castalia sulcata (Krauss, 1849)	0	1	0	0	0	0	0	0	0	1	1	1	1
Castalia undosa Martens, 1885	0	1	0	0	0	0	0	0	0	0	0	0	0
Paxyodon syrmathophorus (Meuschen, 1781)	0	1	0	0	1	0	1	0	1	1	0	0	1
Prisodon obliquus Schumacher, 1817	0	1	0	0	0	0	1	1	1	1	0	0	1
Triplodon corrugatus (Lamarck, 1819)	0	1	0	0	0	0	1	1	1	0	0	0	1
Triplodon chodo Mansur & Pimpão, 2008	0	1	0	0	0	0	0	0	0	0	0	0	0
Veneroida													
Dreissenidae													
Mytilopsis lopesi Alvarenga & Ricci, 1989	0	1	0	0	0	0	0	0	0	0	0	0	0
Mytilopsis trautwineana (Tryon, 1866)	0	0	0	0	0	0	1	1	0	0	0	0	0
Congeria hoeblichi Schütt, 1991	0	0	0	0	0	0	1	0	0	1	0	0	1
Corbiculidae													
Cyanocyclas amazonica (Prime, 1870)	0	1	0	0	0	0	0	0	0	0	0	0	0
Cyanocyclas bavayi (Ancey, 1880)	0	0	0	0	0	0	0	0	0	0	0	1	1
Cyanocyclas brasiliana (Deshayes, 1854)	0	1	0	0	0	0	0	0	0	0	0	0	0
Cyanocyclas cuneata (Jonas, 1844)	0	0	0	0	0	0	0	0	0	0	0	0	1
Cyanocyclas limosa (Maton,1811)	1	1	1	0	0	0	0	0	0	0	0	0	0

Table 2 continued

Species	South American countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Cyanocyclas paranaensis (Orbigny, 1835)	1	1	1	1	0	0	0	0	0	0	0	0	0
Cyanocyclas rotunda (Prime, 1860)	0	0	0	0	0	0	0	0	0	1	1	0	1
Cyanocyclas surinamica (Clessin, 1879)	0	0	0	0	0	0	0	0	0	0	1	0	1
Corbicula fluminalis (Müller, 1774)	0	1	0	0	0	0	0	0	0	0	0	0	1
Corbicula fluminea (Müller, 1774)	1	1	1	0	0	0	1	0	1	0	0	0	1
Corbicula largillierti (Philippi, 1844)	1	1	1	0	0	0	0	0	0	0	0	0	0
Corbicula sp.	0	1	0	0	0	0	0	0	0	0	0	0	0
Polymesoda solida (Phillipi, 1846)	0	1	0	0	0	0	1	0	0	0	0	0	1
Polymesoda aequilatera (Deshayes, 1854)	0	1	0	0	0	0	0	0	0	1	1	1	1
Sphaeriidae													
Byssanodonta paranensis Orbigny, 1846	1	1	0	0	0	0	0	0	0	0	0	0	0
Eupera bahiensis (Spix, 1827)	0	1	0	0	0	0	0	0	0	0	0	0	1
Eupera doellojuradoi Klappenbach, 1962	1	1	1	0	0	0	0	0	0	0	0	0	0
Eupera elliptica Ituarte & Dreher-Mansur, 1993	1	1	0	0	0	0	0	0	0	0	0	0	0
Eupera guaraniana Ituarte, 1994	1	1	0	0	0	0	0	0	0	0	0	0	0
Eupera iguazuensis Ituarte, 1989	1	1	0	0	0	0	0	0	0	0	0	0	0
Eupera klappenbachi Mansur & Veitenheimer, 1975	0	1	1	0	0	0	0	0	0	0	0	0	0
Eupera modioliforme (Anton, 1837)	0	0	0	0	0	0	0	0	0	0	0	0	1
Eupera platensis Doello-Jurado, 1921	1	1	1	1	0	0	0	0	0	0	0	0	0
Eupera primei Klappenbach, 1967	0	0	0	0	0	0	0	0	1	0	0	0	0
Eupera simoni (Jousseaume, 1889)	0	1	0	0	0	0	0	0	1	0	0	0	1
Eupera tumida (Clessin, 1879)	0	1	0	0	0	0	0	0	0	0	0	0	1
Musculium argentinum (Orbigny, 1835)	1	1	1	0	0	1	0	0	0	0	0	0	0
Musculium patagonicum Pilsbry, 1911	1	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium bejumae Baker, 1930	0	1	0	0	0	0	0	0	0	0	0	0	1
Pisidium boliviense Sturany, 1900	0	1	0	0	0	0	0	1	1	0	0	0	0
Pisidium chicha Ituarte, 2005	1	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium chilense (Orbigny, 1846)	0	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium chiquitanum Ituarte, 2001	1	0	0	0	1	0	0	0	0	0	0	0	0
Pisidium dorbignyi Clessin, 1879	0	1	1	0	0	0	0	0	0	0	0	0	0
Pisidium forense Meier-Brook, 1967	0	1	0	0	0	0	0	0	0	0	0	0	0
Pisidium globulus Clessin, 1888	0	1	0	0	0	0	0	0	0	0	0	0	0
Pisidium huillichum Ituarte, 1999	1	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium inacayali Ituarte, 1996	1	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium iquito Ituarte, 2004	0	0	0	0	0	0	0	0	1	0	0	0	0
Pisidium lebruni Mabille, 1884	1	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium llanquihuense Ituarte, 1999	0	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium magellanicum (Dall, 1908)	1	0	0	0	0	1	0	0	0	0	0	0	0
Pisidium meierbrooki Kuiper & Hinz, 1984	0	0	0	0	1	1	0	0	1	0	0	0	0
Pisidium ocloya Ituarte, 2005	1	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium omaguaca Ituarte, 2005	1	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium patagonicum Pilsbry, 1911	1	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium pipoense Ituarte, 2000	1	0	0	0	0	0	0	0	0	0	0	0	0

Table 2 continued

Species	South American countries												
	AR	BR	UY	PY	BO	CH	CO	EQ	PE	GU	SU	GF	VE
Pisidium plenilunium (Melvill & Standen, 1907)	1	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium punctiferum (Guppy, 1867)	0	1	0	0	0	0	0	0	0	0	0	0	1
Pisidium sterkianum Pilsbry, 1897	1	1	1	1	1	0	0	0	0	0	0	0	0
Pisidium taraguyense Ituarte, 2000	1	1	1	0	0	0	0	0	0	0	0	0	0
Pisidium vile Pilsbry, 1897	1	1	1	1	1	0	0	0	0	0	0	0	0
Sphaerium aequatoriale Clessin, 1879	0	0	0	0	0	0	0	1	0	0	0	0	0
Sphaerium cambaraense Mansur et al., 2008	0	1	0	0	0	0	0	0	0	0	0	0	0
Sphaerium forbesi (Philippi, 1869)	0	0	0	0	1	1	1	0	1	0	0	0	0
Sphaerium lauricochae (Philippi, 1869)	0	0	0	0	0	1	0	0	1	0	0	0	0
Sphaerium titicacense (Pilsbry, 1924)	0	0	0	0	1	0	0	0	1	0	0	0	0
Myoida (?)													
Lyonsiidae (?)													
Anticorbula fluviatilis (Adams, 1860)	0	1	0	0	0	0	0	0	0	0	0	0	0
Species richness (S)	60	117	46	31	27	12	29	18	33	17	9	6	49

Atlantic, Uruguay, Paraguay, and Amazon Rivers (>40 species). In Uruguay, the continuation of the Uruguay River basin presents the greatest wealth, followed by the basin of the La Plata River. In Argentina, the Uruguay River and the rivers of Paranoplatense System are the richest in species. Further North of this continent, the Orinoco River in Venezuela and Amazon River, in Peru are quite relevant. In rivers, generally there is a greater species richness in the middle and lower zones (Mansur & Pereira, 2006; Pereira et al., 2011), where the primary production is higher. Moreover, in these areas, a floodplain with oxbow lakes containing many species of bivalves (Colle & Callil, 2012) is very common. Very low richness is probably related to small Pacific drainages, to arid domains from the Andes, to the semiarid at Brazilian Northeast Atlantic or salty endorheic systems in Argentina (Fig. 2).

Only 43 native species occur in more than 10% of the hydrographic regions inventoried, while the other species occur in only 5 of 131 hydrographic regions inventoried (<10%) (Fig. 3). It means that there is an expressive and large zone of endemisms forming mosaics with different richness levels and taxocenosis compositions. *Anodontites* (*A*). *trapesialis* (Lamarck, 1819) and *C. fluminea* are widely distributed in South American hydrographic regions. The respective frequency of occurrence figures for these species in the basins analyzed are 59.6 and 53.8%. The following species should also be mentioned: *M. siliquosa* (Spix, 1827) (44.2%); *Anodontites* (*A*). *elongatus* (Swainson, 1823); *Anodontites* (*A*). *trapezeus* (Spix, 1827) and *C. largillierti* (32.7%); *Anodontites* (*A*). *patagonicus* (Lamarck, 1819) (28.8%); *Anodontites* (*L*). *ensiformes* (Spix, 1827) (26.9%); *L. fortunei* (25.7%); *Anodontites* (*A*). *crispatus* Bruguière, 1792; *Anodontites* (*A*). *tenebricosus* (Lea, 1834) and *Pisidium sterkianum* Pilsbry, 1897 (25.0%); *M. soleniformis* and *Castalia ambigua* Lamarck, 1819 (21.1%).

A. trapesialis is widely spread in hydrographic regions of the South America, occurring in sandy/muddy or muddy-only sediment, with deposits of silt and clay, in regions of lower water velocity as side channels or in marginal lakes, where it finds food (phytoplankton) in abundance (Bonetto & Di Persia, 1975; Hebling, 1976; Simone, 1994; Pereira et al., 2011; Colle & Callil, 2012). The species had dispersed further due to fish farming. The lasidia of this species appear not to show specificity with hosts (Callil et al., 2012), facilitating the dispersion in the fish farms, causing damage on fish production (Guardia-Felipi & Silva-Souza, 2008). *C. fluminea*, which has been reported in South America since the 70s has invaded all the large basins of the continent from Colombia to the North of Patagonia where it became quickly dominant (Santos et al., 2012). *M. siliquosa* is not abundant but present in most of the South American basins living in small aggregate populations that prefer

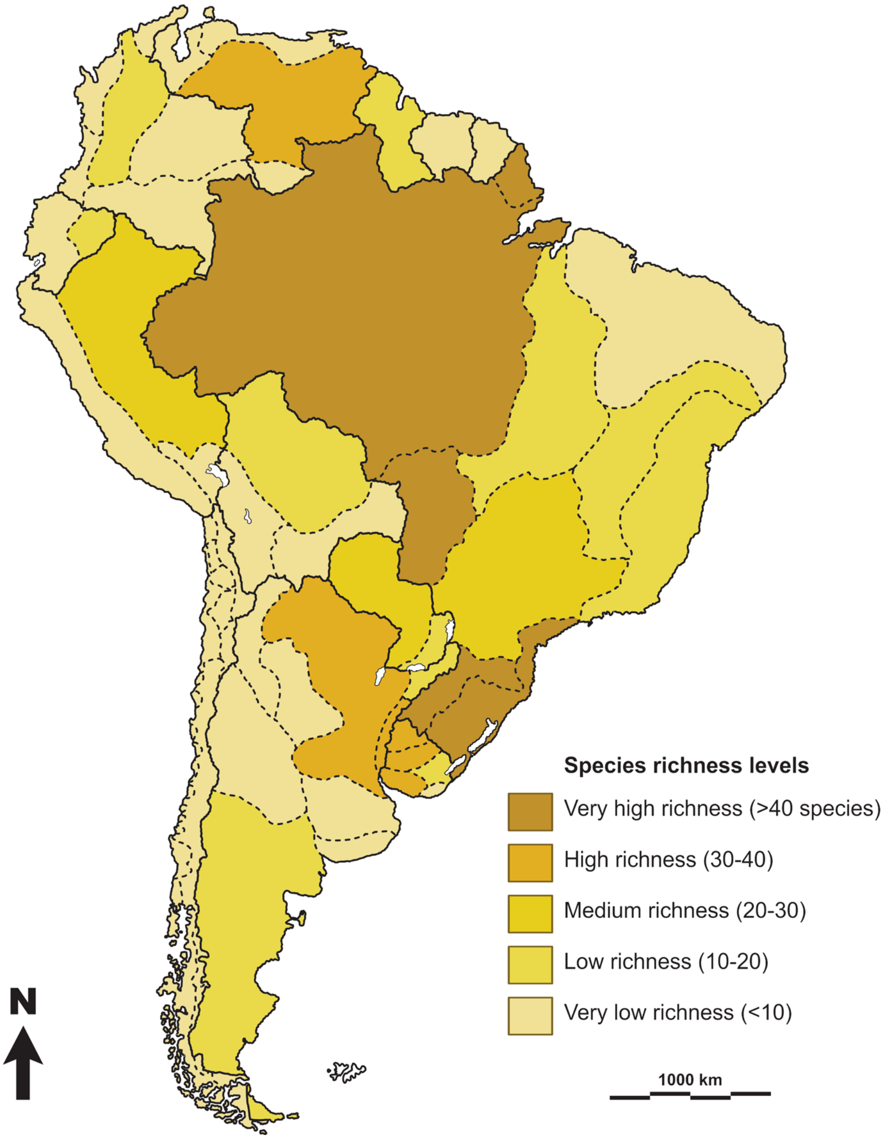

Fig. 2 Species richness (S) zonation of freshwater bivalves in the hydrographic regions in South America

compacted substrate of marginal areas. *A.* (*A*). *elongatus* is present in many basins from the North at the Magdalena, Orinoco, and Amazon basins to the South in the Uruguay River. It usually occurs together with *A.* (*A*). *trapesialis* and *Castalia* spp. sharing the same habitat in areas of marginal lakes and side channels, especially in the region of the Pantanal on the upper Paraguay River (Colle & Callil, 2012). *A.* (*A*). *trapezeus* is very common in the basins of the Eastern and Southern Atlantic, Paraná, Paraguay, and Uruguay, and is rare in Tocantins, Amazonas, and Orinoco.

The distribution of two *Corbicula* species does show no significant ($P < 0.01$) correlation with species richness in the different hydrographic regions in South America: *C. fluminea* ($r = 0.11$; $P = 0.012$) and *C. fluminalis* ($r = 0.07$; $P = 0.31$). However, *C. largillierti* demonstrates significant and poor positive correlation ($r = 0.32$; $P = 0.0001$) with species richness. *C. largillierti* was the first species of the genus to invade South America through the La Plata River. Subsequently, *C. largillierti* decreased in density and distribution after the arrival of another invasive species, *C. fluminea*. *A.*(*A*). *patagonicus* is very common in the Southern American hydrographic regions as Paraná, Uruguay, and South Atlantic River basins. *A.* (*L.*) *ensiformis* is common in the middle Paraná in Argentina,

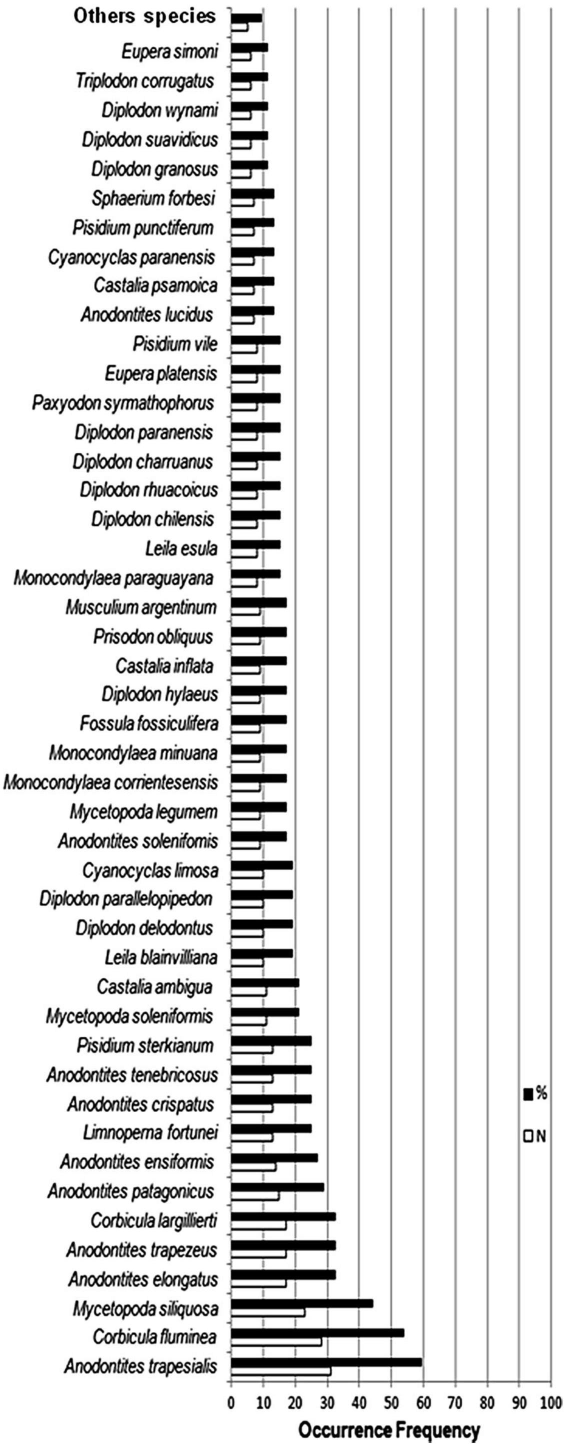

Fig. 3 Occurence frequency (N and %) of freshwater bivalves in hydrographic regions of South America

in Paraguay River of Brazil and Paraguay and in a small part of middle Uruguay River bordering Argentina and Brazil. Northwards, it is observed in the Madeira River in Bolivia, in the Amazon, Tocantins, and Orinoco basins. Like *M. siliquosa*, it lives in small populations on muddy river margins.

The distribution of *L. fortunei* does show no significant correlation ($r = 0.02$; $P = 0.69$) with species richness in different hydrographic regions in South America. After the first record of *L. fortunei* in the La Plata River near Buenos Aires, the species was rapidly dispersed with the help of the boats that flow through waterways of the Uruguay, Paraná, and Paraguay rivers invading Argentina, Brazil, Uruguay, Paraguay, and Bolivia. So far it has not been reported in the Amazon River Basin despite the proximity. It has been recorded in the upper Paraná River, downstream of the dam of St. Simon at Paranaiba River, bordering the state of Goiás, Brazil. This region is very close to the headwaters of the Tocantins River which flows in the delta of the Amazon River (Santos et al., 2012).

A. (*A*). *crispatus* is more frequent in the basins of the Northern part of the continent, and the upper tributaries of the Paraguay river. *A.* (*A*). *tenebricosus* is very common on the lower part of the Uruguay river, where it appears in a very robust form. It also occurs in the south Atlantic drainage of Brazil but at a lower extent, and in the basins of Plata and Paraná becoming more scarce to the north. The record of this species for the Orinoco must be revised because it may have been confused with the related species *A.* (*A*). *crispatus* or *A. elongatus*.

Pisidium sterkianum is often present and abundant in sandy bottoms of lakes and lower parts of the rivers of Paraguay, Paraná, upper Paraná in Brazil, and Uruguay basins. It has also been reported for the Amazon Basin in Brazil and Bolivia.

Mycetopoda soleniformis just like the other species of this genus, lives in clusters forming small populations. It is most frequently found in the basin of the Paraná River, and much less common in the Uruguay River. As for the Amazonas River, there are records for Peru, Bolivia near the Madeira River, and in the state of Acre in Brazil. *C. ambigua* is common in large parts of the Orinoco and the Amazon Rivers even along the Andes in Peru and Ecuador, and has been reported for the Pacific basin in Ecuador. It occurs also in the rivers of Suriname and Guyana. The citations of *C. ambigua* to La Plata, Paraná and Paraguay rivers, and the lower reach of the Uruguay River must be carefully studied with the support of genetics considering the similarities to *Castalia inflata* Orbigny, 1835 which predominates in these Southern hydrographic regions. It is possible that both species could be considered as synonyms.

Endemisms can be easily observed in some species that live on stones in running waters like: *A. rivolii* (Magdalena River at Colombia), *Bartlettia stefanensis* (Moricand, 1856) (High Amazon and Paraguay rivers), *Byssanodonta* (Ihering, 1893) (Middle Paraná River), and *M. lopesi* (lower part of Amazon and Tocantins rivers). *Triplodon*, *Paxyodon* Schumacher, 1817 and *Prisodon* Schumacher, 1817 only appear in the Amazon and Orinoco rivers. *H. balzani* lives in very restricted areas of the Paraguay River that present calcareous water. Endemisms are even more evident among Sphaeriidae. *Eupera iguazuensis* Ituarte, 1989 is restricted to Iguazú falls (area bordering Brazil and Argentina) and *Pisidium pipoensis* Ituarte, 2000 found only in the region of Missiones (Argentina). In the region of Patagonia in Argentina and Chile, there are many proper species of *Pisidium* and at Lake Titicaca (area bordering between Peru and Bolivia) some endemic species of *Sphaerium* can be found.

Regarding Dreissenidae, the native *M. lopesi*, from the lower part of the Amazon River and Tocantins/Araguaia Rivers is adapted to freshwater forming small and low clusters on submerged rocks (Alvarenga & Ricci, 1989). Embryos and larvae develop outside the gills, inside the pallial cavity, fixed to the mantle of parental individuals, and are released as they are young (Mansur, 2012). They differ considerably from estuarine dreissenids as *Mytilopsis sallei* (Recluz, 1849) and *Mytilopsis leucophaeata* (Conrad, 1831) with planktotrophic larvae. Both species are from North America: the former was detected in Venezuela and the latter has been most recently collected in the mangroves of Recife (Souza et al., 2005). *A. fluviatilis* is an endemic species of Amazonas River occurring from Peru to river mouth on the main channel (Simone, 1999, 2006).

Phylogenetic composition and origin of the hydrographic regions

The principal coordinate's analysis for phylogeny-weighted species composition generated 51 PCPS. The first two PCPS contained, respectively, 53.6 and 33.8% of the total variation in the phylogenetic composition matrix. The ordination scatter plot (Fig. 4) shows that the first PCPS was positively related to hydrographic regions characterized by the predominant occurrence of Veneroida + *A. fluviatilis*, and negatively related to predominant occurrence of Mycetopodidae and Hyriidae. On the other hand, the second PCPS split hydrographic regions characterized by predominant occurrence of Hyriidae (positive values) and Mycetopodidae (negative values).

