Universidade Federal do Rio Grande
Instituto de Ciências Biológicas
Pós-graduação em Biologia de
Ambientes Aquáticos Continentais

Diversidade e dinâmica de microcrustáceos em áreas úmidas intermitentes

Maiby Glorize da Silva Bandeira

Orientadora: Profª. Dra. Edélti F. Albertoni
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Dedico ao meu querido Andirobal (Monte Alegre-PA)
Cujos moradores são a minha motivação diária
Eles me mantém focada nos meus objetivos
E me fazem ser mais persistente com os meus sonhos
Que de certa forma são deles também.

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Primeiramente a Deus que nunca desiste de mim. Segundo, à queridíssima profª. Edélti Albertoni que desde o meu primeiro email (no início de 2016), me aceitou e permitiu que eu realizasse mais um grande sonho na minha vida. Nunca terei palavras para expressar o carinho que ela, o prof. Cleber, a Manu e o Leandro tiveram comigo quando cheguei ao tenebroso frio do Sul. A Edélti não foi só uma orientadora, também foi mãe, amiga, conselheira e sempre nos acolheu com muito carinho, seja no laboratório ou no aconchego do seu lar. Sempre me apoiou nas minhas decisões, nas desilusões, nas conquistas, e soube me frear quando achou necessário. Muitíssimo obrigada, vou levar você como exemplo de mulher guerreira e batalhadora por toda minha vida.

A Universidade Federal do Rio Grande (FURG), em especial ao PPG em Biologia de Ambientes Aquáticos Continentais (PPG-BAC) pela oportunidade de cursar um doutorado. Isso representa muito, não só para mim, mas para inúmeras pessoas da minha pequena cidade do meio da Amazônia. Isso é um grande estímulo, principalmente para aqueles que estão trilhando o mesmo caminho (Neto e Melina, vocês serão os próximos). Sou grata pela FURG/PPGBAC me proporcionar uma inesquecível trajetória e toda estrutura necessária para realizar minha tese, que só foi possível graças ao seu incansável corpo docente (em especial, Leandro, Samantha, Garcia e Rogério), aos técnicos (Cláudio, Léo e Clara) e coordenadores (em especial, Juliano e Fabiana), além do memorável secretário Leonardo. Agradeço a Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), que aos trancos e barrancos, me proporcionou auxílio financeiro até o final dessa jornada.

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Aos meus pais Maria da Glória e Miguel Hélio que estão constantemente incentivando os meus sonhos, mesmo que isso me leve para mais longe deles, eu não seria nada se não fosse por vocês, e é como sempre digo, meu único "arrependimento de vida" foi ter que abrir mão de conviver com vocês para seguir os meus sonhos, mas sei que me entendem, pois são a minha fonte de inspiração. Aos meus incríveis irmãos Miguel Jr., Marcelo John, Maria Glorice, Misael Wayllon, Márcia Glorily e Mykson Wyrlley, vocês me inspiram e estão sempre me incentivando, assim como incentivo vocês.