The Veneroida had higher species richness in the hydrographic regions located in the Andes Mountains on the far Southwest, and coastal areas of the continent. This order is represented basically by several species of *Pisidium* genus concentrated mainly in Andean area. These are cooler regions, where rivers are born in mountainous areas. These are very similar environments to the frozen rivers of the Paleartic Region, where many species of *Pisidium* are sympatric. However, the species of *Pisidium* are rarely sympatric in South America and show a great variation within populations (Kuiper, 1983). In streams and lakes of the Andean highlands, they are more numerous and concentrated (Kuiper & Hinz, 1984; Ituarte, 2007). Species of *Sphaerium*, are practically only present in the Andean highlands. An exception is *Sphaerium cambaraense* Mansur et al., 2008, which occurs in the highlands (above 800 m) in Southern Brazil at the *Araucaria angustifolia* forest (Mansur et al., 2008). Fitkau (1981) mentioned that the Amazon does not have habitats suitable for the occurrence of Sphaeriidae except for *E. simoni*, which is adapted to the fluctuations of the water level and long drought periods. In the coastal environment of Northern Brazil and Venezuela, species of *Cyanocyclas* and *Polymesoda* genus are predominant.

Parodiz & Bonetto (1963) presented distribution maps of Hyriidae and Mycetopodiade in South America which coincide with the distribution of species observed in this study. Some species of Hyriidae and Mycetopodidae have also been reported in rivers located in mountainous areas which are not so elevated like Andes area. *D. chilensis* is the only species of Unionoida inhabiting Andine Rivers and lakes in the Patagonian region found in Chile, Argentina, and Peru. This is the most frequent species in lakes near the cities of Temuco, Valdivia, and Puerto Montt at Chile (Parada & Peredo, 2002; Parada et al., 2007).

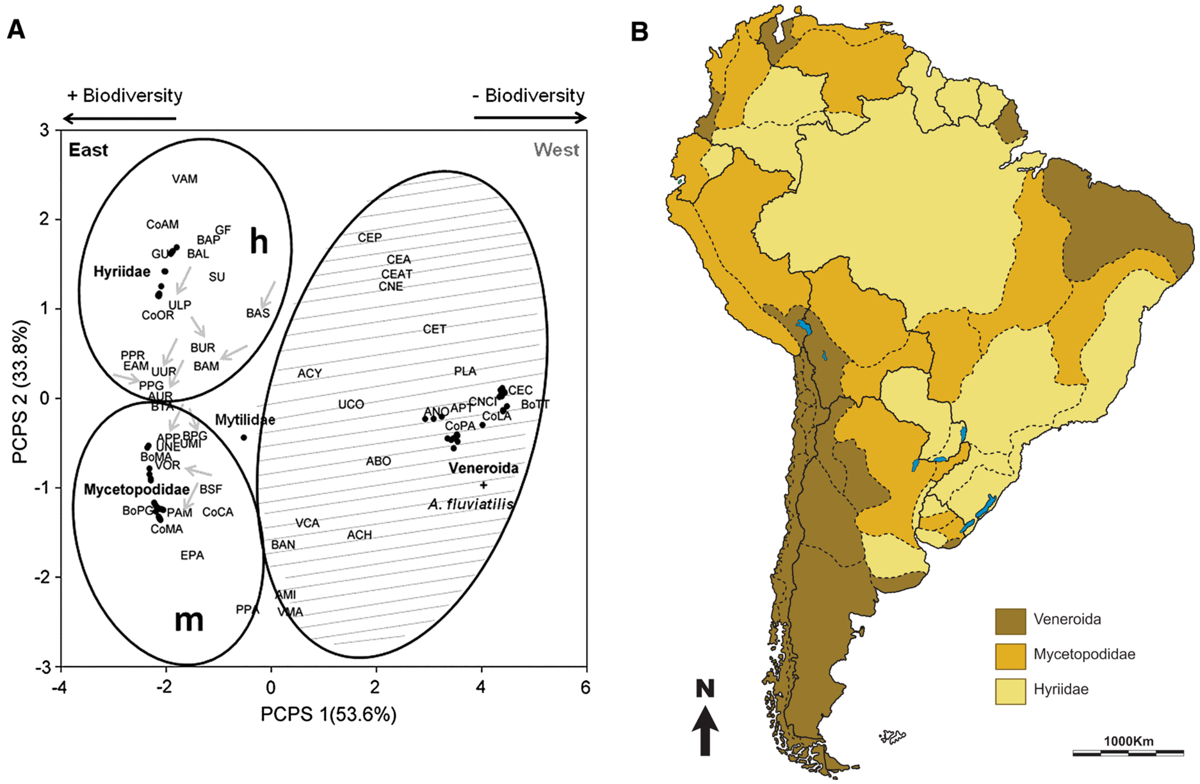

Fig. 4 Principal coordinates analysis of phylogenetic structure (PCPS) for each hydrographic regions of South America. **A** Ordination scatter plot. **B** Phylogenetic structure of hydrographic regions. *Arrow* indicates very high richness. Hyriidae (*h*) and Mycetopodidae (*m*)

A. (*A*). *tenebricosus*, *B. stefanensis*, and *A. rivoli* are typical waterfall species. However, the highest richness of Mycetopodidae and Hyriidae is to be found in lowland rivers, oxbow lakes, lakes, and costal lakes. Very inflated species, such as *Castalia inflata*, float over the mud of river margins and lakes. The elongated forms like *Mycetopoda*, *Mycetopodella falcata* (Higgins, 1868), *A.* (*L*). *ensiformis* bury themselves in the compacted substrate of wet river banks.

To understand the patterns of distribution of species, it is necessary to know the geological events that gave rise to the current configuration of the landscape and hydrographic regions in South America. According to Leal (2011), during the breakup of the Gondwana Paleocontinent in the Mesozoic (Cretaceous period, ~100 Ma), the main drainage of the South American plate was directed to the West. This pattern changed due to geotectonic episodes like: separation of South America from Africa with the opening of the South Atlantic Ocean, the Andean uplift, and the closure of the Panamanian Isthmus. Since the upper Mesozoic era (83–67 Ma), three separate large river basins were present, two located at the current Amazon River Basin (one part which flowed East and another West), and another drainage which flowed South and originated the Paraná–Paraguay river system.

According to Hubert & Renno (2006), successive geological events determined the genesis of the current South American basins in the Cenozoic era (Tertiary period) as follows: (1) 15 and 10 Ma: the last event of great marine incursion, before the final establishment of the Amazon, previously dated between and was postulated to lead to a 150-m marine highstand forming a big sea called Pebas. At least one continental sea, the Paranean Sea between Southern Brazil and Northern Argentina, was formed. The Magdalena basin was isolated after the uplift of the Northwestern Andes changing the direction of river flow to the west; (2) 10 and 8 Ma: marine regressions and Andean foreland dynamics are associated with the final establishment of the Amazon basin. The Paraná–Paraguay split from the protoAmazon at 10 Ma; (3) 8 and 5 Ma: separation of the Orinoco occurred on the Vaupes arch. The modern course of Amazon River appeared with the final uplift of the central Andean cordillera related to the rise of the Purus arch. The Maracaibo Lake was formed after the final uplift of the Northwestern Andes. The Upper Amazon was isolated from the remainders of the Orinoco and Paraná rivers; and (4) 4 Ma: after marine regressions and Andean dynamics, the Upper Amazon was fragmented. The formation of the Pebas sea got several rivers isolated and consequently got their populations of freshwater bivalves isolated, too. According to Wesselingh (2006), the Western Amazonian became a mosaic of lakes, swamps, and meander belts splitting the mains river in different subsystems. According to Wares & Turner (2003), the freshwater habitats are typically connected in a hierarchical, fractal geometric fashion with low-order streams draining into larger streams and rivers. This physical configuration offers a great diversity of habitats for freshwater clams. The compartmentation of hydrographic regions in South American basins promoted different ways to diversification of both invertebrate and vertebrate fauna like fishes, and this fact is closely associated with hydrogeological history of the continent (Hubert & Renno, 2006). According to the same authors, "the patchy nature of freshwater habitats, may in some respects account for the high species diversity encountered there considering that opportunity for geographic isolation (and presumably alopatric speciation) is greater than in marine habitats". For million years in the Mioceno, there was also probably sufficient time for diversification of freshwater bivalves. By virtue of the formation of Pebas, the Andean uplift and erosion changed the fluvial landscapes of South America again resulting in more intensive diversification of freshwater bivalves. Events similar to the formation of Pebas occured in the Southern part of the continent in the Paraná–Paraguay with formation of Paranean Sea. Events like these probably promoted the fauna diversification in water courses as Rivers of the South and Southeast Atlantic, and coastal lakes. Lanzer (2001) verified that the distribution of freshwater clams in lake systems of the coast of Rio Grande do Sul, in Southern Brazil, is related to the genesis of those systems that resulted from the processes of marine transgressions and regressions.

In addition to the geological events, other factors are important for the distribution of bivalves. Freshwater clams cited for South America can also be scattered across the stomach contents of fish, but are limited to the distribution areas of these vectors. They can also be transported over long distances by birds, crossing geographical barriers. These birds eat large bivalves, but normally they break the shell eating only the soft part. However, smaller bivalves can remain unscattered through the gut, mainly Corbiculidae, and Mytilidade, or transported fixed on feathers, mainly Corbiculidae and Sphaeriidae.

Knowledge gaps

The lack of basic knowledge on freshwater clams is a reality that hinders the categorization of species conservation status in South America. This paucity is in part due to the lack of organized and representative collections of the freshwater bivalves species of the main hydrographic regions in South America, difficulties in obtaining type material or respective good illustrations, lack of identification keys and publications on the reproduction, ecology, morphology, and on the affinity of the species with the host fish of gloquidia and lasidia, besides the scarcity of limnological institutions or biological stations dealing with mussels. Many hydrographic regions are underrepresented in scientific collections, especially those located in the Northern part of the continent.

By comparing the study of freshwater bivalves in South America with the one developed in other continents, especially Europe and North America, we can see that in the period of the early naturalists (Haag, 2012), the difficulties encountered there, such as the scarcity of morphological data and the lack of sampling locality of the species, were similar to ours. But in South America, we have aggravating circumstances that type material and additional collections were donated or sold to museums in Europe or North America. In the subsequent periods, the first museums and scientific collections were formed in the countries of the Northern hemisphere. At that time, studies on mussels compared morphologies, ecology, and phylogeny saw a period of major development (Haag, 2012). In South America, the studies leave something to be desired by the lack of comparative material, and again, important collections as the one from Ihering were still sold to Europe. Ortmann (1921), who started and strongly encouraged malacology and mussel ecology in North America (Haag, 2012), did not collect in our watersheds. He described relatively few species from some basins, mainly those mussels collected by his colleague Ichthyologist J. D. Hasemann, with their testimonies reported at the Carnegie Museum, Pittsburgh, again outside South America.

In recent decades, genetic studies have shed light on the phylogenetic and evolutionary relationships inside Unionoida. However, the presence of unionoidean doubly uniparental inheritance of mtDNA (DUI) make evolutionary interpretations difficult mainly by the South American Hyriidae that are scarcely evaluated. Genetic studies are also necessary in order to differentiate similar or cryptic species of Mycetopodidae as, *Anodontites* (*A.*) *iheringi* (Clessin, 1882), and *Anodontites ferrarisii* (Orbigny, 1835); *A. tenebricosus* and *A. soleniformis*; and of Hyriidae as, *D. granosus* and *D. multistriatus*; *C. ambigua*, and *C. inflata*. Many species are morphologically unknown and rare in scientific collections like, *Anodontites* (*A.*) *aroanus* Baker, 1930; *Anodontites* (*A.*) *carinatus* (Dunker, 1858); *Anodontites* (*A.*) *colombienses* Marshall, 1922; *Anodontites* (*A.*) *guanarensis* Marshall, 1927; *Anodontites* (*A.*) *puelchanus* Orbigny, 1835; *Monocondylaea costulata* (Moricand, 1858); *Monocondylaea franciscana* (Moricand, 1837); *Monocondylaea guarayana* (Orbigny, 1835); *Tamsiella amazonica* Bonetto, 1972 and, *Tamsiella schroeteriana* (Lea, 1852). It would be necessary to conduct new expeditions in the type localities in order to obtain topotypes to support the redescription of these species.

Many species of *Diplodon* genus cited for the basins of the Eastern Atlantic, Upper Paraná River, and North and Northeast Atlantic are hardly differentiated. Until now, the diagnostic criteria are not well established, thus requiring adequate morphological studies for the recognition of their taxonomic status: *Diplodon* (*D.*) *caipira* (Ihering, 1893); *Diplodon* (*D.*) *expansus* (Kuester, 1856); *Diplodon* (*D.*) *ellipticus* (Spix, 1827); *Diplodon* (*R.*) *funebralis* (Lea, 1860); *Diplodon* (*D.*) *multistriatus* (Lea, 1831); *Diplodon* (*D.*) *granosus* (Bruguière, 1792); *Diplodon* (*D.*) *paulista* (Ihering, 1893), and *Diplodon* (*D.*) *rhombeus* (Spix, 1827). In addition, *Diplodon* (*D.*) *imitator* Ortmann, 1921 was described from the Jacuí River in the South Atlantic Basin; however, it has not been found ever since. Some species of genus *Diplodon* were not yet framed within subgenera due to lack of knowledge of glochidia morphology (Table 2).

The species, *C. ambigua*, *C. inflata*, *Castalia quadrata* Sowerby, 1869, *Castalia schombergiana* Sowerby, 1869 and *Castalia sulcata* (Krauss, 1849) show a wide morphological variation, with a particular shape of the shell for each different basin, which also hampers the recognition of these species by non-specialists. The internal anatomy is unknown for the most part of the species and the glochidium is not a good intraspecific character in this genus.

Prisodon obliquus Schumacher, 1817 and *Paxyodon syrmatophorus* (Gmelin, 1791) are very similar species with winged hinge, no umbonal sculpture and the same color and periostracum brightness. The upper Amazon River sees a predominance of *P. obliquus*, whereas in the low Amazon River, *P. syrmatophorus* prevails. However, intermediate forms occur in sympatry in some parts of the lower Amazon River. Therefore, questions remain to be answered about the identity of both species, raising suspicions of the existence of only one species with a wide morphological variation along the basin. Pimpão et al. (2012) observed that the glochidia of both species are also very similar.

All species of the genus *Cyanocyclas* should be reviewed. Mainly species of northern part of the continent and *C. limosa*, which shows a wide morphological variation and may represent a large number of species.

Considering Sphaeriidae in the Southern hemisphere, Kuiper (1983) emphasizes the fact that the paucity of species with conspicuous interpopulational variation in the same environment is regarded as a rule. This morphological variation makes difficult the definition of diagnostic criteria and consequently the species recognition. The species of the *Pisidium* genus cited for Argentina, Bolivia, Chile, Peru, and Uruguay were reviewed by Ituarte (2007), and all other hydrographic regions in South America require similar revisions and more collections.

Considering the abovementioned amount of gaps of knowledge, we can recognise that *D. chilensis* is one exception and probably the best known species of Hyriidae in the continent.

Risks for the biodiversity of freshwater bivalves

The main threats to the conservation of freshwater bivalves are related to habitat destruction, water pollution, and the invasion of exotic bivalves (Mansur et al., 2003a; Machado et al., 2008; Pereira et al., 2012). Among the causes of habitat destruction, we can highlight the deforestation of riparian vegetation, damming and channeling rivers, wetland drainage, siltation of rivers and lakes, sand mining, etc. The bivalves are filter feeders that have little or no mobility in adulthood. As a consequence, they are very sensitive to changes in river flow, sediment grain size, water level, slope and shading on the margins. The destruction of the terrestrial environments entails drastic consequences to hydrographic regions. Until today, the practice of burning forests and savannah environments are common in many South American countries and territories despite the restrictions imposed by environmental agencies sponsored by the government. This practice disrupts the soil, facilitating erosion and siltation. Thus, all processes that modify and destroy the vegetation cover also have a negative impact on hydrographic regions, affecting the assemblage of bivalves.

Miyahira et al. (2012a, b) made some comments on the habitat degradation and their effects on freshwater mussels in the state of Rio de Janeiro. Water pollution is an important factor in the population decline of native bivalves. The high organic contamination decreases the oxygen dissolved in the water, keeping these mollusk from surviving. Contamination from industrial effluents and solid waste generates metals that are incorporated by the bivalves and accumulated in the food chain. The agricultural activity also impacts on this fauna which is poisoned by pesticides.

In South America, the main source of energy is provided by hydroelectric plants. In Brazil, the construction of reservoirs to meet the energy demands required for the accelerated development of this country is encouraged by the government. However, when it comes to mollusks, the terms of reference that guide the implementation of the environmental studies for licensing ventures require only a survey of the snails vector of zoonosis. In addition to that, the construction of dams causes environmental changes in making a river into a lake. This fact changes the patterns of connectivity of the wet drainage and affects the structure of the fish fauna (composition and abundance of fish), and their migratory routes. The majority of the Unionoida use fish as dispersal vectors. With the interruption of the migration route of host fishes, the dispersion of mollusks is compromised.

Historical data (Takeda et al., 2005; Pereira et al., 2012) revealed that the construction of 70 reservoirs in a system of waterfalls along the most populated area of Brazil, in high Paraná River, changed the lotic environment to lentic, favoring the colonization of the Corbiculidae invasive species and *L. fortunei*, as well as the gastropod *Melanoides tuberculata* (Müller, 1774). The river segments that allow the survival of native bivalves in their natural habitats are rare. Furthermore, the fish that dispersed bivalve larvae are unable to move upstream along rivers. Consequently, all Unionoida species reported in this area are endangered, though many of them do not appear on official red lists.

The freshwater bivalves have been adapted to drought and flood of the rivers for millions of years. With the construction of reservoirs, the natural flood pulse that occurred in the floodplains of the rivers has become artificially regulated. In many of those rivers, the overflow of the channel during the rainy season is stopped, so there is no more communication with floodplain lakes. This change in water dynamics of rivers impacts the life cycle of bivalves that depend on fish for their dispersal. The disconnection of these environments limits the lasidia and glochidia dispersion through the fish.

Moreover, the bivalves can not keep up with sudden emptying of reservoirs in times of intense rainfall. Two types of impacts are known to be related to that. One occurs in the reservoir when it is quickly emptied by opening the floodgates. The water level decreases dramatically exposing the entire bank, resulting in the death of bivalves that can not keep up with the speed of emptying. The same impact can be observed in the Northeast of Brazil at the times of severe droughts, when reservoirs became empty due the absence of rains. The other impact occurs downstream the reservoir when the water is released at high speed dragging all the marginal fauna and flora, often throwing the bivalves out of the system.

The dispersion of the invasive bivalve species in several hydrographic regions of South America constitutes a threat to the conservation of native clams. The golden mussel produces byssus threads that enable the incrustation on the various types of hard substrates forming macrofouling. This structure of aggregates alter different types of substrate-forming mussel beds on sediment and between rhizomes of the *Schoenoplectus californicus* (C.A. Mey.) Palla

(Cyperaceae), a kind of emergent shoreline vegetation common in South America (Santos et al., 2012). Also, it forms macroclusters over other types of free-floating and amphibious macrophytes, such as species of trees from the banks of rivers and lakes. All these habitats are modified and so is the entire benthic fauna composition. In addition to the habitat loss, the bivalves are choked by the incrustation of mussels on their shells, keeping the valves from opening, and in some cases, from closing, too. So the native bivalves can not perform filtering and become exposed to predators.

The golden mussel occurs predominantly on hard substrates, and to a lesser extent on sandy bottoms. On the other hand, the Corbiculidae invasive species occurs predominantly on sandy bottoms dominating the benthic communities. Thus, the pressure of invasive species on native clams is intense. *L. fortunei* can reach 500,000 ind m^{-2} (Bergonci et al., 2009) and *C. fluminea* just to 5,295 ind m^{-2} (Mansur & Garces, 1988).

L. fortunei form macrofouling on hard substrate covering great areas of rivers and lake bottoms altering the benthic fauna structure. The great density of *L. fortunei* related to the high filtration rates have an impact on the planktonic community and food chain (Darrigran & Damborenea, 2011). The macrofouling also impact the equipments of hydroelectric and thermoelectric plants. However, until now new designs for power plants do not present solutions to minimize the effects of biofouling.

Conservation strategies

Since the 1990s there has been a great effort from most South American countries for the preparation of their official lists of endangered species of their fauna. However, most of these lists include only vertebrate species. Out of the 12 South American countries and 1 territory, only 4 have published lists of endangered species of mollusks: Brazil, Colombia, Paraguay, and Uruguay. The Brazilian list of threatened fauna (Machado et al., 2008) includes the following species: *Diplodon* (*R.*) *koseritzi* (Clessin, 1888) (critically endangered, CEN); *A.* (*A.*) *ferrarisi*, *A.* (*A.*) *iheringi*, *D. caipira*, *D.* (*D.*) *dunkerianus*, *D. fontainianus*, *D. pfeifferi*, *D. rotundus*, *C. undosa*, *A.* (*A.*) *trapezeus*, *Fossula fossiculifera* (Orbigny, 1835), *L. blainvilliana* (endangered, EN); *A.* (*A.*) *elongatus*, *A.* (*L.*) *ensiformis*, *A.* (*A.*) *soleniformis*, *A.* (*A.*) *tenebricosus*, *A.* (*A.*) *trapesialis*, *M. legumen*, *M. siliquosa*, *Monocondylaea paraguayana* (Orbigny, 1835), *Leila esula* (Orbigny, 1835), *B. stefanensis*, *D.* (*D.*) *expansus* (Vulnerable, VU). The species *A.* (*A.*) *soleniformis*, *A.* (*A.*) *trapezeus*, *F. fossiculifera*, *H. balzani*, *B. stefanensis*, *D.* (*D.*) *expansus*, *C. inflata* and *C. nehringi* were considered in the Paraguayan list (Ministerio de Agricultura y Ganaderia, 1998) in only one category defined as "endangered". *Polymesoda solida* (Philippi, 1946) was considered to be a vulnerable species in the threatened fauna list of Colombia (Ardila et al., 2002). The list of the IUCN (2012) includes only *D.* (*D.*) *dunkerianus* and *D. fontainianus* (endangered, EN); *Diplodon* (*D.*) *expansus*, *D. pfeifferi*, and *Castalia martensi* (Ihering, 1891) (vulnerable, VU). The National list of priority species (Scarabino & Clavijo, 2009) recognized that 93% of the species of bivalves (37) from the freshwater environments from Uruguay are priority for conservation. Later Clavijo et al. (2010) prioritized three other species for conservation.

Pereira et al. (2012) listed all species of freshwater bivalves from Brazil and their conservations status based on an official list. According to the authors, 1% of species is critically endangered, 10% are endangered, 9% are vulnerable, and 37% need a new evaluation and should be included in the revised list. Many other species need more information for the adequate determination of their conservation status. The quotation of *A.* (*A.*) *trapesialis* in the list of Brazilian threatened fauna should be revised because this species has dispersed through aquaculture systems as well as invasive species. *A.* (*A.*) *trapesialis* adapts to different environmental conditions and probably does not fit into any category of endangered species.

The lack of basic knowledge on freshwater clams is a general reality that hinders the categorization of the conservation status of the species. There are too many gaps in collection records in Northern South America. These regions are underrepresented in scientific collections; however, in better represented South regions that are many gaps, too.

For the purposes of conservation and management, Parada & Peredo (2005) and Peredo et al. (2005) made an experience with relocation of two populations of *D. chilensis* through a long-term evaluation of survival and recruitment. After 18 years, the relocated population remained at the same site. At one site, the authors did not found recruits but the individuals were greater than at the original site. At the other site, the recruitment has resulted from the dispersion of larvae by the host fish. The size of the juveniles suggested that recruitment took place in the previous reproductive season.

In Brazil, Beasley et al. (2000) studied the reproductive cycle of the harvested salmon pink mussel *P. syrmatophorus*, giving strategies for conservation and management of the species in the Tocantins River Basin, in Brazil. Later, Beasley (2001) studied the density, size frequency distribution, the habitat structure, and the impact of exploitation of these bivalves by industries of pearl buttons aiming to define management strategies. Initiatives on relocation, translocation, and repopulation of the freshwater mussels are unknown in Brazil.

There is little information on the conservation status of freshwater bivalves in Uruguay. Scarabino & Mansur (2007) listed the species of bivalves in Uruguay with the intent of supporting the conservation of this fauna. Scarabino (2004) reviewed for the first time the conservation status of Uruguayan malacofauna and highlighted the priority actions to be taken in order to conserve this fauna. Currently, there are several initiatives to improve and disseminate the knowledge base and implement conservation measures for freshwater bivalves in Uruguay (Clavijo et al., 2010). The first and only experience of relocation was held in Uruguay in 2010 based on a private initiative. As a result of this experience, a total of 133 specimens of *D.* (*R.*) *charruanus*, *D.* (*D.*) *rhuacoicus* (Orbigny, 1835), *A.* (*A.*) *trapesialis* and *A.* (*A.*) *patagonicus* ended up endangered by a dam construction were relocalized to a natural place (Clavijo et al., 2012).

The concern on bivalve conservation in Argentina begins with the implementation of database systems for the malacological scientific collections. Rumi et al. (2008) evaluated the richness of mollusk species in continental Argentina, and mapped their distribution. The authors offered subsidies for prioritizing areas for conservation.

Final considerations

The number of 111 Uninoid species places South America as a very rich continent, but not richer than North America. According to Graf & Cummings (2007), North America presents the highest diversity of mussels on Earth (~300 species). Our results came to 63 mussel species of Hyriidae and 48 Mycetopodidae, a number which is a bit higher than the figures presented by Graf & Cummings (2007) for both families (40 and 32 species, respectively) in South America.

The most diverse hydrographic regions in South America are: (1) very high richness, Amazon River, Paraguay River, Uruguay River, and Rivers of the South and Southeast Atlantic in Brazil; (2) high richness, Orinoco River in Venezuela; Paranoplatense System in Argentina; Uruguay River, La Plata River, and Negro River in Uruguay; and (3) medium richness (Amazon River in Peru, Upper Parana River in Brazil, and Paraguay River in Paraguay). These hydrographic areas are located within the two richest South American macroregions identified by Graf & Cummings (2007): Amazon–Orinoco (on the Peba System) and Paraná–Paraguay (on the Paranean System).

The hydrographic regions present distinct phylogenetic and species composition regardless of the level of richness. Therefore, not only should the richness be considered to be as a criterion for prioritizing areas for conservation, but also the phylogenetic diversity of communities engaged in services and functional aspects relevant to ecosystem maintenance.

The wide distribution of some native species can be attributed to their high tolerance to environmental factors, transposition of geographical barriers, and persistence in face of geological events in the past. Native species with wide distribution, such as *Anodontites trapesialis*, may have similar properties to invasive species, which would explain its wide distribution along to hydrographic regions and success in its current dispersion in the fish farms. However, more studies are needed on the biology of this species for us to understand their mechanisms of dispersion and whether these mechanisms are related to a certain degree of invasiveness.

Another issue to be considered is that the small number of invasive species seems not to interfere in the patterns of species composition and phylogenetic lineages in the different hydrographic regions looked at. *L. fortunei* does not contribute to the dominance of Mytilidae lineage in none of the hydrographic regions assessed with complex assemblages of native mollusks. On that line, it can be inferred from the occurrence of Corbiculidae invaders, among the Veneroida, which are widely distributed in South America, that they appear also in areas dominated by Mycetopodidae and Hyriidae. It is also to consider that the number of corbiculid invaders is much smaller than the total number of species of Veneroida recorded in the continent. However, it is important to raise awareness to the potential impact of invasive species that are dispersing by South American water courses. The golden mussel invasion may result in the reduction of the diversity of bivalve mollusks in the different addressed areas with the capacity to modify the patterns of species richness, species composition, and phylogenetic lineages. Considering this possibility, efforts should be made in order to control the dispersion and population growth of invasive species. The control of the spread of invasive species depends primarily on educational actions intended to raise awareness of boatmen, fishermen, and farmers, who use the water for irrigation; their procedures and equipment must be revised in an attempt to minimize the danger of contamination of new bodies of water.

The distribution of invasive species *L. fortunei*, *C. largillierti*, *C. fluminea*, and *C. fluminalis* is not related to species richness in the different hydrographic regions in South America. This distribution does not corroborate to the assumption that the poorest communities in species would be more susceptible to bioinvasion (Wolfe, 2002; Bohn et al., 2004).

However, the Andean region does not seem to be inviting to the invasion of *L. fortunei* according to Darrigran et al. (2011). The same authors identified three environmental parameters that are barriers to invasion in this region: salinity, river flow intermittence (in different sectors of Pilcomayo and Salado del Norte Rivers), and concentration of suspended sediments (in the Bermejo River and in the upper reaches of the Salado del Norte and Pilcomayo Rivers).

Detailed inventories of native bivalve fauna in different hydrographic regions are also needed, as well as the identification of habitats, with the environmental variables that govern the distribution of the species, the patterns of diversity, and the provision of deeper insights into the reproductive cycle and morphological characters which are determinants for species recognition. This is essential for the establishment of management strategies, identification of potential areas for the conservation, breeding and relocation of endangered species. The species composition and phylogenetic patterns identified in this study will contribute to the definition of priority actions for the conservation of the native mollusks fauna and the control of invasive species. They can also help to direct more studies in order to understand this diversity and to review the lists of endangered species.

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Anexo 3 –
Publicações resultantes da tese:

Pereira, D. et al., 2012. Planejamento experimental para a seleção de métodos de controle populacional de moluscos invasores. In Mansur, M. C. D., C. P. Santos, D. Pereira, I. C. P. Paz, M. L. L. Zurita, M. T. R. Rodriguez, M. V. Nehrke & P. E. A. Bergonci (org), Moluscos Límnicos Invasores no Brasil: Biologia, Prevenção, Controle. Redes Editora, Porto Alegre: 279-293.

CAPÍTULO 26

Planejamento experimental para a seleção de métodos de controle populacional de moluscos invasores

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Sávio Henrique Calazans Campos
Livia Viana de Godoy Fernandes
Isabel Cristina Padula Paz
Cintia Pinheiro dos Santos
Flavio da Costa Fernandes
Maria Teresa Raya Rodriguez
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Quando um cientista elabora uma hipótese de trabalho é necessário que estabeleça critérios que validem de forma irrefutável se a mesma é válida ou não, e é neste ponto que o delineamento experimental entra no processo, visto que experimentos mal projetados ou mal conduzidos podem levar a conclusões errôneas.

O delineamento experimental é a base onde está apoiado todo o sistema científico, e consiste no planejamento e condução de experimentos de modo que seja possível o recolhimento de dados que possam ser analisados, usando métodos estatísticos apropriados e que conduzam a conclusões válidas e objetivas.

O desenvolvimento e adaptação de tecnologias que promovam o controle populacional de espécies invasoras, com a minimização de impacto de subprodutos e metabólitos tóxicos, requerem métodos científicos adequados. Para tal, a correta abordagem experimental requer um planejamento otimizado visando obter respostas rápidas e precisas quanto à eficácia de métodos de controle, dosagens adequadas e suas implicações ambientais.

As espécies de moluscos invasores límnicos que têm sido alvo de preocupação quanto aos impactos econômicos são *Limnoperna fortunei* (Dunker, 1857), *Corbicula largillierti* (Philippi, 1844) e *Corbicula fluminea* (Müller, 1774). Portanto, a maior parte do conhecimento experimental resulta de projetos de pesquisa e desenvolvimento no controle destes bivalves. Desta forma muitos dos exemplos citados neste capítulo se referem a estas espécies, mas podem ser utilizados como referência no planejamento de experimentos que visem testar métodos de controle para outras espécies invasoras.

1. Tipos de experimentos

A experimentação do uso de substâncias químicas, radiações, ondas sonoras ou até mesmo, inimigos naturais, no controle de moluscos invasores, pode ser realizada de diferentes formas com diferentes métodos e tempos de execução. O objetivo, o custo e viabilidade são as características que costumam limitar os experimentos (Zagatto & Bertoletti, 2006).

Gambetta (2011) define muito bem as fases de uma pesquisa experimental desde as fases de laboratório até a sua aplicação na indústria, como segue:

* **Escala de bancada.** Os experimentos conduzidos em laboratório são geralmente referenciados como “em escala de bancada” e se caracterizam pela escala reduzida de uma situação hipoteticamente real. Em linhas gerais uma boa fase de pesquisa em bancada gera resultados sólidos e confiáveis que permitem afirmar que a tecnologia é promissora.

* **Escala piloto.** Os estudos em escala piloto são a solução adotada para sanar os limitantes encontrados em escala de bancada. O principal entrave à utilização dessas plantas-piloto são os custos envolvidos no desenvolvimento, montagem e operação de tais unidades. Esses custos, entretanto, são ordens de grandeza acima dos investimentos na montagem de uma unidade de bancada, mas muito inferiores aos de uma tentativa frustrada de construir uma planta industrial com base em premissas equivocadas ou em informações obtidas em escala de bancada.

* **Escala industrial.** A partir do projeto da planta-piloto e das informações obtidas ao longo de sua operação, pode-se iniciar um projeto de planta industrial, levando em conta as características técnicas e econômicas, que permitirão construir uma planta industrial competitiva. O marco final de uma pesquisa científica bem sucedida é exatamente quando essa nova tecnologia é adotada em uma planta industrial de forma que seja competitiva frente a outros processos e ou produtos e se complete o ciclo da inovação. Dessa forma, recupera-se o investimento realizado na pesquisa e no desenvolvimento, garantindo a sustentabilidade do empreendimento em termos econômicos, ambientais e sociais.

2. Fases de desenvolvimento do organismo alvo

O planejamento de experimentos com moluscos invasores límnicos implica em uma primeira pergunta: qual fase de desenvolvimento do animal deve ser exposta ao agente controlador em meu experimento? Os moluscos límnicos invasores (bivalves e gastrópodes) apresentam uma fase planctônica, na forma larval, e, duas fases bentônicas: recruta e adulta. A escolha das fases adequadas para a experimentação deve considerar uma série de fatores, dentre eles, a disponibilidade da mesma no ambiente aquático para coleta. A Tabela I discrimina as vantagens e desvantagens de cada fase em experimentos de seleção de agentes controladores.

3. Manutenção dos organismos-alvo em laboratório

Escolhida a fase a ser testada em um experimento, um novo desafio surge: como manter o organismo vivo em meu laboratório?

Até o momento não foi possível reproduzir o mexilhão-dourado em laboratório, assim como as espécies do gênero *Corbicula*. Desta forma, os organismos-teste não são reproduzidos, mas apenas mantidos em laboratório sob condições adequadas à sua sobrevivência. O sucesso da manutenção de organismos-alvo em laboratório depende de várias etapas desde sua coleta, transporte e manutenção para a sobrevida, até o seu uso.

3.1. Coleta do organismo-alvo

A coleta de larvas de *L. fortunei* é feita diretamente no plâncton e as amostras devem ser transportadas sob refrigeração (ver Capítulos 10 e 11). Alguns cuidados devem ser tomados durante o transporte de indivíduos adultos: no caso de espécies do gênero *Corbicula*, o ideal é coletar os organismos e enrolar em algodão ou gaze umedecida e acondicioná-los em potes plásticos, que são posteriormente colocados em isopor com gelo em escamas. Desta forma se reduz o metabolismo do animal, que não realizará a filtração. E não havendo água não se observa efeitos da degradação da qualidade da mesma sobre os bivalves. Esta forma de acondicionamento é apropriada para larvas de espécies do gênero *Corbicula*, que tem curta permanência no plâncton. Quando o animal é desembalado e colocado em bandeja com água reconstituída (ver item 4.2.3 deste capítulo) acrescida de alimento com base em algas e ração de peixe, as larvas são liberadas logo em seguida na bandeja e po-

Tabela I. Vantagens e desvantagens do uso de diferentes fases de desenvolvimento de moluscos invasores em experimentos visando à seleção de métodos de controle populacional.

Fases	Vantagens	Desvantagens
Larvas	A coleta é facilmente realizada com rede de plâncton. É a fase inicial do desenvolvimento, desta forma o controle das larvas inibe a incrustação ou acumulação. Poderá requerer concentrações ou doses letais menos elevadas.	A presença de larvas no plâncton pode ser determinada pela sazonalidade. Indivíduos muito pequenos dificultando a avaliação da letalidade. Quando grandes volumes de água são tratados, a seleção e quantificação de organismos são mais difíceis. A utilização de amostras concentradas de plâncton nos experimentos impossibilita a utilização de um número padrão de indivíduos gerando muita variabilidade nos dados. Difícil manutenção em laboratório o que implica em coleta de organismos a cada experimento.
Recrutas	Organismos recrutados em substratos artificiais tem tamanho mais uniforme do que indivíduos recrutados em substratos naturais. É uma das fases de maior mobilidade, sendo interessante compreender a ação dos métodos de controle nesta fase. É possível padronizar o número de indivíduos nos testes com facilidade. Manutenção em laboratório é possível.	A presença de recrutas no macrofauna bentônica pode ser determinada pela sazonalidade. O recrutamento de organismos incrustantes ocorre em substratos artificiais num tempo mínimo de exposição de três meses. Indivíduos muito pequenos dificultando a avaliação da letalidade.
Adultos	A coleta é facilmente realizada manualmente ou por meio de amostradores e substratos artificiais. Indivíduos grandes facilitam a avaliação da letalidade. Organismos recrutados em substratos artificiais tem tamanho mais uniforme do que indivíduos recrutados em substratos naturais. O controle dos adultos inibe a produção larval. Os organismos podem ser coletados durante todo o ano. É possível padronizar o número de indivíduos nos testes com facilidade. Manutenção em laboratório é possível.	Requer maiores cuidados com manutenção (alimentação, renovação do meio, etc). Poderá requerer concentrações ou doses letais mais elevadas.

dem ser facilmente removidas com pipeta de *Pasteur*. Pouco se conhece sobre a reprodução destes organismos sendo difícil reproduzi-los em laboratório.

Quanto ao mexilhão-dourado (*L. fortunei*), com base no conhecimento de sua capacidade de resistência ao dessecamento (Montalto & Drago, 2003), o transporte sem a imersão em água oferece uma condição adequada sem perdas consideráveis (Campos, 2009). Transporte similar ao relatado para os bivalves do gênero *Corbicula* também podem ser realizados desde que os aglomerados sejam bem lavados e desmembrados, cuidando-se para não danificar o pé do animal no momento da desagregação. O transporte em água é possível, mas requer atenção à degradação da qualidade da mesma que depende do tempo de deslocamento.

3.2. Condições de manutenção

A manutenção do mexilhão-dourado em laboratório depende do controle da qualidade da água, a qual está diretamente relacionada a alguns parâmetros tais como temperatura (24-26ºC), pH (6,5-7,5), oxigenação (Saturado), acúmulo de metabólitos (troca de água).

3.3. Alimentação

As relações ideais para sustentar uma população de mexilhões em função de volumes de água não são definitivas. Em seu estudo, Campos (2009) utiliza caixa de água para manutenção e aclimatação dos organismos em laboratório, alimentando-os com um composto à base de *Saccharomyces cerevisae* fornecidas duas vezes ao dia e complementada com as microalgas *Ankistrodesmus sp.* e *Pseudokirchneriella subcapitata*

3.4. Cuidados de biossegurança: o que fazer para o organismo não fugir do laboratório?

Quanto à biossegurança, deve-se adotar medidas para a manipulação adequada de agentes biológicos, químicos e físicos para prevenir acidentes e reduzir riscos inerentes às atividades desenvolvidas. Tratando-se de um organismo invasor torna-se necessário adotar práticas para a sua contenção dentro do laboratório, principalmente em áreas que tenham ambientes não invadidos e propícios para que o mexilhão possa se estabelecer (rios, lagos e lagoas). A adoção de boas práticas laboratoriais é essencial para que se evite a dispersão de larvas, juvenis ou mesmo adultos na drenagem urbana. Algumas práticas recomendadas para manter um nível adequado de biossegurança e evitar a dispersão deste organismo para outros corpos hídricos são listadas a seguir.

* Capacitação das pessoas que manipulam os moluscos invasores;

* Controle do acesso ao laboratório de experimentos, cultivo/manutenção;

* Limpeza adequada dos estabelecimentos e equipamentos do laboratório com agentes (substância oxidante) minimizando a possibilidade de transporte de larvas e juvenis;

* Uso de EPIs, vidrarias e equipamentos minimizando a possibilidade de dispersão do organismo para fora da área controlada do laboratório;

* Tratar a água descartada do cultivo, que deve ser renovada a toda semana, tratar descartes de resíduos, como conchas e animais mortos, com substâncias oxidantes;

* Controlar e tratar efluentes mantendo um sistema sanitário diferenciado.

4. Planejando um experimento

O planejamento do experimento começa com a seleção adequada dos indivíduos da espécie-alvo, sua adequada manutenção em sistema de cultivo, tipo de meio de cultivo, desenho experimental (delineamento), escolha dos testes estatísticos a análise de dados, e, finalmente, a validação dos métodos com base em testes ecotoxicológicos, visando avaliar os possíveis danos ambientais potenciais do tipo de método de controle populacional sobre a biota aquática ou até mesmo sobre operadores do sistema de controle. A desconsideração de qualquer um destes passos pode invalidar os dados obtidos em um experimento mal planejado.

Figura 1. Sistema de tanques para manutenção de mexilhões em laboratório (Características: 500 Litros; 24-26°C; pH: 6,5-7,5; Oxigênio saturado por aeração constante; Circulação de água constante; Filtração em sistema de filtro biológico e substituição semanal de um terço do volume dos tanques) (Campos, 2009).

4.1. Seleção e preparação dos organismos alvos

Para experimentos com larvas do mexilhão-dourado, são geralmente escolhidas larvas véliger de charneira reta e véliger umbonada de acordo com Santos et al. (2005). Para os experimentos com adultos, dentre os critérios de seleção, devem ser considerados além do tamanho (Fig. 2), características vitais como produção de bisso, filtração e locomoção. Os organismos que não produzem bisso ou que apresentam suas conchas abertas sem atividade filtrante devem ser descartados. No caso de organismos adultos, é aconselhável a limpeza das conchas com escova de dente para que se removam algas perifíticas com potencial de desenvolvimento dentro da unidade experimental.

4.2. Meio de Cultivo

No caso dos organismos aquáticos o meio de cultivo é o tipo de água na qual o mesmo vai permanecer durante todo o experimento. A qualidade desta água implica em diferentes interferências nos resultados finais do experimento. Portanto a escolha de um determinado meio de cultivo deve considerar os objetivos do experimento, o tempo de duração do mesmo, a viabilidade técnica e possíveis implicações da qualidade do meio sobre o desenvolvimento e manutenção do organismo alvo e na qualidade dos resultados.

4.2.1. Água bruta

A utilização da água bruta em experimentos tem como objetivo avaliar a interferência da qualidade da água do local sobre o método de controle (físico, químico ou biológico). A água bruta pode ser um meio utilizado em testes de bancada e estação piloto. Santos, C. P. (2011) avaliou a ação da luz ultravioleta sobre larvas do mexilhão-dourado em água bruta em experimento utilizando estação-piloto, com o objetivo de avaliar a relação da turbidez com a eficiência do tratamento. Soares et al. (2009) utilizaram água bruta para avaliar a toxicidade do sulfato de cobre sobre indivíduos adultos do mexilhão-dourado em testes de bancada. Os autores escolheram utilizar água bruta, devido à presença de sólidos suspensos. A presença de sólidos na água é um fator determinante para a incorporação de metais por organismos filtradores (Callil & Junk, 1999).

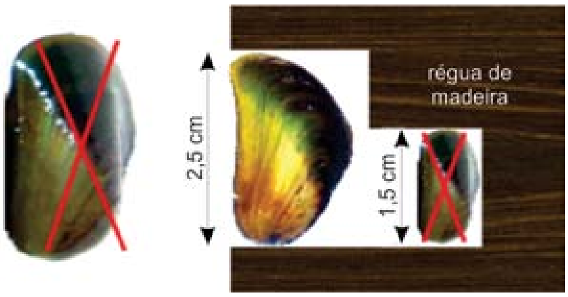


Figura 2. Seleção de tamanho de *L. fortunei* para experimentos em laboratório (Fernandes & Coutinho, 2008).

4.2.2. Água deionizada

A utilização da água deionizada em experimentos busca eliminar a interferência da qualidade da água sobre o método de controle (físico, químico ou biológico). A água deionizada pode ser utilizada em testes de bancada e estação-piloto, onde o tempo de residência do fluido nos canos e muito pequeno e o experimento de curto período de duração. Santos, C. P. (2011) avaliou a ação da luz ultravioleta sobre larvas do mexilhão-dourado em água deionizada, em experimento utilizando estação-piloto, com o objetivo de eliminar turbidez e aumentar eficiência do tratamento. A desvantagem da água deionizada é que pode causar desequilíbrio osmótico nos organismos-alvo mais sensíveis, principalmente em experimentos com maior duração. No entanto, Santos, C. P. (2011) não detectou diferenças significativas quanto à mortalidade entre grupos controle com água bruta e água deionizada em seus experimentos.

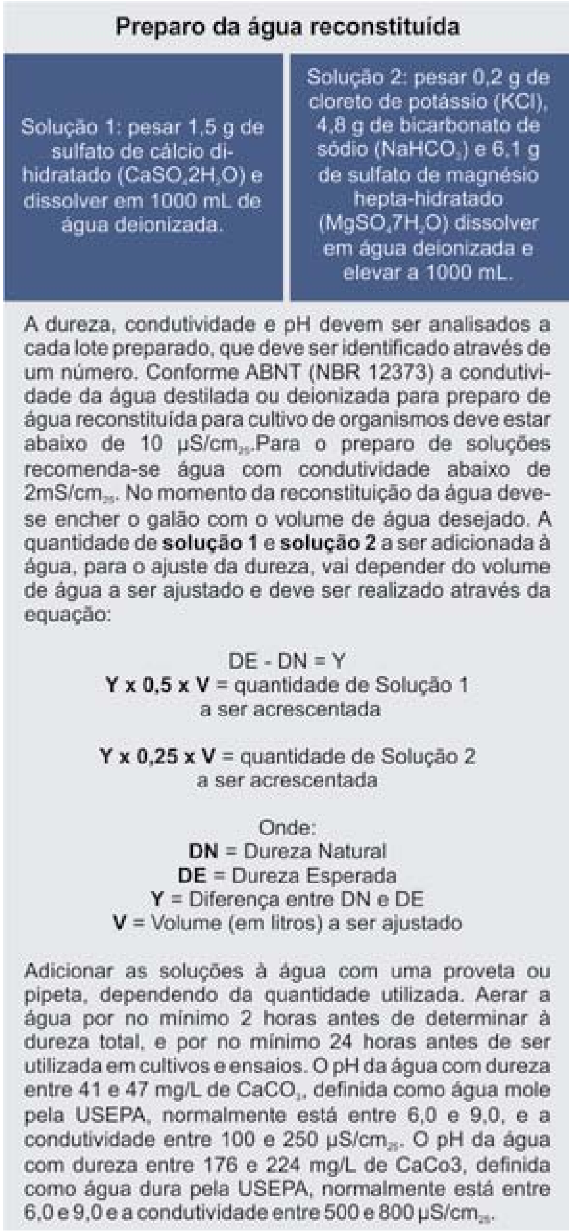
4.2.3. Água reconstituída

O uso de água reconstituída (Fig. 3) em ensaios com organismos aquáticos é padrão em ensaios ecotoxicológicos, pois suas características físico-químicas são mais estáveis devido ao tamponamento. Águas podem se reconstituídas a partir de águas brutas ou águas deionizadas. Desta forma as características químicas das águas são ajustadas para aquelas desejadas no experimento. No caso da reconstituição da água a partir da água deionizada, é garantida a ausência de matéria orgânica, que pode degradar-se e alterar a qualidade da água. Pereira et al. (2011b) utilizaram água reconstituída para a realização de testes visando à seleção de agentes microbianos no controle de *L. fortunei*.