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RESUMO

Áreas úmidas são ambientes aquáticos considerados *hotspots* de biodiversidade, esses ambientes apresentam características hidrológicas diferentes, podendo ser permanentes ou temporários, dependentes principalmente das condições climáticas sazonais da região. Entre os grupos aparentes, os microcrustáceoas apresentam adaptações que permitem sua permanência nesses sistemas. Então, analisar a diversidade e dinâmica das espécies nesses ambientes possibilita entender os mecanismos que ditam os padrões espaciais e temporais da organização das comunidades em áreas úmidas, particularmente nas intermitentes. Com isso, o objetivo geral dessa tese foi estudar a diversidade e dinâmica dos microcrustáceos em áreas úmidas intermitentes, respondendo as seguintes questões: i) Qual a tendência global dos estudos com microcrustáceos em cultivos de arroz, e o potencial deste ambiente como estoque de biodiversidade? Para isso, foi realizada uma análise cienciométrica global e compilados 77 estudos com microcrustáceos de cultivos de arroz, nas bases de dados Web of Science e Scopus, entre 1977 e 2019. Destes, foram quantificadas 301 espécies de seis grupos de microcrustáceos, distribuídas em 18 países. Com isso, foi possível registrar que os cultivos de arroz têm potencial para estocar a diversidade desses organismos. ii) Como as espécies endêmicas (*Branchinecta iheringi* e *Eulimnadia pampa*) da região subtropical do hemisfério Sul estão respondendo aos diferentes hidroperíodos do ano? Para isso, foram acompanhados quatro hidroperíodos consecutivos, onde o tempo de permanência da água e a variação de temperatura tiveram efeito significativo no restabelecimento das espécies. Com acompanhamento das estratégias de eclosão, foi visto que *B. iheringi* responde de imediato aos estímulos de eclosão enquanto *E.pampa* precisa de um tempo maior para eclodir. iii) Qual a influência do tempo de hidratação e da temperatura na eclosão de microcrustáceos, comparando abordagens *in situ* e *ex situ*? Para isso, foram acompanhados 34 dias de hidroperíodo *in situ* e testadas três temperaturas em 30 dias no laboratório. Em ambas abordagens, foram registrados 41 táxons de cinco grupos de microcrustáceos, e o tempo de hidratação foi o fator mais importante na eclosão. Em laboratório, o aumento da temperatura afetou positivamente a eclosão e nas duas abordagens, o início do tempo de hidratação foi o período mais importante para a eclosão.

Palavras-chave: ambientes aquáticos; dormência; estímulos de eclosão; ecologia de comunidades; zooplâncton

ABSTRACT

Wetlands are aquatic environments considered hotspots of biodiversity, these environments have different hydrological characteristics, which may be permanent or temporary, depending mainly on the seasonal climatic conditions of the region. Among the apparent groups, microcrustaceans have adaptations that allow them to remain in these systems. Then, analyzing the diversity and dynamics of species in these environments makes it possible to understand the mechanisms that dictate the spatial and temporal patterns of the organization of communities in wetlands, particularly in intermittent areas. With that, the general objective of this thesis was to study the diversity and dynamics of microcrustaceans in intermittent wetlands, answering the following questions: i) what is the global trend of studies with microcrustaceans in rice fields, and the potential of this environment as a stock of biodiversity? For this purpose, a global scientometric analysis was carried out and 77 studies with rice field microcrustaceans were compiled in the Web of Science and Scopus databases between 1977 and 2019. Of these, 301 species from six groups of microcrustaceans, quantified in 18 countries, were quantified. With that, it was possible to register that the rice fields have the potential to store the diversity of these organisms. ii) How are endemic species (*Branchinecta iheringi* and *Eulimnadia pampa*) from the subtropical region of the southern hemisphere responding to the different hydroperiods of the year? For this, four consecutive hydroperiods were followed, where the water permanence time and the temperature variation had a significant effect on the restoration of the species. With monitoring of hatching strategies, it was seen that *B. iheringi* responds immediately to hatching stimuli while *E.pampa* needs more time to hatch. iii) What is the influence of hydration time and temperature on the hatching of microcrustaceans, comparing *in situ* and *ex situ* approaches? For that, 34 days of hydroperiod *in situ* were followed and three temperatures were tested in 30 days in the laboratory. In both approaches, 41 taxa from five groups of microcrustaceans were recorded, and the hydration time was the most important factor in hatching. In the laboratory, the increase in temperature positively affected hatching and in both approaches, the beginning of the hydration time was the most important period for hatching.

Key-words: aquatic environments; dormancy; hatching stimuli; community ecology; zooplankton

APRESENTAÇÃO

Esta tese é produto do projeto que desenvolvi no curso de Doutorado em Biologia de Ambientes Aquáticos Continentais (PPGBAC), na Universidade Federal do Rio Grande (FURG), entre 2016 e 2020. Nesta, busquei conhecer a diversidade de microcrustáceos de áreas úmidas intermitentes e como esses organismos se estruturam e permanecem nesses ambientes tão instáveis e frágeis. Ao logo dos capítulos, abordei aspectos ecológicos e reprodutivos de seis grupos de microcrustáceos, incluindo dados globais, até espécies endêmicas de áreas úmidas subtropicais.

A tese está estruturada em introdução geral, três capítulos, considerações finais e perspectivas. A **introdução geral** está formatada nas normas da Associação Brasileira de Normas Técnicas (ABNT). Nesta seção, é onde contextualizo os capítulos, abordando a caracterização das Áreas Úmidas intermitentes, aspectos ecológicos e reprodutivos dos microcrustáceos, e a importância de estudar a diversidade e a dinâmica desses organismos nesses ambientes.

O Capítulo 1 é intitulado **"Microcrustaceans in rice fields: a scientometric analysis"**, e foi submetido nos *Anais da Academia Brasileira de Ciências*. Neste capítulo nós avaliamos as tendências mundiais em estudos das formas ativas e dormentes de microcrustáceos em cultivos de arroz e o potencial desse ambiente como estoque de diversidade por meio de uma análise cienciométrica. Verificamos que apenas 15,5% dos países produtores de arroz identificaram a riqueza de microcrustáceos em suas lavouras. Embora sejam ambientes artificiais, os cultivos de arroz possuem alto potencial para armazenar a diversidade de microcrustáceos.

O Capítulo 2 é intitulado **"Strategy for the hatching of microcrustaceans endemic to intermittent environments along hydroperiods"**, e foi publicado como capítulo no livro 'Crustáceos: ecossistema, classificação e reprodução', organizado por Luciana do Nascimento Mendes, e editado pela *Atena Editora*, em 2019. Neste capítulo nós acompanhamos a estratégia de eclosão de *Branchinecta iheringi* LILLJEBORG, 1889 (Branchiopoda: Anostraca) and *Eulimnadia pampa* MARINONE; URCULA; RABET, 2016 (Branchiopoda: Diplostraca), em diferentes hidroperíodos do ano. As duas espécies apresentaram respostas diferentes aos hidroperíodos anuais, mesmo quando aparecem no mesmo hidroperíodo, cada uma predomina em tempos diferentes. Essas espécies aparentemente estão investindo principalmente na produção de ovos dormentes, fortalecendo a manutenção do banco de ovos dos sedimentos nas áreas úmidas intermitentes.

O Capítulo 3 é intitulado "**Hydration time influences microcrustacean hatching in intermittent wetlands: *in situ* and *ex situ* approaches**" e foi publicado no periódico

Hydrobiologia em 2020. Nós analisamos a influência do tempo de hidratação e da temperatura na eclosão de microcrustáceos, comparando as abordagens *in situ* e *ex situ*. Nossos resultados exploraram alguns mecanismos gerais do processo de eclosão que podem se aplicar a áreas úmidas intermitentes em regiões subtropicais, onde a variação diária de luz e temperatura é menos aguda do que a disponibilidade de água. Nosso registro de 41 táxons em três áreas úmidas reforça a importância de mais estudos e da conservação de áreas úmidas intermitentes em regiões subtropicais. Esses ambientes são frequentemente ameaçados pela agricultura e urbanização, além disso, mudanças no clima global podem alterar os estímulos de eclosão e afetar negativamente o surgimento de microcrustáceos, especialmente para espécies que precisam de um tempo de hidratação maior para emergir.

As **considerações finais e perspectivas** estão formatadas nas normas da ABNT. Nesta seção apresento uma breve discussão dos principais achados ao longo dos capítulos e o impacto desses resultados para a conservação da diversidade de microcrustáceos e das áreas úmidas intermitentes. Além disso, na apresentação de cada capítulo estão disponíveis os dados dos manuscritos publicados, além do local de publicação e as normas de formatação.