4.3. Delineamento

4.3.1. Número de indivíduos

O número de indivíduos usados em experimentos necessita ser considerado em função da variabilidade e representatividade obtida dentro das análises estatísticas a serem adotadas. Estudos de experimentos desenhados para cálculos de concentração letal (CL_{50}) com o mexilhão-dourado geralmente utilizam um número de 10 ou 20 indivíduos em todas as réplicas e de 3 a 5 replicações das concentrações (Patrício et al., 2003; Soares et al., 2009; Campos, 2009). Pereira et al. (2011b) utilizaram 10 indivíduos e 5 replicações para cada tratamento. Um caminho a ser adotado antes da definição do delineamento do experimento é realizar experimentos pilotos com 10, 20 ou 30 indivíduos e 3 a 5 replicações das concentrações e escolher o modelo mais otimizado do experimento com menor variação dos dados.



Preparo da água reconstituida

Solução 1: pesar 1,5 g de sulfato de cálcio di-hidratado ($CaSO_4 2H_2O$) e dissolver em 1000 mL de água deionizada.

Solução 2: pesar 0,2 g de cloreto de potássio (KCl), 4,8 g de bicarbonato de sódio ($NaHCO_3$) e 6,1 g de sulfato de magnésio hepta-hidratado ($MgSO_4 7H_2O$) dissolver em água deionizada e elevar a 1000 mL.

A dureza, condutividade e pH devem ser analisados a cada lote preparado, que deve ser identificado através de um número. Conforme ABNT (NBR 12373) a condutividade da água destilada ou deionizada para preparo de água reconstituída para cultivo de organismos deve estar abaixo de 10 $\mu S/cm_{25}$.Para o preparo de soluções recomenda-se água com condutividade abaixo de 2mS/cm_{25}. No momento da reconstituição da água deve-se encher o galão com o volume de água desejado. A quantidade de **solução 1** e **solução 2** a ser adicionada à água, para o ajuste da dureza, vai depender do volume de água a ser ajustado e deve ser realizado através da equação:

DE - DN = Y
Y x 0,5 x V = quantidade de Solução 1
a ser acrescentada

Y x 0,25 x V = quantidade de Solução 2
a ser acrescentada

Onde:
DN = Dureza Natural
DE = Dureza Esperada
Y = Diferença entre DN e DE
V = Volume (em litros) a ser ajustado

Adicionar as soluções à água com uma proveta ou pipeta, dependendo da quantidade utilizada. Aerar a água por no mínimo 2 horas antes de determinar à dureza total, e por no mínimo 24 horas antes de ser utilizada em cultivos e ensaios. O pH da água com dureza entre 41 e 47 mg/L de $CaCO_3$, definida como água mole pela USEPA, normalmente está entre 6,0 e 9,0, e a condutividade entre 100 e 250 $\mu S/cm_{25}$. O pH da água com dureza entre 176 e 224 mg/L de CaCo3, definida como água dura pela USEPA, normalmente está entre 6,0 e 9,0 e a condutividade entre 500 e 800 $\mu S/cm_{25}$.

Figura 3. Procedimento para a preparação de água reconstituída.

4.3.2. Repetição

O experimento deve ser repetido no mínimo três vezes para validação dos resultados, confirmando que os mesmos são devido ao agente testado, e não fruto do acaso.

4.3.3. Controle negativo e positivo

É fundamental que todo planejamento de experimento inclua um controle (testemunha) que seja mantido sobre as mesmas condições dos organismos-alvo, apenas sem a inserção do composto/organismo a ser avaliado. Esse tipo de controle também é chamado controle negativo. Em ensaios onde já são conhecidos compostos ou organismos que não apresentem efeitos sobre o organismo-alvo (efeito neutro), esses são utilizados nas mesmas condições de todas as réplicas do ensaio, sendo denominado controle positivo.

4.3.4. Aleatorização

Impedir que a heterogeneidade de fatores ambientais que ocorrem de forma diferencial no espaço possam influenciar os resultados dos ensaios.

4.3.5. Condições ambientais da sala de experimentos

Por se tratar de experimentos com organismos aquáticos não é necessário controle da umidade da sala. A temperatura da sala deve permanecer entre 21 e 22°C. Não é necessária a iluminação (fotoperíodo), já que as condições de aplicação em campo, onde as incrustações ocorrem muitas vezes em tubulações e equipamentos, não apresentam luminosidade.

4.3.6. Exemplos de experimentos

São descritos a seguir alguns modelos de experimentos realizados para selecionar métodos de controle de moluscos invasores.

4.3.6.1. Controle biológico: seleção de agentes microbianos

Um exemplo de experimento, em escala de bancada, para a avaliação da ação de agentes microbianos e ou produtos formulados sobre indivíduos adultos do mexilhão-dourado é descrita a seguir (Fig. 4).

4.3.6.2 Controle físico

Dentre os métodos de controle físico são descritos abaixo, dois exemplos de experimentos, um com ondas ultrassônicas e outro com luz ultravioleta.

4.3.6.2.1. Ultrassom

Um exemplo de experimento, em escala de bancada, para a avaliação da ação de ondas ultrassônicas sobre larvas de *L. fortunei* e *C. fluminea* é descrita a seguir (Fig. 5).

4.3.6.2.2. Luz ultravioleta (UV)

Um exemplo de experimento, em escala piloto, para avaliação da ação germicida de luz ultravioleta sobre larvas do mexilhão-dourado é descrita a seguir (Fig. 6) de acordo com Santos, C. P. (2011).

4.3.6.3. Controle químico: substâncias moluscidas

Um exemplo de experimento, em escala de bancada, para a avaliação da ação de um moluscida (sulfato de cobre) sobre indivíduos adultos de *L. fortunei* é descrito a seguir (Fig. 7), de acordo com Soares et al. (2009). O exemplo descrito pode ser adaptado para avaliação de outras substâncias químicas.

5. Avaliação

A avaliação dos resultados dos experimentos requer, primeiramente, o estabelecimento de critérios de avaliação da mortalidade, bem como cálculos e procedimentos estatísticos adequados para consolidar o experimento através da correta interpretação dos resultados,

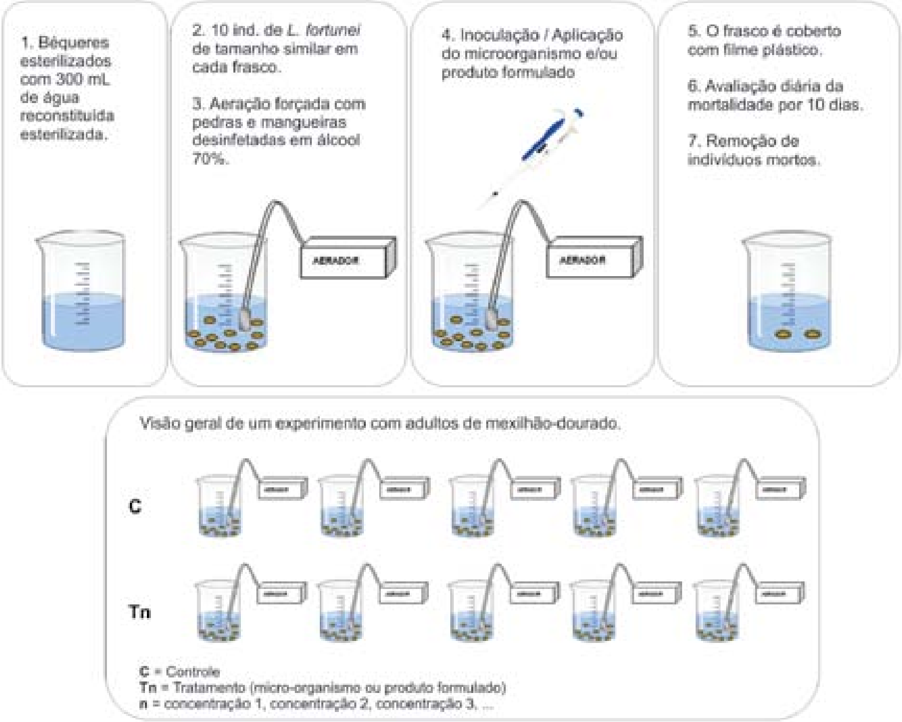


Figura 4. Procedimento para a preparação de experimento para seleção de agentes microbianos.

1. Coleta de organismos testes

* Primeiramente é necessário coletar larvas no ambiente e quantificá-las (procedimento descrito no Capítulo 10).

2. Concentração Teste (CT)

Béqueres de 1000 mL são preenchidos com água filtrada do local com larvas em uma concentração conhecida.

3. Experimento

- Sondas de aparelhos de diferentes frequências são aplicados à solução, sendo anotada a mortalidade (seis réplicas por frequência).
- Selecionada a frequência que provoca a maior mortalidade, são testados diferentes volumes (ex: 0,5L; 1L; 1,5L; 2L; etc.).
- Cada volume é novamente testado em diferentes tempos de imersão da sonda na solução.
- Para cada tempo e volume são testadas diferentes potências.
- O cálculo da dosagem é feito considerando-se o volume, o tempo e a potência (ver Capítulo 35).
- Deve-se repetir o experimento no mínimo seis vezes em cada dosagem e também no controle.

4. Avaliação da mortalidade

* Imediatamente, ao término do experimento, as larvas são pipetadas do fundo do béquer e são avaliadas quanto à mortalidade; cada larva avaliada é retirada da amostra com uma pipeta de *Pasteur*, evitando-se assim a recontagem de um mesmo indivíduo.

Figura 5. Procedimento para a preparação de experimento para avaliar a atuação de ondas ultrassônicas no controle da população larval de *L. fortunei* e *C. fluminea*.

bem como fornecer subsídios para a tomada de decisão referente à aplicação da tecnologia em campo.

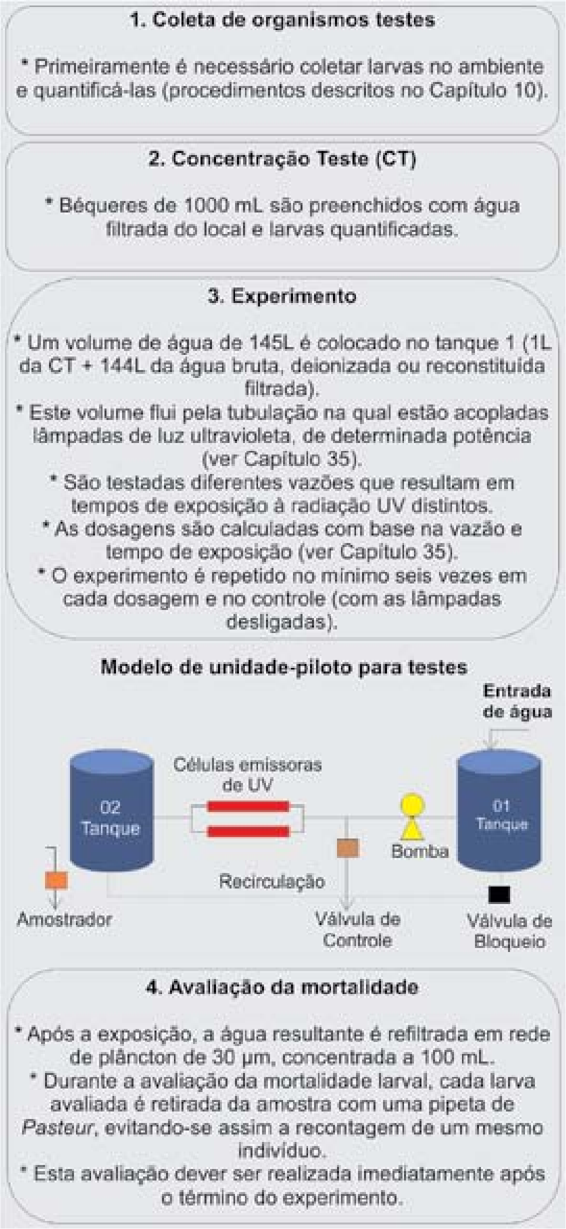
5.1. Critérios de letalidade

Testes de toxicidade realizados com mexilhões, geralmente causam uma grande variabilidade devido à capacidade de isolar-se do meio externo (Cataldo et al., 2002a; Rajagopal et al., 2003), necessitando de uma atenção maior no momento da definição da condição de vida do mexilhão, após a sua exposição a um biocida. Torna-se necessário, neste período, a observação das reações vitais do mexilhão o qual, muito vezes, permanece em estado de defesa, mantendo as valvas fechadas. Sendo assim, alguns estudos inserem um período (geralmente 48h), após a exposição, para confirmar as reações vitais dos organismos sobreviventes. Dentro deste período consideram a morte do organismo, ao confirmar sua inércia, falta de reação a estímulos (como um toque com bastão de vidro) e, também, apresentar valvas abertas e o manto exposto (Darrigran & Damborenea, 2001; Campos, 2009; Soares et al., 2009).

Santos, C. P. (2011) avalia a mortalidade de larvas do mexilhão-dourado com base nos critérios de mobilidade, adução valvar e ausência de batimentos do estilete cristalino (Tab. II). Soares et al. (2009) definem alguns critérios, com base em Morton (1973), para uma avaliação quali-quantitativa do comportamento de *L. fortunei* exposto ao sulfato de cobre. Com esses critérios os autores buscaram não apenas avaliar a mortalidade, mas compreender a ação da substância sobre o comportamento do molusco (Tab. II).

5.2. Confirmação da ação letal de microrganismos

Após a constatação da morte de um organismo-alvo é necessário confirmar se este foi morto realmente pelo microrganismo inoculado. Uma maneira clássica é o reisolamento do microrganismo após a inoculação do organismo-alvo em um meio de cultura apropriado para o crescimento do microrganismo testado



1. Coleta de organismos testes

* Primeiramente é necessário coletar larvas no ambiente e quantificá-las (procedimentos descritos no Capítulo 10).

2. Concentração Teste (CT)

* Béqueres de 1000 mL são preenchidos com água filtrada do local e larvas quantificadas.

3. Experimento

* Um volume de água de 145L é colocado no tanque 1 (1L da CT + 144L da água bruta, deionizada ou reconstituída filtrada).
* Este volume flui pela tubulação na qual estão acopladas lâmpadas de luz ultravioleta, de determinada potência (ver Capítulo 35).
* São testadas diferentes vazões que resultam em tempos de exposição à radiação UV distintos.
* As dosagens são calculadas com base na vazão e tempo de exposição (ver Capítulo 35).
* O experimento é repetido no mínimo seis vezes em cada dosagem e no controle (com as lâmpadas desligadas).

Modelo de unidade-piloto para testes

4. Avaliação da mortalidade

* Após a exposição, a água resultante é refiltrada em rede de plâncton de 30 µm, concentrada a 100 mL.
* Durante a avaliação da mortalidade larval, cada larva avaliada é retirada da amostra com uma pipeta de *Pasteur*, evitando-se assim a recontagem de um mesmo indivíduo.
* Esta avaliação dever ser realizada imediatamente após o término do experimento.

Figura 6. Procedimento para a preparação de experimento para avaliar a atuação de radiação ultravioleta no controle da população larval de *L. fortunei* e *C. fluminea*.

(Fig. 9). Esta confirmação também pode ser feita por métodos moleculares e histológicos (Molloy & Mayer, 2007).

5.3. Interpretação de resultados

Em ensaios de avaliação de produtos e/ou microrganismos para o controle de pragas se utilizam alguns cálculos padrões e procedimentos estatísticos que permitem a inferência sobre a efetividade dos mesmos sobre a praga-alvo.

5.3.1. Mortalidade absoluta (MA)

Número absoluto de indivíduos mortos no experimento para cada tratamento (Alves, 1998).

5.3.2. Mortalidade corrigida (MC)

Considera a mortalidade ocorrida no tratamento-testemunha (sem aplicação do agente estressor) no cálculo. A correção da mortalidade pode ser feita pelo uso da fórmula de Abbott, como segue abaixo, (Alves, 1998).

Importante destacar que experimentos com mortalidade maior de 10% no tratamento controle devem ser excluídos e repetidos.

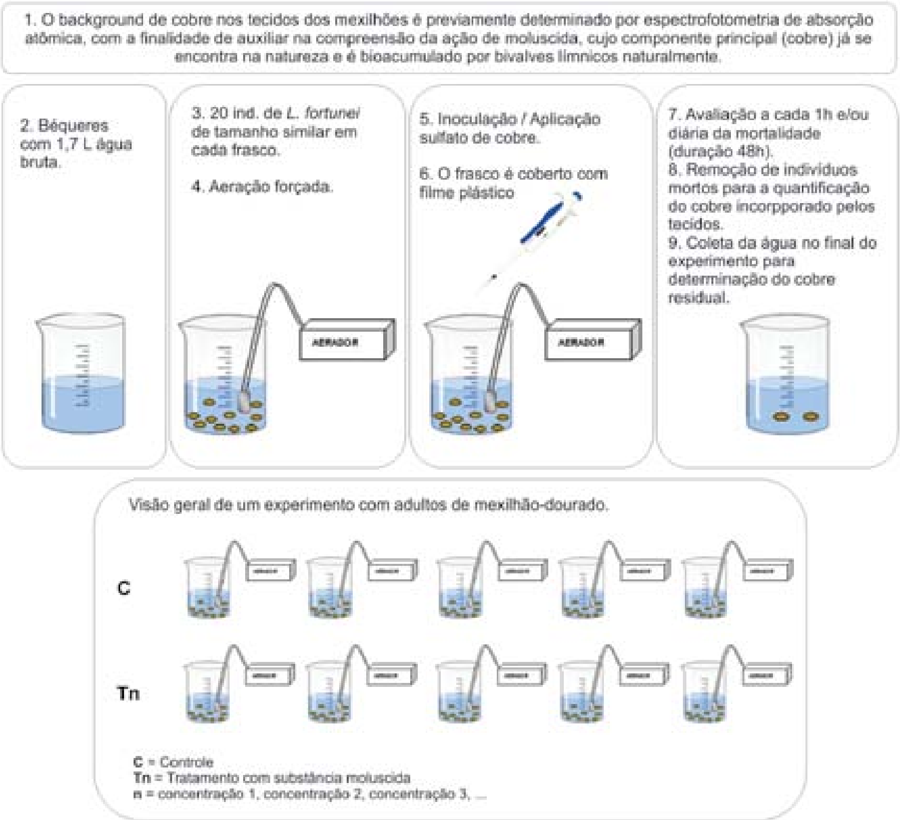
$$MC = \frac{\text{\% Mortalidade no Tratamento} - \text{\% Mortalidade no Testemunho}}{100 - \text{\% Mortalidade no Testemunho}}$$

5.3.3. Relação dose-resposta ou concentração-resposta

Descreve a mudança em efeito sobre um organismo causado por diferentes níveis de exposição (ou concentrações) a um estressor (que pode ser químico, físico ou biológico), após certo tempo de exposição (Crump et al., 1976). O termo **dose** pode ser utilizado quando se sabe exatamente a quantidade de substância a que os organismos foram submetidos, quando não se conhece a quantidade de agente estressor que atingiu diretamente o organismo-alvo, o termo correto é **concentração** (Alves, 1998). Em experimentos com substâncias químicas, ondas ultrassônicas e radiações ultravioleta, é possível obter a dosagem. Já aqueles realizados com agentes microbianos, apenas a concentração é obtida.

O estudo de dose-resposta e desenvolvimento de modelos de dose-resposta é primordial para determinar as doses “seguras” e “letais” das substâncias as quais os organismos são submetidos.

Graficamente, os dados de dose-resposta são demonstrados em uma curva de dose-resposta como um gráfico X-Y relacionando a magnitude do agente de controle (ex.: concentração de bactérias/ml, dose radiação ultravioleta) à resposta dos organismos (no caso, mexilhão-dourado). A resposta é avaliada como


1. O background de cobre nos tecidos dos mexilhões é previamente determinado por espectrofotometria de absorção atômica, com a finalidade de auxiliar na compreensão da ação de moluscida, cujo componente principal (cobre) já se encontra na natureza e é bioacumulado por bivalves límnicos naturalmente.

2. Béqueres com 1,7 L água bruta.

3. 20 ind. de *L. fortunei* de tamanho similar em cada frasco.

4. Aeração forçada.

5. Inoculação / Aplicação sulfato de cobre.

6. O frasco é coberto com filme plástico

7. Avaliação a cada 1h e/ou diária da mortalidade (duração 48h).
8. Remoção de indivíduos mortos para a quantificação do cobre incorpporado pelos tecidos.
9. Coleta da água no final do experimento para determinação do cobre residual.

Visão geral de um experimento com adultos de mexilhão-dourado.

C = Controle
Tn = Tratamento com substância moluscida
n = concentração 1, concentração 2, concentração 3, ...

Figura 7. Procedimento para a preparação de experimento para avaliar a atuação de substâncias químicas no controle da população adulta de *L. fortunei*.

Figura 8. Mexilhões mortos após infecção por microrganismo (isolado Bb7B) e reisolamento em placa com meio de cultura. Fotos: A.S. de Oliveira e D. Pereira.

Tabela II. Indicadores comportamentais e de letalidade para *L. fortunei* em experimentos: larvas de acordo com Santos, C. P. (2011) e adultos de acordo com Soares et al. (2009), com base em Morton (1973).