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INTRODUÇÃO GERAL

Compreender os mecanismos que determinam a interação das espécies com o ambiente em que vivem representa um dos principais desafios da Ecologia de Comunidades (ROSENZWEIG, 1995). Este assunto é de amplo interesse devido ao reconhecimento de que o aumento do impacto antrópico no meio ambiente afeta a diversidade, distribuição e dinâmica das espécies (CARDINALE et al., 2012). Assim, analisar a diversidade e dinâmica das espécies pode fornecer *insights* sobre os mecanismos subjacentes que ditam os padrões espaciais e temporais de organização das comunidades (COTTENIE, 2005). Além disso, pode resultar na previsão de como as comunidades podem potencialmente responder a mudanças nos fatores abióticos dos ambientes (CHASE, 2007; VAN ALLEN et al., 2017), principalmente em ambientes aquáticos instáveis como as áreas úmidas (DAVIS et al., 2016; MARTINS et al., 2019; BUSH et al., 2020).

Áreas úmidas: definições, classificações, funções e ameaças

As áreas úmidas (AUs) são mundialmente distribuídas (Figura 1) estando entre os ecossistemas aquáticos mais ameaçados do mundo (HEITMEYER et al., 2013). Esses ambientes são considerados como *hotspot* de biodiversidade, pois apresentam uma grande biodiversidade e alto endemismo (VAN COPPENOLLE; TEMMERMAN, 2020), características hidrológicas naturalmente instáveis, além de em sua maioria estarem frequentemente expostas às ações antrópicas, (JUNK et al., 2013). Para proteger esses ambientes, foi estabelecida a Convenção de Ramsar, tratado intergovernamental estabelecido em fevereiro de 1971, na cidade iraniana de Ramsar (MMA, 2020) visando a proteção de áreas úmidas de importância internacional, criada inicialmente para proteger os habitats aquáticos importantes para a conservação de aves migratórias (JUNK et al., 2013). Ao longo do tempo, houve um aumento na preocupação com as demais áreas úmidas, ocorrendo à ampliação do Tratado para promover a conservação e o uso sustentável, assim como o bem-estar das populações humanas que dependem desses ambientes (MMA, 2020).

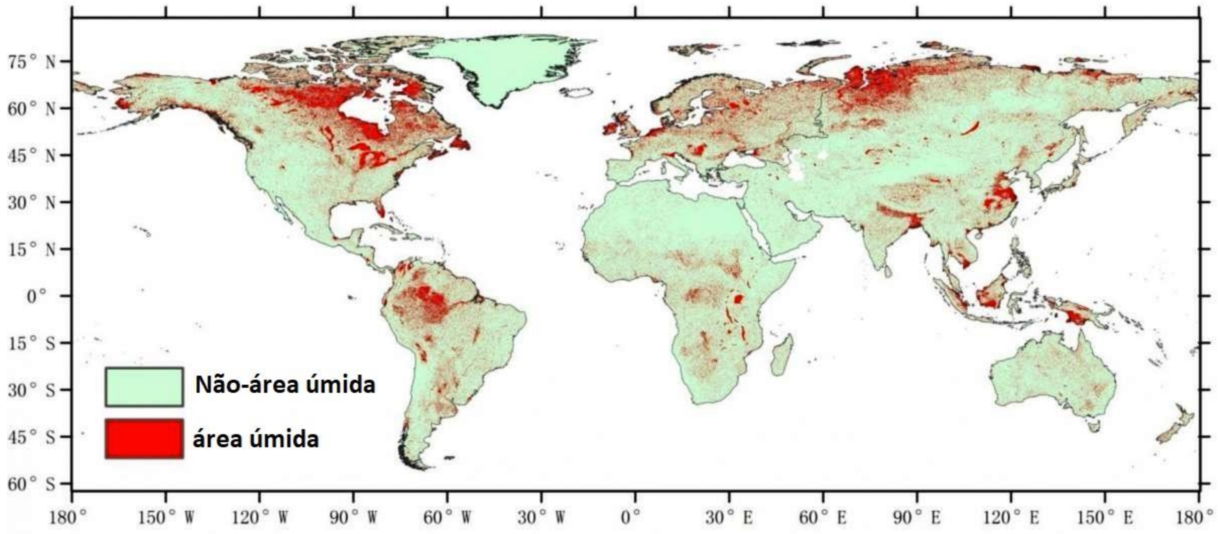


Figura 1: Distribuição das áreas úmidas no globo terrestre (Modificada de ZHU; GONG, 2014).