Indicadores	Definição
Larvas	
M	Presença de mobilidade (M).
AV	Adução valvar após estímulo mecânico.
AB	Ausência dos batimentos do estilete cristalino após estímulo mecânico.
Adultos	
M	Número de indivíduos em deslocamento (M) pela superfície de vidro do aquário.
IM	Número de indivíduos sésseis (IM) no aquário.
A	Número de indivíduos com valvas abertas (A).
F	Número de indivíduos com valvas fechadas (F).
DA	A densidade de indivíduos aglomerados (DA) foi obtida pelo somatório de indivíduos aglomerados dividido pelo número de aglomerados.
PE	Número de indivíduos com o pé exposto (PE).
PR	Número de indivíduos com o retraído (PR).
SE	Os sifões expostos (SE) indicam filtração ativa; os sifões são considerados expostos quando ultrapassam a borda posterior da concha.
SR	Os sifões retraídos (SR) indicam filtração não ativa; os sifões são considerados não expostos quando não ultrapassam a borda posterior da concha.
RTP	A reação ao toque positiva (RTP) é indicada pela movimentação das valvas ou pela retração do pé ou sifões, por meio do contato com a extremidade de um palito de madeira.
RTN	A reação ao toque negativa (RTN) é indicada quando as valvas não se fecham ou o pé e sifões não se retraem por meio do contato com a extremidade de um palito de madeira.
V	Os indivíduos vivos (V) retraem o pé e sifões, fechando as valvas, quando tocados com a extremidade de um palito de madeira; quando as valvas estão fechadas, via dissecação se observa a movimentação das brânquias ou retração do pé, quando tocados com a extremidade de uma agulha histológica; os indivíduos vivos apresentam uma cor amarela ou marrom intensa.
MO	Os indivíduos mortos (MO) não retraem o pé e sifões, nem fecham as valvas, quando tocados com a extremidade de um palito de madeira; quando as valvas estão fechadas, via dissecação não se observa movimentação das brânquias ou retração do pé, quando tocados com a extremidade de uma agulha histológica ou de um bisturi; a cor dos indivíduos mortos é esbranquiçada.

mortalidade, e pode ser expressa em números absolutos ou como porcentual de indivíduos mortos.

A dose é geralmente plotada no eixo X, enquanto a mortalidade é plotada no eixo Y. O primeiro ponto no gráfico onde a resposta é acima de zero (ou acima da resposta do tratamento controle), é denominado dose limiar.

A mortalidade também varia em função do tempo. Sendo assim, estudos preliminares devem testar diferentes tempos de exposição dependendo do objetivo do experimento e dos agentes de controle testados. No caso do controle microbiano, a ação tóxica da bactéria evolui com o passar do tempo, sendo necessário de 8 a 10 dias para se verificar uma ação efetiva (Fig. 11).

5.3.4. Concentração Letal Média (CL_{50}) e Tempo Letal Médio (TL_{50})

Análise estatística de curvas de dose resposta pode ser realizada por métodos de regressão como *Probit* e *Logit*. Além desta análise, são calculados as regressões lineares e os coeficientes de determinação, com base nos dados de mortalidade e concentrações do agente estressor. Regressão do tipo Probit é a mais utilizada para determinação da Concentração Letal Média (CL_{50}) e Tempo Letal Médio (TL_{50}) a partir das curvas de dose resposta.

Os cálculos de concentração letal (CL) determinam a quantidade necessária do agente estressor para que ocorra a mortalidade de 50% (CL_{50}) ou 95% (CL_{95}) da população ensaiada. Os cálculos de tempo letal (TL) determinam o tempo necessário de exposição do organismo-alvo ao agente estressor para que ocorra a mortalidade de 50% (TL_{50}) ou 95% (TL_{95}) da população ensaiada. Devem ser considerados os limites de confiança e a significância do teste.

A análise conjunta dos parâmetros descritivos de mortalidade absoluta e corrigida, juntamente com os dados obtidos via regressão de *Probit*, permite a visualização de quais tratamentos e concentrações são mais efetivos no controle de determinada praga-alvo (Tab. III).

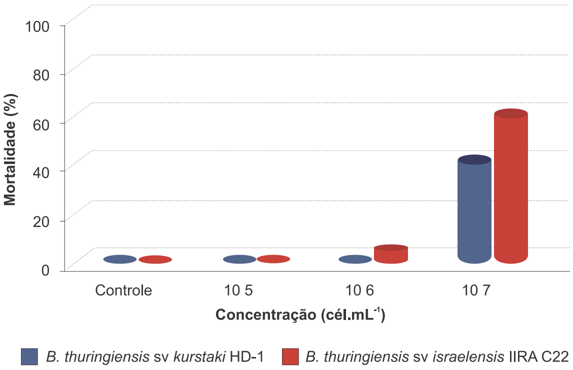


Figura 9. Mortalidade de *Limnoperna fortunei* exposto a *Bacillus thuringiensis* sv. *Israelensis* IIRAC 22 em experimento de bancada: relação dose-resposta

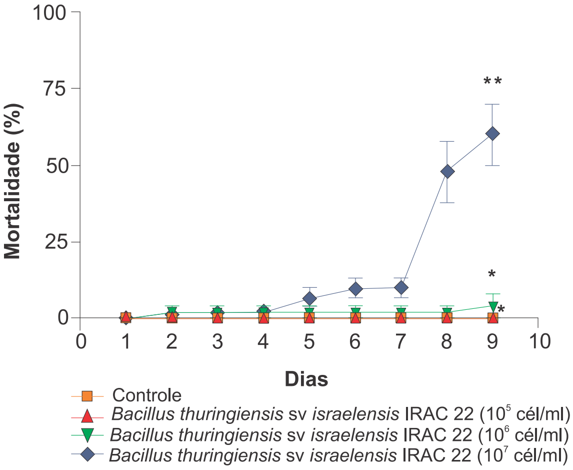


Figura 10. Mortalidade de *Limnoperna fortunei* exposto a *Bacillus thuringiensis* sv. *Israelensis* IIRAC 22 em experimento de bancada: relação dose-resposta ao longo do tempo.

5.3.5. Análise de dados

Soares et al. (2009) utilizaram diferentes abordagens na análise de dados de mortalidade e de critérios de letalidade do mexilhão-dourado exposto ao sulfato de cobre. Por meio da análise de variância (ANOVA, *Dunnet a posteriori*), com nível de significância de 95%, compararam tratamentos e controles quanto à mortalidade. Utilizaram análise multivariada para avaliar os dados obtidos pelas observações do comportamento (com base nos critérios discriminados na Tab. II) do mexilhão-dourado frente à exposição ao controlador químico em duas etapas: a primeira, análise de agrupamento (matriz de correlação de Pearson entre variáveis; agrupamento pelo método do centroide) (Fig. 12) e por meio da Análise de Componentes Principais (ACP) (Fig. 13), com a finalidade de ordenar e agrupar as variáveis que melhor explicam o comportamento; a segunda, por meio de análise de discriminante (AD) (Fig. 14), com a finalidade de discriminar os diferentes tratamentos quanto aos padrões de comportamento.

Os autores acima verificaram, por meio da ACP (Fig. 12), que os componentes 1 e 2 responderam por 55,96% da variância dos indicadores comportamentais e de letalidade. O componente 1 (35,05%) apresentou forte correlação positiva com o número de indivíduos com sifões expostos – SE (0,935); com o número de indivíduos com valvas abertas – A (0,926); com a densidade de indivíduos aglomerados – DA (0,604) e o número de indivíduos com reação ao toque positiva – RTP (0,573). Também apresentou forte correlação negativa com o número de indivíduos com sifões não expostos – SNE (-0,935); o número de indivíduos com valvas fechadas – F(-0,926); com o número de indivíduos com reação ao toque negativa – RTN (-0,641) e com concentrações de sulfato de cobre utilizadas – C (-0,600). O componente 2 (20,91%) apresentou forte correlação positiva com o número de indivíduos mortos – MO (0,949); com a temperatura do aquário –T (0,865) e com o tempo de exposição – TE (0,844). Este componente também apresentou forte correlação negativa com o número de indivíduos vivos – V (-0,949). A ACP (Fig. 12) ordenou os indicadores comportamento e letalidade de *L. fortunei* em concordância com os grupos (G1 a G5) formados por meio da análise de agrupamento hierárquico (Fig. 13) dos mesmos indicadores: G1 (F, SNE, RTN e C); G2 (MO, T e TE); G3 (número de indivíduos com o pé retraído – PNE, número de indivíduos com o pé exposto – PE, número de indivíduos sésseis – IMV e o número de indivíduos em deslocamento – MV); G4 (RTP, DA, A e SE) e G5 (V). O G1 reuniu as variáveis que indicaram filtração inativa e altas concentrações de sulfato de cobre. Ao contrário do G1, o G4 reuniu variáveis que indicaram filtração ativa e a formação de aglomerados. O G2 reuniu variáveis que indicaram a mortalidade ao longo do tempo associada ao aumento da temperatura nos aquários. O G3 reuniu variáveis relacionadas à mobilidade, que não contribuíram para a descrição dos padrões de comportamento dos organismos testes, pois os mexilhões apresentaram pouca mobilidade durante os experimentos. O G5 refere-se os organismos vivos. A avaliação comportamental do mexilhão durante os experimentos permitiu definir parâmetros de comportamento para o entendimento do efeito moluscida da substância testada. Os organismos quando expostos reagiram imediatamente fechando as valvas. Após alguns minutos abriam as valvas e iniciavam novamente a atividade de filtração de forma pouco intensa, como pode ser observado por meio do nível de exposição dos sifões. No entanto, com o passar do tempo de exposição, o efeito das concentrações sobre os moluscos inibiu a atividade de filtração e a mobilidade dos mexilhões. A análise multivariada demonstrou claramente a distinção entre grupos de filtração ativa e inativa. Após a exposição ao cobre os mexilhões diminuíram a atividade de filtração, a mobilidade e a reação ao toque, demonstrando um estado letárgico. Outros indivíduos mantiveram as

Tabela III. Mortalidade corrigida de *L. fortunei* e concentração letal (CL_{50}) de duas variedades de *B. thuringiensis*. Experimentos de bancada realizados por Pereira et al. (2011b).

Tratamento	Mortalidade corrigida (%)	CL_{50}
B. thuringiensis sv. *israelensis* IRAC22 (10^7 cél./ml)	72	7,6 x 10^6 cél/mL
B. thuringiensis sv. *kurtaski* HD-1 (10^7 cél./ml)	62,5	8,65 x 10^6 cél/mL

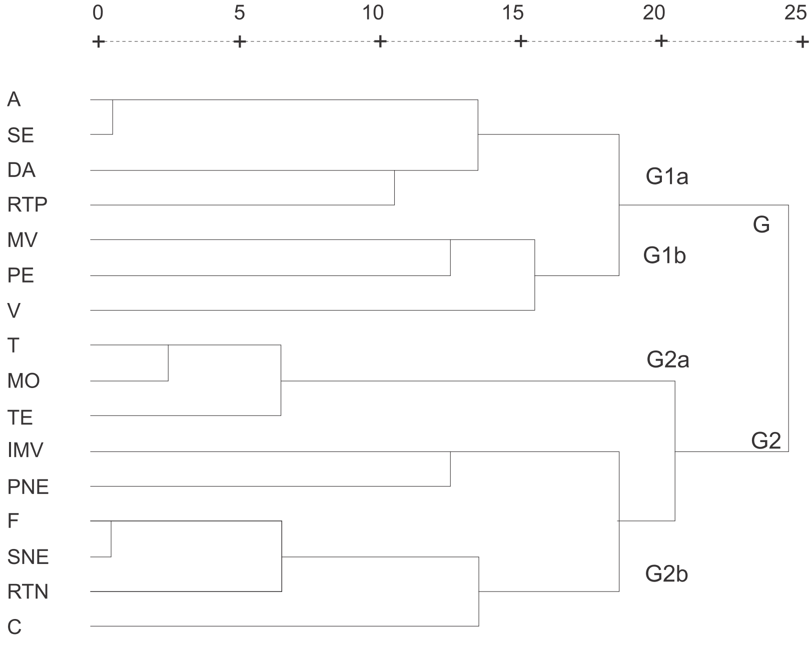


Figura 11. Análise multivariada dos indicadores comportamentais e de letalidade de *Limnoperna fortunei*: agrupamento hierárquico (método do centroide) com base em matriz de correlação (Pearson) entre os indicadores comportamentais e de letalidade (grupos 1 e 2: G1 e G2) (Fonte: Soares et al., 2009).

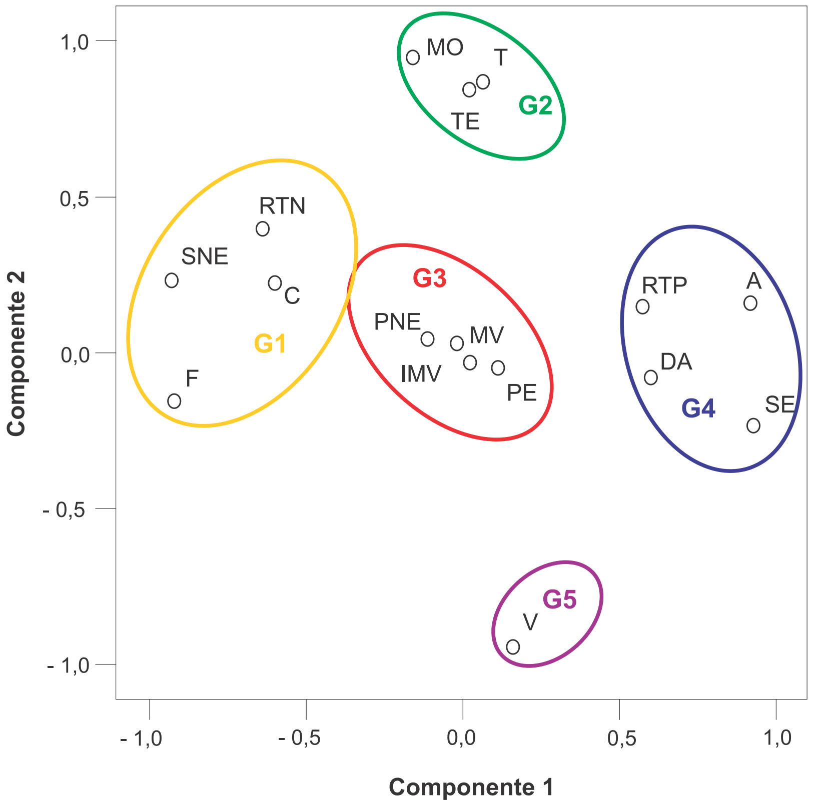


Figura 12. Análise multivariada dos indicadores comportamentais e de letalidade de *Limnoperna fortunei*. As variáveis agrupadas no dendograma ilustrado na figura anterior apresentam a mesma relação na ordenação obtida por análise de componentes principais (ACP). (grupos 1 a 4 do dendograma, G1 a G4) dos indicadores de letalidade. (Fonte: Soares et al., 2009).

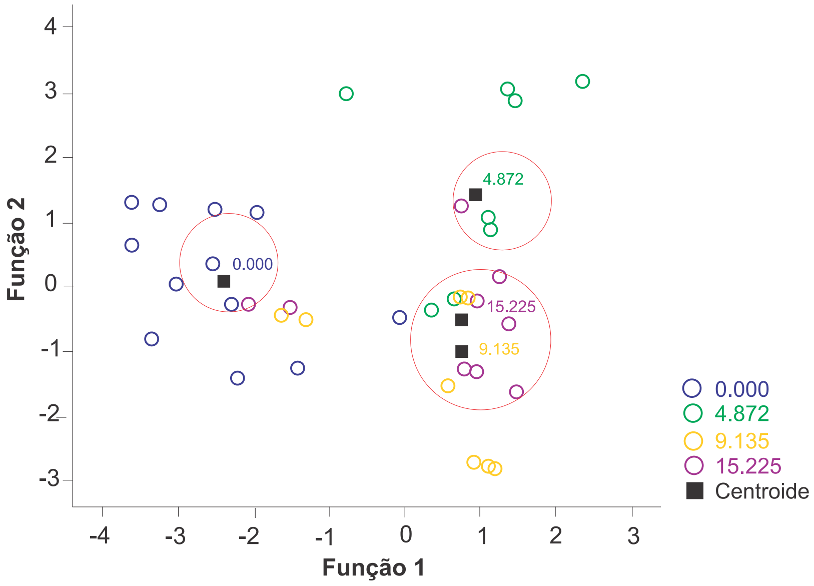


Figura 13. Ordenação (análise de discriminante canônica) dos tratamentos e controles quanto aos indicadores de comportamento e letalidade de *Limnoperna fortunei*. (Fonte: Soares et al., 2009).

valvas fechadas. Esse comportamento indicou provavelmente um mecanismo de reação do bivalve diante da sinalização da presença de uma substância de elevada toxicidade.

Por meio da AD (Fig. 14), as funções 1 e 2 responderam 94,8% da variância dos tratamentos quanto aos indicadores comportamentais e de letalidade. A função 1 (67,8%) apresentou forte correlação positiva com a variável discriminante RTN (0,464) e negativa com A (-0,600). A função 2 (27,0%) apresentou forte correlação positiva com a variável discriminante RTP (0,488) e negativa com TE (-0,331). Com base nesta análise foi possível diferenciar as observações referentes ao controle (sem adição de sulfato de cobre) do tratamento 4,872 mg L-1, e estes dos demais tratamentos (9,135 mg L-1 e 15,225 mg L-1). A avaliação proposta por meio de indicadores de comportamento e letalidade do mexilhão-dourado, durante os testes de toxicidade consistiu num complemento eficiente da avaliação da toxicidade do sulfato de cobre ao mexilhão-dourado e pode ser adaptada em experimentos com outras substâncias que causam efeitos diferenciados sobre a fisiologia e comportamento das espécies alvos. Também pode ser adaptada aos experimentos realizados com outras espécies de bivalves. Critérios específicos a espécies de gastrópodes devem ser desenvolvidos ou e/ou adaptados.

5.4. Avaliação ecotoxicológica

Duas abordagens ecotoxicológicas finalizam a avaliação e seleção de métodos de controle populacional de moluscos invasores: uma, a avaliação da toxicidade do meio (água) no qual é aplicado o tratamento; outra, a avaliação ecotoxicológica da substância moluscida ou do produto formulado.

5.4.1. Avaliação ecotoxicológica da água tratada

Visa verificar se a presença de subprodutos ou metabólitos no meio tratado confere toxicidade a organismos representantes da biota aquática. Santos, C. P. (2011) avaliou a toxicidade de água submetida à radiação ultravioleta, para o controle de larvas do mexilhão-dourado, por meio de ensaios ecotoxicológicos crônicos com organismos-teste de três níveis tróficos (*Pimephales promelas*, *Ceriodaphnia dubia* e *Pseudokirchneriella subcapitata*).

5.4.2. Avaliação ecotoxicológica de substâncias moluscidas ou produto formulado

Visa verificar se a substância moluscida ou produtos formulados apresentam toxicidade às espécies não-alvo. Várias espécies de organismos-teste não-alvo podem ser utilizadas aqui, incluindo espécies exóticas e nativas. A maioria das espécies utilizadas como organismos-teste no Brasil hoje, é exótica, mas os métodos para utilizá-las são padronizados pela ABNT, o que garante uma maior confiabilidade e repetibilidade dos resultados.

Seria interessante padronizar testes ecotoxicológicos com espécies de bivalves nativos, mas muitas dificuldades podem ser encontradas neste sentido. Um fato a se considerar é que os bivalves nativos, em sua maioria, não são facilmente criados em laboratório e seus aspectos reprodutivos são muito pouco conhecidos. No caso do mexilhão-dourado, a escolha de um organismo-teste não alvo filogeneticamente relacionado se torna impossível, uma vez que as demais espécies da família Mytilidae são todas marinhas. Quanto aos corbiculídeos, a padronização de testes com espécies do gênero *Cyanocyclas* pode ser uma alternativa, mas requer estudos prévios sobre a criação e reprodução desta espécie em laboratório. A busca de indicadores representantes das famílias Hyriidae e Mycetopodiade também se torna uma tarefa difícil, pois muitas das espécies utilizam peixes em seu desenvolvimento larval parasitário. Além disso, muitas espécies destas duas últimas famílias apresentam populações reduzidas ou enquadradas em alguma categoria de ameaça de extinção. Uma alternativa seria padronizar testes com espécies da família Sphaeriidae que são mais abundantes, não apresentam ciclo parasitário e apresentam ampla distribuição no Brasil.

Anexo 4 –
Publicações resultantes da tese:

Pereira, D., M. C. D. Mansur & D. M. Pimpão, 2012. Identificação e diferenciação dos bivalves límnicos invasores dos demais bivalves nativos do Brasil. In Mansur, M. C. D., C. P. Santos, D. Pereira, I. C. P. Paz, M. L. L. Zurita, M. T. R. Rodriguez, M. V. Nehrke & P. E. A. Bergonci (org), Moluscos Límnicos Invasores no Brasil: Biologia, Prevenção, Controle. Redes Editora, Porto Alegre: 75-94.

CAPÍTULO 5

Identificação e diferenciação dos bivalves límnicos invasores dos demais bivalves nativos do Brasil

Daniel Pereira
Maria Cristina Dreher Mansur
Daniel Mansur Pimpão

Com a introdução de espécies de moluscos límnicos invasores de origem asiática no Brasil, a busca por métodos de controle populacional, visando à minimização dos danos econômicos, tem sido alvo de investimentos prioritários pelos setores de geração de energia hidrelétrica e termoelétrica, bem como de captação e tratamento de água para abastecimento público. Os programas de controle populacional de espécies de moluscos invasores envolvem desde métodos simples, como remoção mecânica, até métodos mais complexos de controle físico (UV e Ultrassom), químico (cloração, ozonização, aplicação de sulfato de cobre, etc.) e biológico (bactérias malacopatogênicas).

A eficácia do controle populacional dos moluscos invasores requer o conhecimento prévio das características biológicas e ecológicas da espécie-alvo. E o primeiro passo é reconhecer a identidade taxonômica da espécie. Mesmo sendo as espécies invasoras muito peculiares e distintas das espécies nativas, a identificação taxonômica errônea é muito comum. Deve-se considerar que nem sempre o controle é realizado por biólogos, pois diferentes profissionais atuantes na área de meio ambiente coordenam atividades em plantas industriais e nos sistemas naturais nos quais estas estão inseridas.

Além disso, é cada vez mais preocupante o estado de conservação das espécies nativas de bivalves límnicos, que vêm sofrendo redução populacional em decorrência de diferentes atividades humanas impactantes aos ecossistemas aquáticos continentais, são elas: destruição de habitats marginais, assoreamento, alteração da qualidade da água, eutrofização, barramentos, alterações populacionais e das rotas migratórias da ictiofauna, bem como a competição por recursos e habitats com espécies de moluscos límnicos invasores.

Com base nessas considerações, tomou-se a iniciativa de elaborar uma chave dicotômica para a identificação e diferenciação dos bivalves invasores introduzidos no Brasil dos bivalves nativos encontrados no país.

A determinação específica de espécies de bivalves de água doce não é uma tarefa fácil.

Muitas espécies foram descritas para o Brasil e o grande número de sinônimos é um fato marcante, sendo necessária a revisão taxonômica deste grupo.

Estruturas e orientação da concha para estudo

As principais estruturas da concha utilizadas na diferenciação de gêneros e espécies de moluscos nativos e invasores encontram-se discriminadas na Tabela I e na Figura 1.

A orientação da concha para a tomada de medidas biométricas para fins de diferenciação estatística dos gêneros e espécies é realizada da seguinte forma: toma-se a concha (Fig. 6A), orientando-se os umbos para cima e a lúnula para frente; o ligamento e o escudo devem ficar voltados para o observador; assim, a valva direita será correspondente ao lado direito do observador e vice-versa; portanto, a região anterior estará voltada para frente e a posterior, voltada para o observador; em caso de dúvidas, observar o ligamento que é sempre posterior; para tomar as medidas de uma concha é necessário visualizar duas linhas básicas, x e y; após marcar um ponto central em cada músculo adutor, unindo-se estes pontos se obtêm a linha x; bipartindo o umbo, a linha y passa pelo bico, perpendicularmente a linha x, e finaliza na borda ventral. A largura da concha (z) é tomada com as duas valvas fechadas (Fig. 6B).

Para a diferenciação estatística de espécies e gêneros com base em medidas da concha a análise multivariada de discriminantes canônicas (ADC) é um dos procedimentos mais utilizados (ver Capítulo 6). Pereira et al. (2011a) diferenciou 11 espécies do gênero *Anodontites* com base no comprimento, altura, largura e posição do umbo. Pimpão et al. (2012) também comparou a morfometria de conchas larvais de espécies amazônicas de Hyriidae por meio do uso da ADC.

Tabela I. Termos malacológicos citados na chave dicotômica.

Termo	Definição
Apófise (a)	Projeção aderida ao septo, junto ao compartimento mais interno da cavidade umbonal, onde se fixa e se sustenta o músculo retrator do pé.
Borda da concha	Extremidade marginal das valvas.
Bico (b)	Extremidade, ápice da prodissoconcha e umbo. Pode ter direcionamento diferente do umbo (Fig. 1B, D e F).
Bisso (bi)	Filamento orgânico ou conjunto de fios fabricados pela glândula do bisso no interior do pé do animal e serve para fixá-lo ao substrato. Presente em *Limnoperna fortunei* (Fig. 2A), *Mytilopsis* e *Eupera spp.*
Borda prismática (bp)	Extremidade marginal interna das valvas, geralmente de aspecto visivelmente diferente do restante da superfície interna das valvas em Mycetopodidae.
Capacete	Prodissoconcha claramente separada e projetada formando uma tampa ou capacete.
Carena (ca)	Saliência externa que parte do umbo em direção a região póstero-inferior. Linha longitudinal que marca a troca de inclinação da superfície externa da concha (Fig. 1A).
Cavidade Subumbonal (csu)	Reentrância interna dorsal, sob os umbos (Fig. 1B).
Charneira (c)	Região de articulação das valvas, situada dorsalmente sob os umbos. Apresenta-se sob diversos aspectos: lisa, estreita espessa, provida de dentes, fossetas ou lamelas cujas disposições variam muito (Fig. 1B, D e F).
Concha oval	Semelhante a um ovo com dois eixos de simetria.
Concha ovoide	Semelhante a um ovo com um eixo de simetria.
Concha romboide	Semelhante a uma elipse com bordas paralelas como um polígono paralelogramo (com quatro lados iguais e paralelos).
Concha triangular	Semelhante a um triângulo.
Dentes cardinais (dc)	Dentes situados na charneira, logo abaixo dos umbos (Fig. 1D e F).
Dente pseudocardinal anterior (dpa) e posterior (dpp)	Dentes da charneira de formato irregular, de difícil individualização e distinção entre eles, em alguns casos. Característicos de Hyriidae (Fig. 1B).
Dentes laterais (dl)	Dentes alongados em forma de lamela, situados na frente e atrás dos cardinais (Fig. 1B, D e F).

Tabela I. Termos malacológicos citados na chave dicotômica.

Termo	Definição
Equilateral	Quando as valvas são simétricas em relação a um plano vertical que passa pelos umbos e perpendicular à charneira.
Escultura umbonal (eu)	Ornamentação externa da concha em forma de proeminências. Pode ser radial (Fig. 1A), concêntrica e reticular.
Escudo	Depressão externa achatada na região posterior delimitada pela carena (Fig. 6B).
Expansão alada	Projeção em forma de asa situada nas extremidades anterior/dorsal ou posterior/dorsal (Fig. 4A).
Fosseta	Cavidade na charneira para o encaixe de dente da valva oposta.
Heterodonte	Tipo de charneira que apresenta dentes cardinais medianos em número máximo de três, com fossetas correspondentes em cada valva e ainda apresentam antero e posteriormente aos cardinais, dentes laterais alongados (Presente em Corbiculidae e Sphaeriidae) (Fig. 1D e F).
Impressão dos músculos anteriores (iaa) e posteriores (iap)	Cicatrizes deixadas na superfície interna da concha, onde os músculos do animal se fixam na mesma (Fig. 1B, D e F).
Impressão dos músculos adutores	Duas impressões grandes de contorno ovalado; uma situada na região anterior e a outra na região posterior da concha (Fig. 1B, D e F).
Impressão dos músculos dorsais	Impressões pequenas na cavidade umbonal.
Inequilateral	Quando as valvas são assimétricas em relação a um plano vertical que passa pelo umbo e perpendicular à charneira.
Ligamento (l)	Estrutura orgânica que une as duas valvas dorsalmente e força a abertura das valvas quando do relaxamento dos músculos adutores. Firme, mas elástica quando o animal está vivo; quebradiça depois do animal morto, com o ressecamento da concha. Geralmente externo (Fig. 1A, B, D e F).
Linhas ou estrias comarginais (ec)	Marcas ou linhas na superfície externa da concha que delimitam a margem de um estágio de crescimento. Paralelas à margem da valva (Fig. 1A e E).
Linha palial (lp)	Linha paralela aos bordos da margem ventral da concha, deixada pela aderência do manto. Liga as duas impressões dos músculos adutores (Fig. 1B, D, F e 3A).
Lúnula	Depressão externa pequena na região anterior logo após os umbos (Fig. 6B).
Nodosidade	Saliência em forma de nódulo na superfície externa da concha (Fig. 4B).
Pé em forma de machado	Pé típico de bivalves Unionoida, em forma de lâmina de machado (Fig. 5A).
Pé com extremidade intumescida	Pé alongado e com a extremidade intumescida, funcionando como uma âncora; não laminar distinto dos demais bivalves (Fig. 5B).
Perióstraco	Camada orgânica, fina, que reveste a superfície externa da concha. Protege as camadas calcárias da dissolução pela água.
Rostro	Projeção da região posterior da valva, que a torna inequilateral (Fig. 4C).
Prodissoconcha (pc)	Concha embrionária dos bivalves, secretada pela larva e geralmente mantida nos indivíduos adultos (Fig. 1E).
Septo (s)	Projeção que divide a cavidade umbonal de cada valva em dois compartimentos. Nele se fixa e se sustenta o músculo adutor anterior. (Fig. 2B).
Sinus palial ou seio palial (sp)	Reentrância de linha palial em forma de "U" ou "V" invertido, junto a impressão do músculo adutor posterior (Presente em *Leila blainvilliana* (Fig. 3A, B) e *Neocorbicula*).
Umbo (u)	Elevação na região dorsal de cada valva (Fig. 1A, D, E e F). Quanto a sua localização podem ser denominados frontais, terminais e subterminais. É a região mais antiga da concha, geralmente gasta em Unionoida.

Diversidade de bivalves límnicos no Brasil: espécies invasoras e nativas

São conhecidos 22 gêneros de bivalves límnicos para o Brasil, sendo que dois destes estão representados apenas por espécies invasoras neste país, são eles: *Limnoperna* (Mytilidae) e *Corbicula* (Corbiculidae). A Tabela II apresenta um resumo da classificação destes gêneros.

A seguir, é apresentada a primeira chave para determinação e diferenciação das espécies de bivalves límnicos invasores dos demais bivalves nativos citados para o Brasil.

A relação das espécies de moluscos citadas para o Brasil encontra-se discriminada na Tabela III. São conhecidas 114 espécies de moluscos bivalves límnicos com registros para o Brasil, sendo que destas, apenas 5 espécies (4% das espécies de bivalves límnicos citados para o país) são invasoras (Fig. 7). No entanto, o impacto deste pequeno número de espécies invasoras aliado aos impactos ambientais de origem antrópica tem contribuído para a diminuição das populações das espécies nativas. Dentre os impactos decorrentes das espécies invasoras podemos citar a competição por espaço, recursos alimentares, bem como pela formação de macroaglomerados bioincrustantes, quando considerado o mexilhão-dourado.

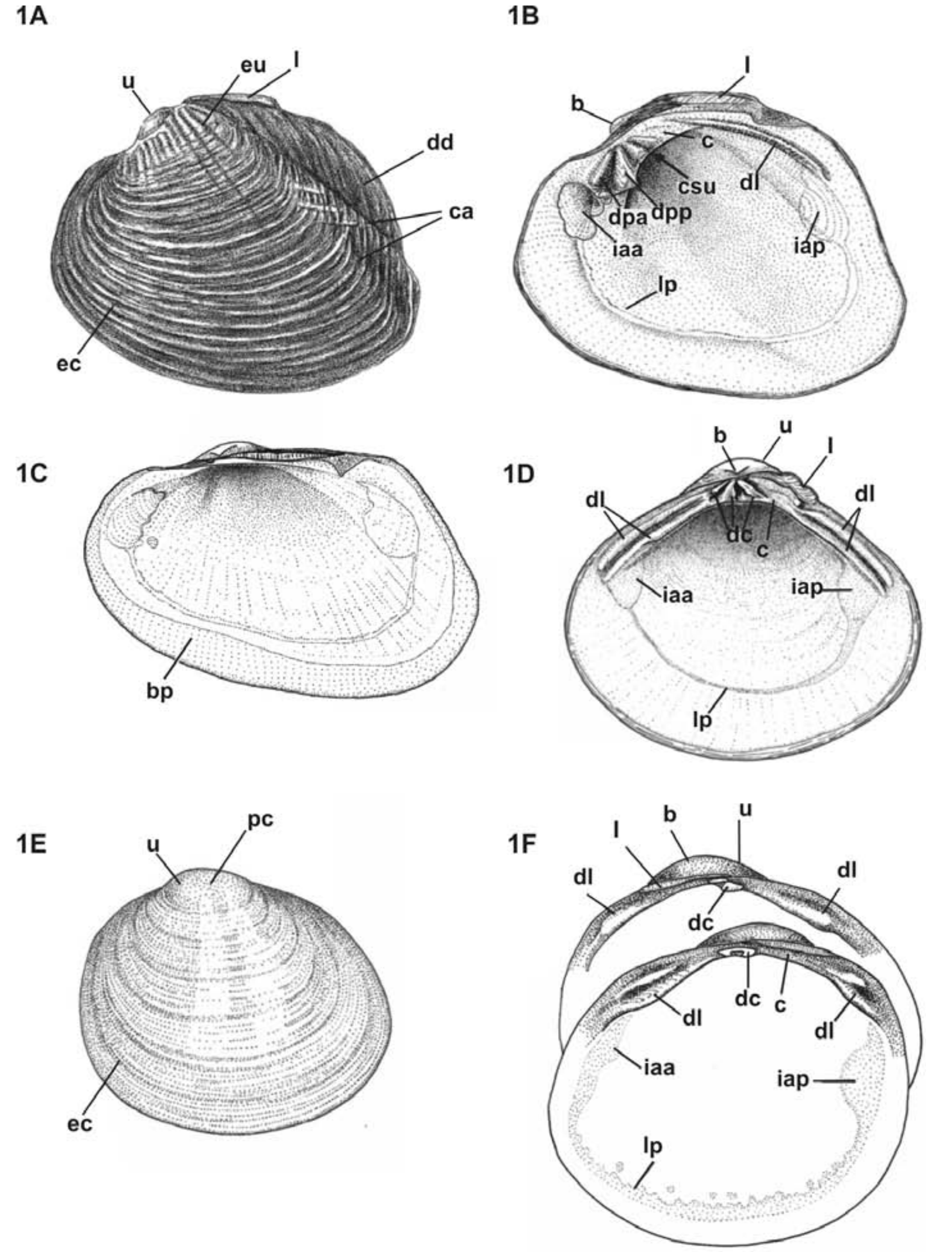


Figura 1. Estruturas da concha de bivalves límnicos: 1A, vista externa da valva esquerda e 1B, interna da valva direita de *Castalia* sp; 1C, vista interna da valva direita de *Anodontites patagonicus*; 1D, vista interna da valva direita de *Corbicula fluminea*; 1E, vista externa da valva esquerda de *Pisidium* sp. e vista interna das valvas esquerda e direita de *Pisidium* sp. Prodissoconcha (pc); umbo (u); bico (b); escultura umbonal (eu); carena (ca); declive dorsal (dd); estrias ou linhas comarginais (ec); ligamento (l); cavidade subumbonal (csu); charneira (c); dente cardinal (dc); dente pseudocardinal anterior (dpa); dente pseudocardinal posterior (dpp); dente lateral (dl); impressão do músculo adutor anterior (iaa); impressão do músculo adutor posterior (iap); linha palial (lp); borda prismática (bp). (Desenho: M.C.D. Mansur).

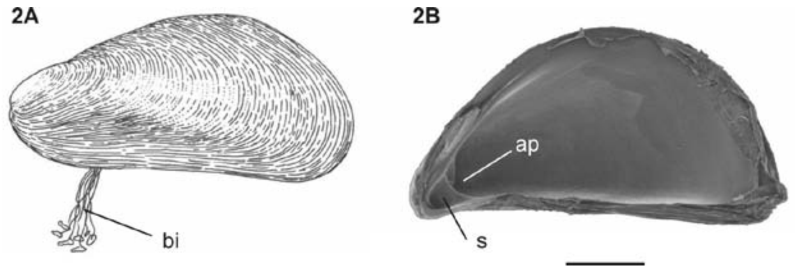


Figura 2. Concha mitiloide: 2A, fios de bisso (bi) em *Limnoperna fortunei*; 2B, septo (s) e apófise (ap) em *Mytilopsis*. Escala: 0,5 cm. (Foto e desenho: M.C.D. Mansur).

Figura 3. Representação da linha palial (lp) e do sinus palial (sp) em conchas do gênero *Leila* (Unionoida, Mycetopodidae): 3A, concha com a linha palial demarcada e 3B, não demarcada. A seta indica o sinus palial. Escala: 1 cm. (Fotos: M.C.D. Mansur).

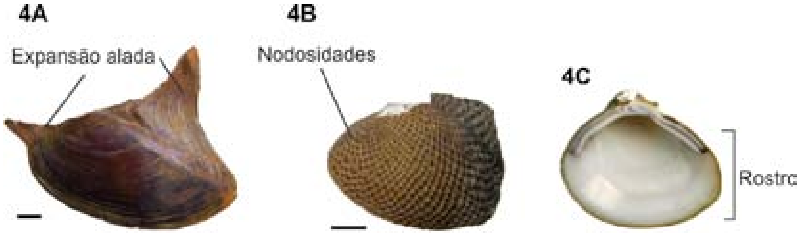


Figura 4. Estruturas da concha: 4A, expansão alada em Hyriidae; 4B, nodosidades sobre o perióstraco de Hyriidae; 4C, rostro em Corbiculidae. Escala: 1 cm. (Fotos: M.C.D. Mansur e D. Pimpão).

Figura 5. Pé de bivalves límnicos: 4A, pé típico dos bivalves límnicos, em forma de machado representado por um indivíduo do gênero *Leila*; 4B, pé de com extremidade intumescida, típico do gênero *Mycetopoda* (Fotos: M.C.D. Mansur).

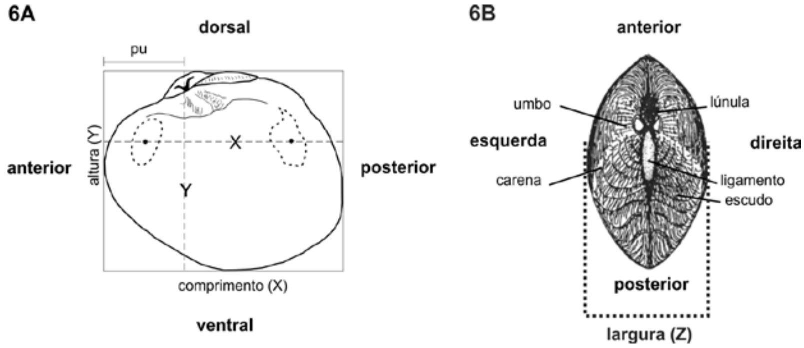
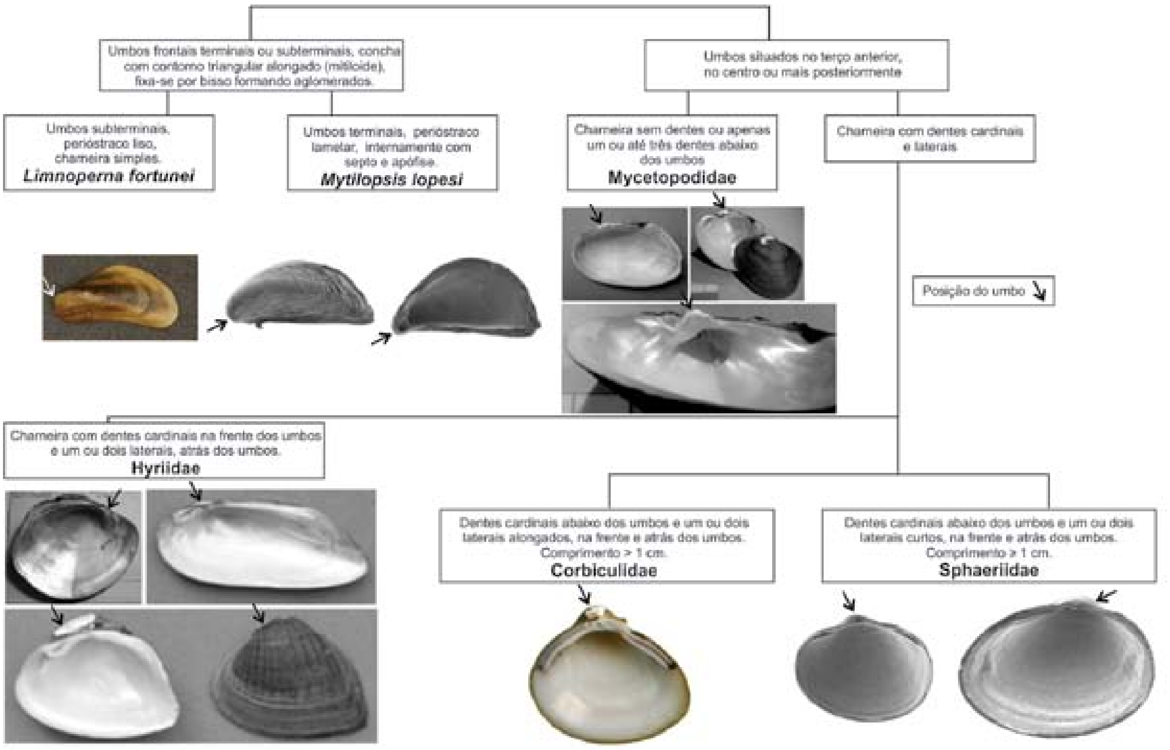


Figura 6. Orientação da concha de um bivalve: 6A, borda dorsal, ventral, anterior e posterior; 6B, vista da largura da concha (z). Posição do umbo (pu) determinada pela distância entre o bico do umbo e o limite anterior perpendicular à linha Y (altura) (Desenhos: M.C.D. Mansur).

Tabela II. Gêneros de bivalves límnicos nativos e invasores citados para o Brasil.

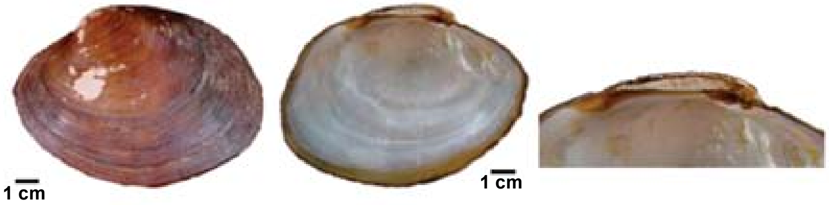
Gêneros	Origem
Classe BIVALVIA Linné, 1758	
Subclasse PTERIOMORPHIA Beurlen, 1944	
Ordem MYTILOIDA Férrusac, 1822	
Superfamília MYTILOIDEA Rafinesque, 1815	
Família MYTILIDAE Rafinesque, 1815	
Subfamília Mytilinae Rafinesque, 1815	
Gênero *Limnoperna* Rochebrune, 1882	Invasor
Subclasse PALAEOHETERODONTA Newell, 1965	
Ordem UNIONOIDA Stoliczka, 1871	
Superfamília UNIONOIDEA Fleming, 1828	
Família HYRIIDAE Fleming, 1828	
Subfamília Hyriinae Swainson, 1840	
Gênero *Diplodon* Spix, 1827	Nativo
Gênero *Castalia* Lamarck, 1819	Nativo
Gênero *Prisodon* Schumacher, 1817	Nativo
Gênero *Paxyodon* Schumacher, 1817	Nativo
Gênero *Triplodon* Spix, 1827	Nativo
Superfamília ETHERIOIDEA	
Família MYCETOPODIDAE Gray, 1840	
Subfamília Anodontitinae Modell, 1942	
Gênero *Anodontites* Bruguière, 1792	Nativo
Subgênero *Anodontites* s.s.	Nativo
Subgênero *Lamproscapha*	Nativo
Subfamília Mycetopodinae Adams & Adams, 1856	
Gênero *Mycetopoda* Orbigny, 1835	Nativo
Subfamília Monocondylaeinae Modell, 1942	
Gênero *Monocondylaea* Orbigny, 1835	Nativo
Gênero *Fossula* Lea, 1870	Nativo
Gênero *Haasica* Strand, 1932	Nativo
Gênero *Tamsiella* Haas, 1931	Nativo
Subfamília Leilinae Morretes, 1949	
Gênero *Leila* Gray, 1840	Nativo
Subfamília Bartlettiinae	
Gênero *Bartlettia* H. Adams, 1866	Nativo
Subclasse HETERODONTA Neumayr, 1884	
Ordem VENEROIDA Adams & Adams, 1858	
Subordem ARCTICINA Newell, 1965	
Superfamília SPHAERIOIDEA Rafinesque, 1820	
Família SPHAERIIDAE Rafinesque, 1820	
Subfamília Sphaeriinae Baker, 1927	
Gênero *Musculium* Link, 1807	Nativo
Gênero *Sphaerium* (Scopoli, 1777)	Nativo
Gênero *Pisidium* C. Pfeiffer, 1821	Nativo
Subfamília Euperinae Heard, 1965	
Gênero *Eupera* Bourguignat, 1854	Nativo
Superfamília CORBICULOIDEA	
Família CORBICULIDAE Gray, 1847	
Gênero *Corbicula* Megerle Von Mühlfeld, 1811	Invasor
Gênero *Cyanocyclas* Blainville, 1818	Nativo
Gênero *Polymesoda* Rafinesque, 1828	Nativo
Superfamília DREISSENOIDEA	
Família DREISSENIDAE	
Gênero *Mytilopsis* Conrad, 1857	Nativo

Chave para determinação de gêneros de bivalves límnicos: diferenciação entre invasores e nativos

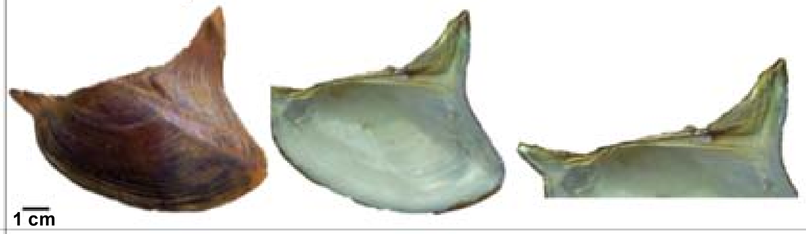


Família MYCETOPODIDAE

Concha fixa ao substrato endurecido ou em perfurações de rochas, através de projeção da região anterior, com contorno muito irregular, lembrando uma ostra em forma de «P» ou machado. SIM ⇨ NÃO ⇩	***Bartlettia stefanensis***  Fotos: M.C.D. Mansur
Concha muita alongada com extremidade anterior capitada e inclinada. SIM ⇨ NÃO ⇩	***Mycetopodella falcata***  Fotos: M.C.D. Mansur
Concha elíptica alongada. Pé muito alongado, com extremidade intumescida. SIM ⇨ NÃO ⇩	***Mycetopoda***  Fotos: C.D. Araujo

Família MYCETOPODIDAE	
SIM ⇨ Sinus palial presente. NÃO ⇩	***Leila***  Fotos: M.C.D. Mansur
SIM ⇨ Com um dente em forma de calo nacarado em cada valva. NÃO ⇩	***Monocondylaea***  Fotos: D. Pimpão
SIM ⇨ Com um dente na valva esquerda e dois na direita, achatados, intercalados por fosseta triangular rasa e escura, perpendicular à charneira. NÃO ⇩	***Fossula fossiculifera***  Fotos: C.D. Araujo
SIM ⇨ Concha semelhante à espécie acima, mas com fosseta estreita e oblíqua à charneira. NÃO ⇩	***Tamsiella***  Fotos: C.D. Araujo
SIM ⇨ Com dois dentes muito robustos e uma fosseta, bem desenvolvidos nas duas valvas, perióstraco com pintas verdes. NÃO ⇩	***Haasica balzani***  Fotos: C.D. Araujo
SIM ⇨ Charneira sem dentes. NÃO ⇩	***Anodontites***  Fotos: D. Pereira

Família HYRIIDAE

Concha com duas expansões aladas nas extremidades da charneira; superfície lisa, sem escultura; borda posterior truncada perpendicularmente; carena saliente. SIM ⇨ NÃO ⇩	***Paxyodon syrmatophorus***  Fotos: C.D. Araújo
Com duas expansões aladas, superfície lisa; borda posterior côncava; carena baixa. SIM ⇨ NÃO ⇩	***Prisodon obliquus***  Fotos: C.D. Araújo
Com uma ou duas expansões aladas; superfície fortemente esculturada por raios e/ou nodosidades. SIM ⇨ NÃO ⇩	***Triplodon***  Fotos: C.D. Araújo
Concha sem asas, triangular, com carena saliente. SIM ⇨ NÃO ⇩	***Castalia***  Fotos: D. Pereira
Concha sem asas, não triangular, ovalada, oval ou romboide, sem carena ou com carena baixa e arredondada. SIM ⇨ NÃO ⇩	***Diplodon***  Fotos: D. Pereira

Família CORBICULIDAE

Com sinus palial, dentes laterais lisos. SIM ⇨ NÃO ⇩	***Polymesoda***  Fotos: M.C.D. Mansur

Família CORBICULIDAE

Com sinus palial, dentes laterais serreados, superfície externa não ondulada (<2cm).

SIM ⇨

NÃO ⇩

Cyanocyclas

Fotos: M.C.D. Mansur

Sem sinus palial, dentes laterais serreados, superfície externa ondulada por linhas comarginais (±4cm).

SIM ⇨

NÃO ⇩

Corbicula

Fotos: M.C.D. Mansur

Família SPHAERIIDAE

Um dente cardinal em cada valva; com pintas pretas ou marrons que atravessam a superfície da concha (±0,7 cm).

SIM ⇨

NÃO ⇩

Eupera

Fotos: M.C.D. Mansur

Dois dentes cardinais na valva esquerda; umbos centrados; charneira muito arqueada.

SIM ⇨

NÃO ⇩

Sphaerium cambaraense

Fotos: C.D. Araújo

Dois dentes cardinais na valva esquerda; charneira pouco arqueada; umbos com capacete.

SIM ⇨

NÃO ⇩

Musculium argentinum

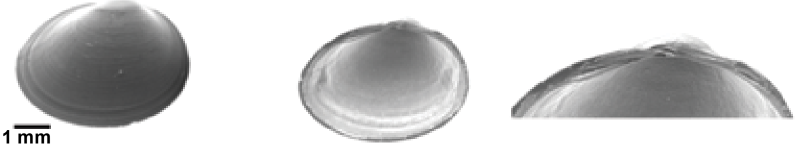
Fotos: D. Pereira

Conchas diminutas (em torno de 2 a 5mm), sem pintas pretas; umbos posteriores ao meio da concha; região anterior bem maior que a posterior.

SIM ⇨

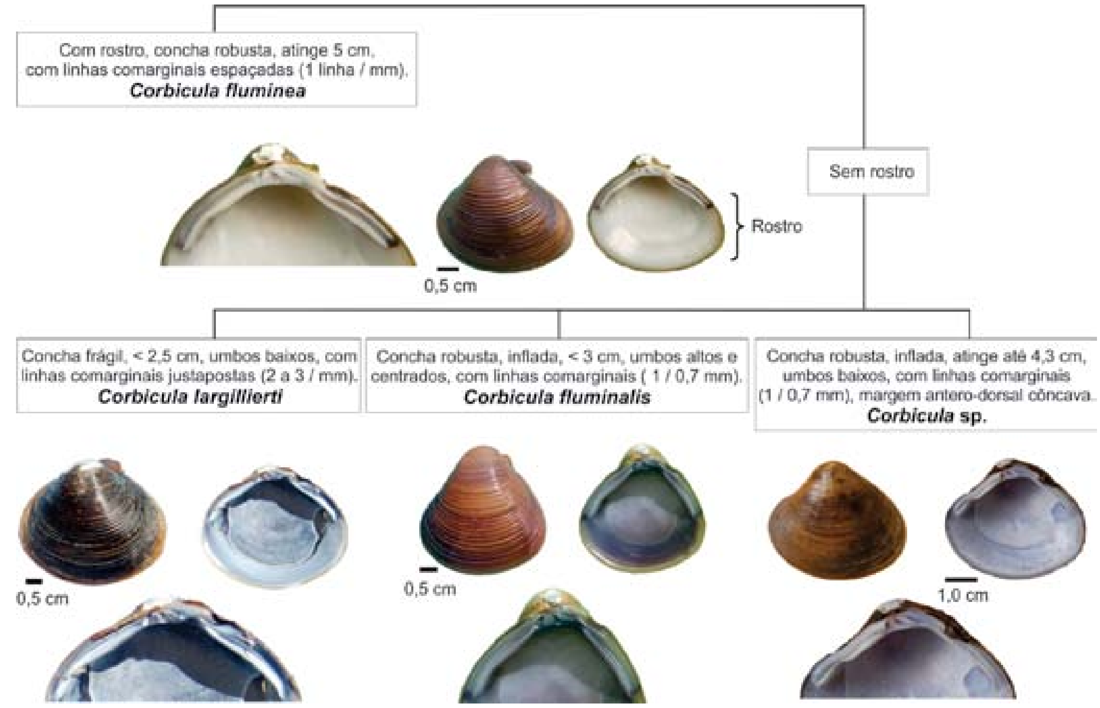
NÃO ⇩

Pisidium



Fotos: M.C.D. Mansur

Chave para determinação das espécies do gênero *Corbicula*



Com rostro, concha robusta, atinge 5 cm, com linhas comarginais espaçadas (1 linha / mm). ***Corbicula fluminea***

Sem rostro

Concha frágil, < 2,5 cm, umbos baixos, com linhas comarginais justapostas (2 a 3 / mm). ***Corbicula largillierti***

Concha robusta, inflada, < 3 cm, umbos altos e centrados, com linhas comarginais (1 / 0,7 mm). ***Corbicula fluminalis***

Concha robusta, inflada, atinge até 4,3 cm, umbos baixos, com linhas comarginais (1 / 0,7 mm), margem antero-dorsal côncava. ***Corbicula* sp.**

Adaptado de Mansur et al., 2011; Fotos: C.D. de Araújo.

Dentre as famílias mais representativas em número de espécies podemos citar Hyriidae (52 espécies; 45% das espécies de bivalves límnicos), Mycetopodidae (32; 28%) e Sphaeriidae (20; 17%), sendo todas estas espécies representantes da malacofauna nativa (Fig. 8).

Dentre os gêneros mais representativos em número de espécies podemos citar *Diplodon* (37 espécies; 32% das espécies de bivalves límnicos), *Anodontites* (14; 12%), *Castalia* (11; 10%), *Eupera* e *Pisidium* (9; 8%), e *Monocondylaea* (7; 6%), sendo todas estas espécies representantes da malacofauna nativa (Fig. 9).

O Brasil apresenta oito grandes bacias hidrográficas dos rios: 1, Amazonas; 2, Tocantins/Araguaia; 3, do Atlântico Norte/Nordeste; 4, São Francisco; 5, do Atlântico Leste; 6, Paraná/Paraguai; 7, Uruguai; e 8, bacia do Atlântico Sul/Sudeste (Fig. 10). O maior número de espécies é verificado nas bacias: Paraná/Paraguai (51 espécies; 22% das espécies de bivalves límnicos citados para o Brasil), Atlântico Sul/Sudeste (43; 18%), Uruguai (42; 18%) e Amazonas (40; 17%) (Fig. 11). No entanto, esses números podem não representar a diversidade real destas bacias, já que as bacias Amazonas, Atlântico Norte/Nordeste, Atlântico Leste, Tocantins/Araguaia e São Francisco carecem de coletas e inventários malacofaunísticos.

Das 114 espécies citadas para o Brasil, 45 carecem de revisão taxonômica (35% das espécies citadas). As maiores dificuldades são verificadas quanto à identidade taxonômica das espécies do gênero *Diplodon* que apresentam ampla variação morfológica. A falta de

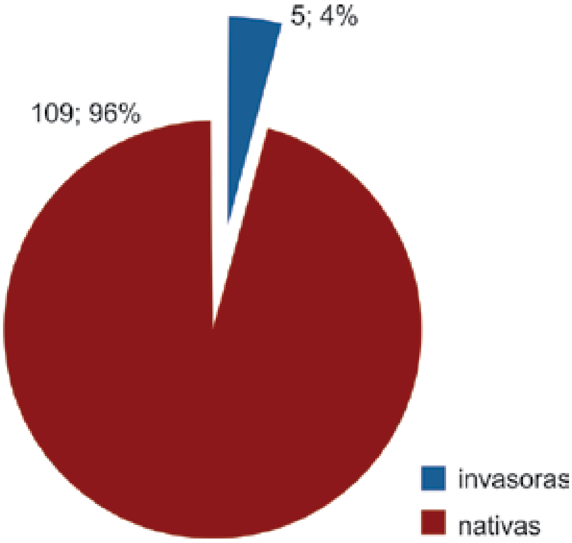


Figura 7. Número e percentual de espécies de moluscos bivalves límnicos nativos e invasores citadas para o Brasil.

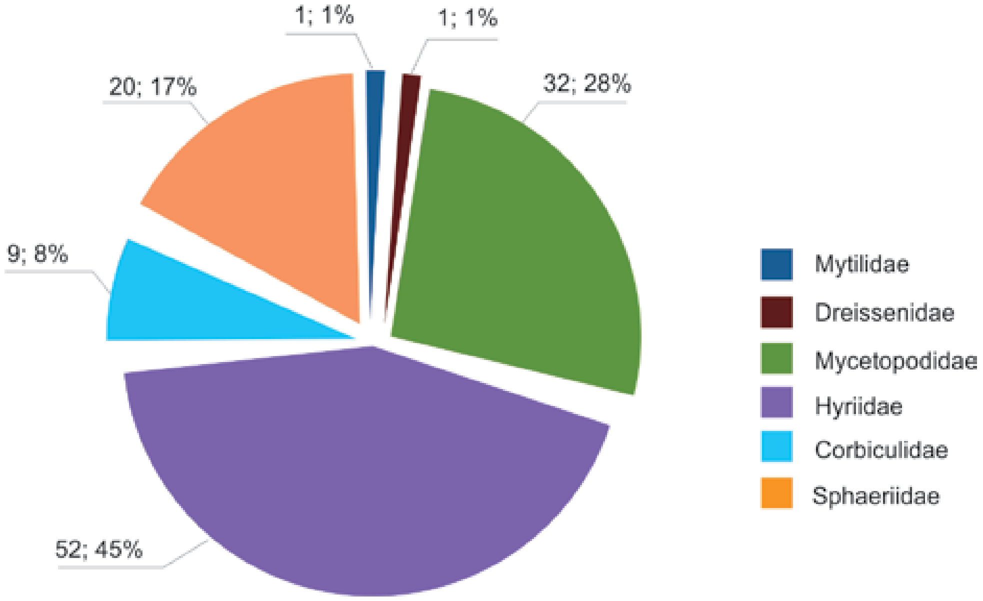


Figura 8. Número e percentual de espécies de moluscos bivalves límnicos conhecidos para as famílias citadas para o Brasil.

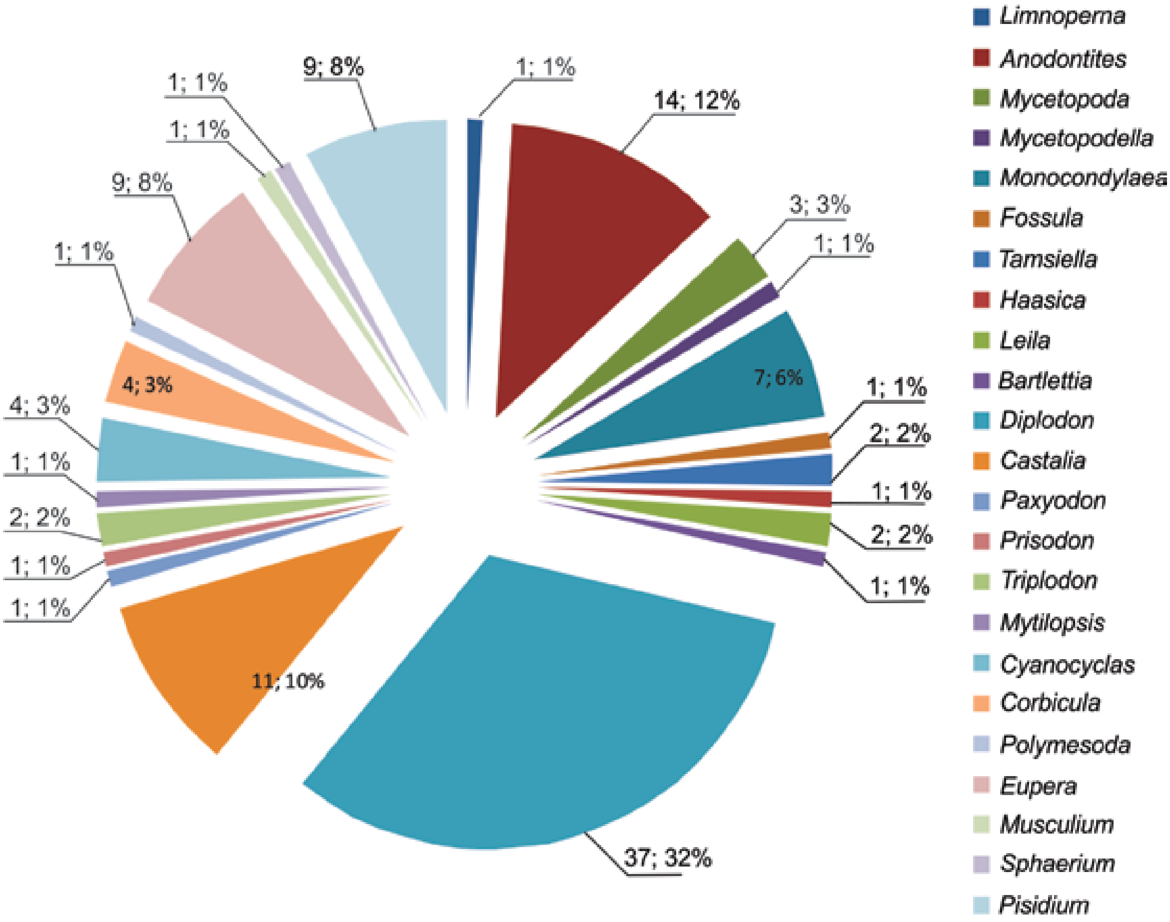


Figura 9. Número e percentual de espécies de moluscos bivalves límnicos conhecidos para os gêneros citados para o Brasil.

conhecimento da real identidade taxonômica das espécies é um agravante no que diz respeito à conservação, sendo que algumas espécies constam em listas vermelhas. Apenas 1% das espécies citadas para o Brasil está enquadrada na categoria Criticamente Em Perigo (CEP) na lista vermelha brasileira de espécies ameaçadas; 11%, na categoria Em Perigo (EP) e 9% em Vulnerável (VU) (Fig. 12). As demais espécies não constam em listas, mas isso não significa que não estejam ameaçadas, pois as listas não foram revisadas desde suas publicações. Além disso, muitas destas espécies têm sofrido ameaças consideráveis, destacando-se a construção de novas barragens, assoreamento, desmatamento, destruição de habitats, poluição e a ampliação da dispersão das espécies de bivalves invasoras. Desta forma, 46 espécies (40,3% das espécies de bivalves límnicos citadas para o Brasil) são sugeridas como candidatas à avaliação criteriosa em nova revisão da lista de espécies ameaçadas da fauna brasileira (Tab. III).

As demais espécies carecem de dados e, assim como as espécies candidatas, deverão ser alvo de pesquisas quanto aos seus níveis populacionais, preferências ambientais e distribuição geográfica atual no país.

Considerando dados históricos da malacofauna límnica do estado de São Paulo (Ihering, 1893; Vaz et al., 1983, 1985, 1986b, 1987, 1992; Teles et al., 1991; França et al., 2007; Suriani et al., 2007) e o diagnóstico apresentado no Capítulo 19 para a bacia do Rio Tietê, além de registros de coleções de museus, é possível estabelecer uma cronologia, a qual ilustra a diminuição da riqueza de moluscos bivalves límnicos ao longo dos anos na bacia do Rio Tietê (Fig. 13). Cabe ressaltar que a construção das barragens situadas nesta bacia ocorreu no período da ditadura militar. Naquela época, o licenciamento ambiental de empreendimentos hidrelétricos era um processo novo no país, carecendo de estudos criteriosos sobre a biota aquática e do estabe-

Figura 10. Bacias hidrográficas do Brasil. Fonte: ANA (http://www.aneel.gov.br/area.cfm?id_area=104).

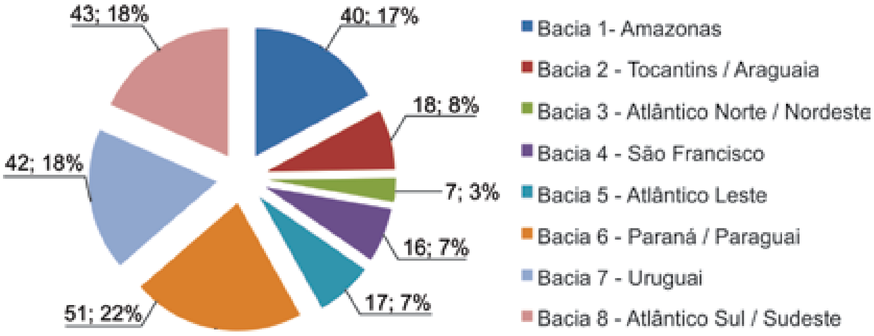


Figura 11. Número e percentual de espécies de moluscos bivalves límnicos citados nas bacias hidrográficas do Brasil.

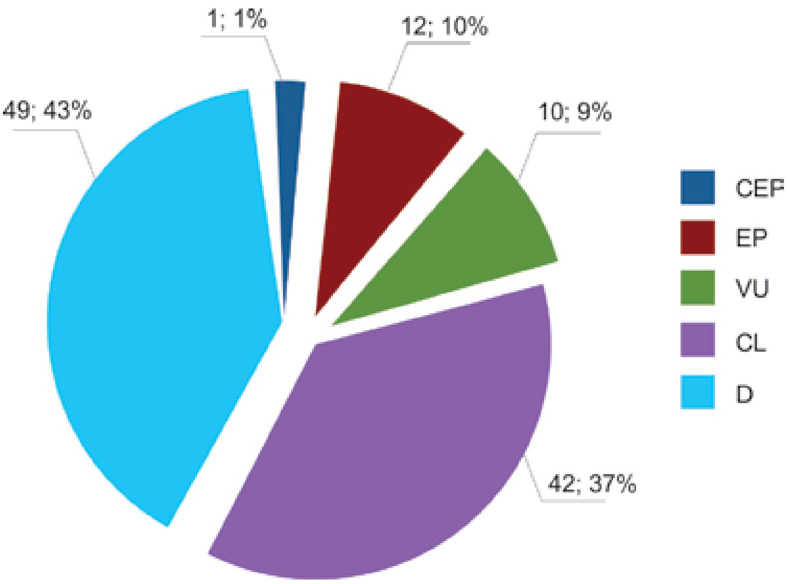


Figura 12. Conservação das espécies de bivalves límnicos citados nas bacias hidrográficas do Brasil. *Status* de conservação das espécies presentes em listas vermelhas de espécies ameaçadas: criticamente em perigo (CEP), em perigo (EP), vulnerável (VU). Espécies candidatas à lista de espécies ameaçadas de extinção do Brasil (CL) que deverão ser avaliadas por meio de critérios apropriados; espécies desconhecidas (D) quanto a quaisquer aspectos da sua conservação.

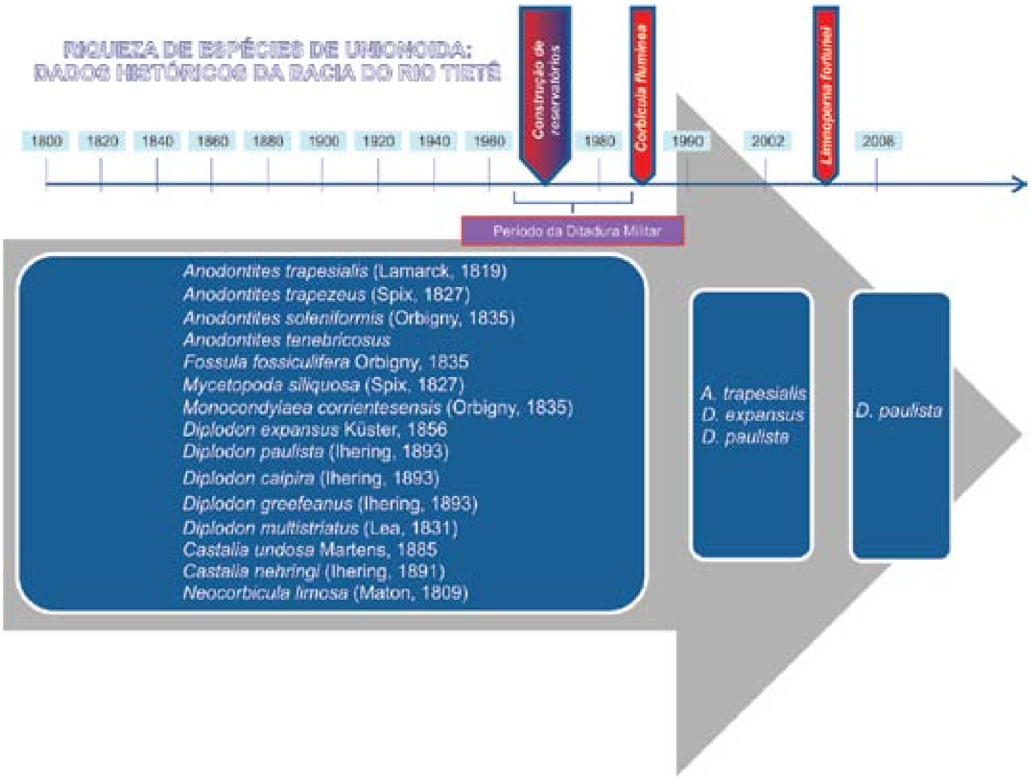


Figura 13. Diversidade histórica de bivalves límnicos na bacia do Rio Tietê com base em revisão bibliográfica.

lecimento de medidas mitigatórias e compensatórias eficazes para promover a conservação da fauna bentônica, em especial os moluscos bivalves de água doce. Além disso, a introdução das espécies invasoras somou outro impacto sobre as espécies nativas, competindo por espaço e recursos alimentares.

Também é importante considerar as estratégias reprodutivas diferenciadas entre as espécies de bivalves límnicos invasores, desenvolvimento direto no plâncton, e dos nativos, que em grande parte é indireto, utilizando os peixes como vetores e dispersores (ver Capítulo 6). As espécies que utilizam os peixes como vetores e dispersores tem relação estreita com a ictiofauna e o plano de ações estratégicas para a conservação destes moluscos deve considerar a conservação das espécies de peixes vetores.

No entanto, a maioria dos vetores é desconhecida, o que demonstra a carência de dados que possam dar suporte à conservação de muitas espécies de moluscos bivalves. A construção de barragens, além de provocar uma alteração ambiental ao transformar um rio em lago, muitas vezes afeta a estrutura da ictiofauna (composição e abundância de peixes), além de suas rotas migratórias. Portanto, é de extrema importância a pesquisa científica sobre a relação larva gloquídio e ou lasídio com o peixe vetor e dispersor, visando descrever detalhadamente o ciclo parasitário no peixe e o desenvolvimento da larva do bivalve até sua fase adulta bentônica, bem como a importância das rotas migratórias de peixes na dispersão desses moluscos.

Tabela III. Espécies de bivalves límnicos citados para as bacias hidrográficas do Brasil com base principalmente nas seguintes obras: Haas (1969); Ihering (1890, 1893, 1910); Ituarte & Mansur (1993); Mansur et al. (1987, 1988, 1991, 1994, 2008a, 2011a); Mansur & Meier-Brook (2000); Mansur & Pereira (2006); Mansur & Silva (1990); Mansur & Valer (1992); Ortmann (1921); Pereira et al. (2000a); Pimpão et al. (2008, 2012); Pimpão & Mansur (2009), Simone (2006), Scarabino & Mansur (2007), além do exame de coleções científicas. *Status* (S) de conservação das espécies: vulnerável (VU), em perigo (EP), criticamente em perigo (CEP), conforme Amaral et al (2008). Candidata à lista de espécies ameaçadas de extinção do Brasil (CL), espécies as quais são desconhecidas (D) quanto a quaisquer aspectos quanto a sua conservação *carece de revisão taxonômica.

Família/Gênero	Espécie	Bacias Hidrográficas	Ameaças	S
Mytilidae				
Lymnoperna Rochebrune, 1882	*Limnoperna fortunei* (Dunker, 1857)	Paraná/Paraguai, Uruguai e Atlântico Sul/Sudeste.	-	D
Mycetopodidae				
Anodontites Bruguière, 1792	*Anodontites (A.) crispatus* Bruguière, 1792*	Amazonas, Paraná/Paraguai, Atlântico Norte/Nordeste.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Anodontites (A.) elongatus (Swainson, 1823)	Amazonas, Paraná/Paraguai, Uruguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	VU
	Anodontites (L.) ensiformis (Spix, 1827)	Amazonas, Tocantins/Araguaia, Paraná/Paraguai, Uruguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	VU
	Anodontites (A.) ferrarisi (Orbigny, 1835)	Uruguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	EP
	Anodontites (A.) iheringi (Clessin, 1882)*	Atlântico Sul/Sudeste.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	EP
	Anodontites (A.) lucidus (Orbigny, 1835)	Uruguai, Atlântico Sul/Sudeste.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Anodontites (A.) moricandi (Lea, 1860)*	São Francisco.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Anodontites (A.) obtusus (Lamarck, 1819)*	São Francisco, Atlântico Norte/Nordeste.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Anodontites (A.) patagonicus (Lamarck, 1819)*	Paraná/Paraguai, Uruguai, Atlântico Sul/Sudeste.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	D
	Anodontites (A.) schombergianus (Sowerby, 1870)*	Amazonas e Tocantins/Araguaia.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Anodontites (A.) soleniformis (Lamarck, 1819)*	Amazonas, São Francisco, Paraná/Paraguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	VU
	Anodontites (A.) tenebricosus (Lea, 1834)*	Paraná/Paraguai, Uruguai, Atlântico Sul/Sudeste.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	VU
	Anodontites (A.) trapesialis (Lea, 1860)	Amazonas, Tocantins/Araguaia, Atlântico Norte/Nordeste, São Francisco, Atlântico Leste, Paraná/Paraguai, Uruguai, Atlântico Sul/Sudeste.	Assoreamento, erosão marginal e poluição.	VU

Tabela III. Continua...

Família/Gênero	Espécie	Bacias Hidrográficas	Ameaças	S
Mycetopodidae				
	Anodontites (A.) trapezeus (Spix, 1827)	Amazonas, Tocantins/ Araguaia, São Francisco, Atlântico Leste, Paraná/ Paraguai, Uruguai, Atlântico Sul/Sudeste.	Assoreamento, erosão marginal e poluição.	EP
Mycetopoda Orbigny, 1835	*Mycetopoda legumen* (Martens, 1888)	Uruguai, Atlântico Sul/Sudeste.	Erosão marginal, poluição, barramento e barreiras à piracema.	VU
	Mycetopoda siliquosa (Spix, 1827)	Amazonas, Tocantins/ Araguaia, Atlântico Norte/ Nordeste, São Francisco, Atlântico Leste, Paraná/ Paraguai, Uruguai, Atlântico Sul/Sudeste.	Erosão marginal, poluição, barramento e barreiras à piracema.	VU
	Mycetopoda soleniformis Orbigny, 1835	Paraná/Paraguai, Uruguai.	Erosão marginal, poluição, barramento e barreiras à piracema.	CL
Mycetopodella Marshall, 1927	*Mycetopodella falcata* (Higgins, 1868)	Amazonas.	Erosão marginal, poluição, barramento e barreiras à piracema.	CL
Monocondylaea Orbigny 1835	*Monocondylaea corrientesensis* Orbigny, 1834	Paraná/Paraguai, Uruguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Monocondylaea costulata Moricand, 1858	Amazonas, Tocantins/ Araguaia.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Monocondylaea franciscana (Moricand, 1837)	São Francisco.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Monocondylaea jaspidea Hupé, 1857	Amazonas, Tocantins/ Araguaia.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Monocondylaea minuana Orbigny, 1835	Uruguai, Atlântico Sul/Sudeste.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	D
	Monocondylaea paraguayana Orbigny, 1835	Paraná/Paraguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	VU
	Monocondylaea parchappi Orbigny, 1835	Paraná/Paraguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
Fossula Lea, 1870	*Fossula fossiculifera* (Orbigny, 1835)	São Francisco, Atlântico Leste, Paraná/ Paraguai, Uruguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	EP
Tamsiella Haas, 1931	*Tamsiella amazonica* Bonetto, 1972*	Amazonas.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Tamsiella schroeteriana (Lea, 1852)*	Amazonas.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
Haasica Strand, 1931	*Haasica balzani* (Ihering, 1893)	Paraná/Paraguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
Leila Gray, 1838	*Leila blainvilliana* (Lea, 1834)	Paraná/Paraguai, Uruguai, Atlântico Sul/Sudeste.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema e espécies invasoras.	EP
	Leila esula (Orbigny, 1835)	Amazonas, Tocantins/ Araguaia.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	VU
Bartlettia H. Adams 1866	*Bartlettia stefanensis* Moricand, 1856	Paraná/Paraguai.	Assoreamento, erosão marginal, poluição e barramento.	VU
Hyriidae			-	

Tabela III. Continua...

Família/Gênero	Espécie	Bacias Hidrográficas	Ameaças	S
Hyriidae			-	
Diplodon Spix, 1827	*Diplodon (D.) aethipos* (Lea, 1860)	Uruguai, Atlântico Sul/Sudeste.	-	D
	Diplodon (D.) berthae Ortman, 1921	Uruguai, Atlântico Sul/Sudeste.	-	D
	Diplodon (D.) besckeanus (Dunker, 1848)	Atlântico Leste.	Assoreamento, erosão marginal e poluição.	CL
	Diplodon (D.) caipira (Ihering1893)*	Paraná/Paraguai.	-	EP
	Diplodon (D.) delodontus (Lamarck, 1919)*	Paraná/Paraguai, Uruguai, Atlântico Sul/Sudeste.	-	D
	Diplodon (D.) dunkerianus (Lea, 1956)*	Atlântico Leste.	Assoreamento, erosão marginal e poluição.	EP
	Diplodon (D.) ellipticus (Wagner, 1827)*	São Francisco, Atlântico Leste, Atlântico Sul/ Sudeste (?)	-	D
	Diplodon (D.) expansus (Küster, 1856)*	Paraná/Paraguai, Atlântico Leste, Atlântico Sul/Sudeste (?).	Assoreamento, erosão marginal e poluição.	VU
	Diplodon (D.) rhombeus (Spix, 1827)*	São Francisco, Paraná/ Paraguai.	-	D
	Diplodon (D.) granosus (Bruguière, 1792)*	Atlântico Leste, Atlântico Sul/Sudeste.	-	D
	Diplodon (D.) imitator Ortman, 1921*	Atlântico Sul/Sudeste.	-	D
	Diplodon (D.) martensi (Ihering, 1893)*	Atlântico Leste, Uruguai, Atlântico Sul/Sudeste.	-	D
	Diplodon (D.) multistratus (Lea, 1834)*	Atlântico Leste, Atlântico Sul/Sudeste.	-	D
	Diplodon (D.) obsolescens (Baker, 1913)	Amazonas.	-	D
	Diplodon (D.) parallelopipedon (Lea, 1834)	Paraná/Paraguai, Uruguai.	-	D
	Diplodon (D.) parodizi Bonetto, 1960	Paraná/Paraguai, Uruguai.	-	D
	Diplodon (D.) paulista (Ihering, 1893)*	Paraná/Paraguai.	-	D
	Diplodon (D.) piceus (Lea, 1860)	Uruguai.	-	D
	Diplodon (D.) rhuacoicus (Orbigny, 1835)*	Uruguai, Atlântico Sul/Sudeste.	-	D
	Diplodon (D.) suavidicus (Lea, 1856)	Amazonas.	-	D
	Diplodon (D.) vicarius Ortmann, 1821*	Paraná/Paraguai.	-	D
	Diplodon (D.) wynami (Lea, 1860)*	Uruguai, Atlântico Sul/Sudeste.	-	D
	Diplodon (R.) burroughianus (Lea, 1834)	Paraná/Paraguai, Uruguai.	Assoreamento, erosão marginal, poluição e barramento.	CL
	Diplodon (R.) charruanus Orbigny, 1835*	Uruguai, Atlântico Sul/Sudeste.	-	D
	Diplodon (R.) deceptus Simpson, 1914 sensu Ortmann, 1921	Atlântico Sul/Sudeste.	-	D

Tabela III. Continua...

Família/Gênero	Espécie	Bacias Hidrográficas	Ameaças	S
Hyriidae			-	
	Diplodon (R.) funebralis (Lea, 1860)*	São Francisco, Paraná/Paraguai.	Assoreamento, erosão marginal e poluição, barramento.	CL
	Diplodon (R.) koseritzi (Clessin, 1882)	Atlântico Sul/Sudeste.	Assoreamento, erosão marginal e poluição, barramento e espécies invasoras.	CEP
	Diplodon (R.) hildae Ortman, 1921	Atlântico Sul/Sudeste.	-	-
	Diplodon (R.) hylaeus (Orbigny, 1835)	Amazonas, Tocantins/Araguaia e Paraná/Paraguai (?).	Assoreamento, erosão marginal e poluição, barramento.	CL
	Diplodon (R.) iheringi (Simpson, 1900)	Atlântico Sul/Sudeste.	Assoreamento, erosão marginal e poluição, barramento.	EP
	Diplodon (R.) peraeformis (Lea, 1860)	Uruguai.	Assoreamento, erosão marginal e poluição, barramento.	CL
	Diplodon fontainianus (Orbigny, 1835)*	Paraná/Paraguai.	Assoreamento, erosão marginal, poluição, barramento.	EP
	Diplodon greeffeanus Ihering, 1893*	Paraná/Paraguai.		
	Diplodon pfeifferi (Dunker, 1848)	Atlântico Leste.	Assoreamento, erosão marginal, poluição, barramento.	EP
	Diplodon paranensis (Lea, 1834)*	Paraná/Paraguai.	Assoreamento, erosão marginal, poluição, barramento.	CL
	Diplodon rotundus Wagner, 1827*	Tocantins/Araguaia, São Francisco e Paraná/Paraguai.	Assoreamento, erosão marginal, poluição, barramento.	EP
	Diplodon uruguayensis (Lea, 1860)*	Uruguai.	Assoreamento, erosão marginal, poluição, barramento.	CL
Castalia Lamarck, 1819	*Castalia ambigua* Orbigny, 1835*	Amazonas e Paraná/Paraguai.	Assoreamento, erosão marginal, poluição, barramento, barreiras à piracema e explotação.	CL
	Castalia duprei (Récluz, 1842)	Tocantins/Araguaia.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Castalia inflata Orbigny, 1835	Amazonas, Paraná/Paraguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Castalia martensi (Ihering, 1891)	Uruguai, Atlântico Sul/Sudeste.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema e espécies invasoras.	CL
	Castalia nehiringi (Ihering, 1893)	Paraná/Paraguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Castalia orbignyi (Deville & Hupé, 1850)	Amazonas.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Castalia psammoica (Orbigny, 1835)	Uruguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Castalia quadrata (Sowerby, 1869)*	Amazonas.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Castalia schombergiana Sowerby, 1869*	Amazonas.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Castalia sulcata (Krauss, 1849)*	Amazonas.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	CL
	Castalia undosa Martens, 1885	Paraná/Paraguai.	Assoreamento, erosão marginal, poluição, barramento e barreiras à piracema.	EP
Paxyodon Schumacher, 1817	*Paxyodon syrmathophorus* (Meuschen, 1781)	Amazonas, Tocantins/Araguaia.	Assoreamento, erosão marginal, poluição, barramento, barreiras à piracema e explotação.	CL

Tabela III. Continua...

Família/Gênero	Espécie	Bacias Hidrográficas	Ameaças	S
Hyriidae			-	
Prisodon Schumacher, 1817	*Prisodon obliquus* Schumacher, 1817*	Amazonas, Tocantins/ Araguaia.	Assoreamento, erosão marginal, poluição, barramento, barreiras à piracema e explotação.	CL
Triplodon Spix, 1827	*Triplodon corrugatus* (Lamarck, 1819)	Amazonas, Tocantins/ Araguaia.	Assoreamento, erosão marginal, poluição, barramento, barreiras à piracema e explotação.	CL
	Triplodon chodo Mansur & Pimpão, 2008	Amazonas.	Poluição e espécies invasoras.	CL
Dreissenidae				
Mytilopsis Conrrad, 1858	*Mytilopsis lopesi* Alvarenga & Ricci, 1989	Amazonas, Tocantins/ Araguaia.	Assoreamento, erosão marginal, poluição, barramento e espécies invasoras.	CL
Corbiculidae			-	
Cyanocyclas Blainville, 1818	*Cyanocyclas amazonica* (Prime, 1870)*	Amazonas.	-	D
	Cyanocyclas brasiliana (Deshayes, 1854)*	Amazonas.	-	D
	Cyanocyclas limosa (Maton, 1809)*	Paraná/Paraguai, Uruguai.	Assoreamento, erosão marginal, poluição e espécies invasoras.	CL
	Cyanocyclas paranensis (d'Orbigny, 1835)*	Paraná/Paraguai.	Assoreamento, erosão marginal, poluição e espécies invasoras.	CL
Corbicula Megerle Von Mühlfeld, 1811	*Corbicula fluminalis* (Müller, 1774)	Atlântico Sul/Sudeste.	-	D
	Corbicula fluminea (Müller, 1774)	Amazonas, Tocantins/ Araguaia, Atlântico Norte/ Nordeste, São Francisco, Atlântico Leste, Paraná/ Paraguai, Uruguai, Atlântico Sul/Sudeste.	-	D
	Corbicula largillierti (Philippi, 1844)	Tocantins/Araguaia, Atlântico Norte/ Nordeste, São Francisco, Atlântico Leste, Paraná/ Paraguai, Uruguai, Atlântico Sul/Sudeste.	-	D
	Corbicula sp.*	Atlântico Sul/Sudeste.	-	D
Polymesoda Rafinesque, 1828	*Polymesoda* sp.*	Amazonas, Atlântico Norte/Nordeste.	-	D
Sphaeridae			-	D
Eupera Bourguignat, 1854	*Eupera klappenbachi* Mansur & Veitenheimer, 1975	Atlântico Sul/Sudeste.	Poluição, drenagem de banhados e remoção de macrófitas.	D
	Eupera platensis Doello-Jurado, 1921	Uruguai, Atlântico Sul/Sudeste.	Poluição, drenagem de banhados e remoção de macrófitas.	D
	Eupera elliptica Ituarte & Dreher-Mansur, 1993	Paraná/Paraguai.	Poluição, drenagem de banhados e remoção de macrófitas.	D
	Eupera doellojuradoi Klappenbach, 1962	Uruguai.	Poluição, drenagem de banhados e remoção de macrófitas.	D
	Eupera bahiensis (Spix & Wagner, 1827)	Atlântico Leste.	Poluição, drenagem de banhados e remoção de macrófitas.	D
	Eupera tumida (Clessin, 1879)	Amazonas, São Francisco, Atlântico Leste, Paraná/Paraguai.	Poluição, drenagem de banhados e remoção de macrófitas.	D

Tabela III. Continua...

Família/Gênero	Espécie	Bacias Hidrográficas	Ameaças	S
Sphaeridae			-	D
	Eupera simoni (Jousseaume, 1889)	Amazonas, Paraná/Paraguai.	Poluição, drenagem de banhados e remoção de macrófitas.	D
	Eupera guaraniana Ituarte, 1994	Uruguai, Atlântico Sul/Sudeste.	Poluição, drenagem de banhados e remoção de macrófitas.	D
	Eupera iguazuensis Ituarte, 1989	Paraná/Paraguai.	Poluição, drenagem de banhados e remoção de macrófitas.	D
Sphaerium (Scopoli, 1777)	*Sphaerium cambaraense* Mansur, Meier-Brook & Ituarte, 2008	Paraná/Paraguai, Uruguai, Atlântico Sul/Sudeste.	Poluição e drenagem de banhados.	D
Musculium Link, 1807	*Musculium argentinum* (D'Orbigny, 1835)	Uruguai, Atlântico Sul/Sudeste.	Poluição e drenagem de banhados.	D
Pisidium C. Pfeiffer, 1821	*Pisidium vile* Pilsbry, 1897	Paraná/Paraguai, Uruguai, Atlântico Sul/Sudeste.	Poluição e drenagem de banhados.	D
	Pisidium dorbignyi Clessin, 1879	Paraná/Paraguai, Uruguai, Atlântico Sul/Sudeste.	Poluição e drenagem de banhados.	D
	Pisidium sterkianum Pilsbry, 1897	Amazonas, Paraná/Paraguai, Uruguai, Atlântico Sul/Sudeste.	Poluição e drenagem de banhados.	D
	Pisidium punctiferum (Guppy, 1867)*	Amazonas, Tocantins/Araguaia, São Francisco, Paraná/Paraguai, Uruguai, Atlântico Sul/Sudeste.	Poluição e drenagem de banhados.	D
	Pisidium taraguyense Ituarte, 2000	Paraná/Paraguai, Uruguai, Atlântico Sul/Sudeste.	Poluição e drenagem de banhados.	D
	Pisidium forense Meier Brook, 1967	Paraná/Paraguai, Atlântico Sul/Sudeste.	Poluição e drenagem de banhados.	D
	*Pisidium globulus**	Atlântico Sul/Sudeste.	Poluição e drenagem de banhados.	D
	Pisidium bejumae H.B. Baker, 1930*	Amazonas.	Poluição e drenagem de banhados.	D
	Pisidium boliviense Sturany, 1900*	Amazonas.	Poluição e drenagem de banhados.	D

Recomendações

Abaixo são listadas algumas ações prioritárias necessárias para minimizar os efeitos das espécies invasoras sobre as espécies nativas, assim como ações complementares visando à conservação dos bivalves nativos por meio da indução de projetos de pesquisa (básica e aplicada) e da apropriação dos dados gerados pelos gestores que atuam em órgãos ambientais, responsáveis pela conservação da biodiversidade e licenciamento ambiental no país.

Os temas prioritários de pesquisa são: impacto das espécies de bivalves límnicos invasores sobre os bivalves nativos; estudo morfológico das espécies nativas e invasoras visando à elaboração de chaves e catálogos; mapeamento das espécies nativas de bivalves citadas para o Brasil, especialmente nas bacias subamostradas; descrição do ciclo de desenvolvimento dos bivalves nativos e reconhecimento das espécies de peixes vetores e dispersores das larvas destes moluscos; relação das rotas migratórias de peixes vetores com a dispersão de bivalves límnicos; criação de espécies de bivalves límnicos para repovoamento de áreas com declínio das populações das mesmas; avaliação do impacto da construção de reservatórios em série (cascata) sobre a distribuição da malacofauna e a busca de estratégias alternativas para a conservação de espécies de bivalves típicos de água corrente, visando subsidiar o estabelecimento de medidas compensatórias e mitigadoras; reconstrução de habitats em represas e nos seus tributários para a conservação da malacofauna; monitoramento populacional das espécies invasoras e nativas; identificação de áreas para a implantação de unidades de conservação; estabelecimento de estratégias de conservação; revisão das listas de espécies ameaçadas estaduais e a nacional, visando rever a categorização das espécies enquadradas e a categorização de espécies que não constam nas listas.