A Convenção de Ramsar tem o propósito de conservação das AUs no nível internacional, porém somente depois de 25 anos foi incorporada no Brasil, pelo Decreto nº 1.905/96 (MMA, 2020). O decreto de inclusão ocorreu depois de realizados inventários, no qual foi descrito que o Brasil tem a maior concentração de AUs do mundo (DIEGUES, 1994; JUNK et al., 2013). A partir disso, se estabeleceram programas como o "IUCN *wetlands programe"*, da União Internacional para Conservação da Natureza (IUCN), representado pela Universidade de São Paulo (JUNK et al., 2013). Programas como este tem o objetivo de estimular organizações governamentais e não governamentais a elaborar propostas de iniciativas para o desenvolvimento sustentável e preservação das áreas úmidas. Com isso, houve um avanço das pesquisas e a maior percepção da necessidade de conservação desses ambientes. Depois disso, ocorreu a criação do Instituto Nacional de Ciência e Tecnologia em Áreas Úmidas (INAU), no pantanal mato-grossense, que vem trabalhando em parceria com grupos de pesquisas de todo território nacional (JUNK et al., 2013). A partir desta parceria foram estabelecidas definições e classificações para servir como base científica para políticas de proteção e manejo sustentável das áreas úmidas brasileiras (JUNK et al., 2013).

De acordo com a Convenção de Ramsar, as áreas úmidas são conceituadas como áreas de pântano, charco, turfa ou água natural ou artificial, permanente ou temporária, com água estagnada ou corrente, doce, salobra ou salgada, incluindo áreas de água marítima com menos de seis metros de profundidade na maré baixa (MMA, 2020). Porém, esse é um conceito genérico, entãoem 2013, considerando suas particularidades no Brasil, as áreas úmidas foram definidas como ecossistemas na interface entre ambientes terrestres e aquáticos, continentais ou costeiros, naturais ou artificiais, permanente ou periodicamente inundados ou com solos encharcados (JUNK et al., 2013). As águas podem ser doces, salobras ou salgadas, com comunidades de plantas e animais adaptados à sua dinâmica hídrica (JUNK et al., 2013). As AUs têm como principais características, uma extensão constante ou provisoriamente alagada, solo saturado e rico em matéria orgânica, características físicas e químicas particulares e a colonização de uma biota adaptada morfológica e fisiologicamente aos períodos com água (hidroperíodos) desses ambientes (CARVALHO; OZORIO, 2007; MALTCHIK et al., 2010; STENERT et al., 2012).

A classificação de AUs é importante para a elaboração de inventários, planejamento de bacias hidrográficas, avaliação da biodiversidade e reconhecimentode suas funções (MALTCHIK et al., 2004). A partir da categorização de MALTCHIK (2003), uma das classificações feita por JUNK et al. (2013) foi a respeito da localização desses ambientes, que podem ser categorizadas como áreas úmidas interiores, encontradas no interior do Brasil e as áreas úmidas costeiras, localizadas nas planícies costeiras do país, além de áreas úmidas antropogênicas (Figura 2). As interiores são as AUs naturais, permanentes ou temporárias, com água doce, salobra e salgada, que se encontram dentro do país e fora da influência direta ou indireta do mar (e.g., pantanal, igapó, várzea, lavrado, banhado e charco). As costeiras são as AUs naturais, permanentes ou temporárias, com água doce, salobra e salgada, sob influência direta do regime de marés, de intrusões salinas, ou de deposição atmosférica de substâncias dissolvidas ou particuladas, ou de propágulos do oceano (e.g., restingas e manguezais). As antropogênicas são as AUs, costeiras ou interiores, que resultam da atividade humana, sejam de forma ordenada (e.g., tanques de piscicultura, açudes e cultivos de arroz) ou não ordenada (e.g., AUs no entorno de represas hidrelétricas e represamentos pela construção de estradas).

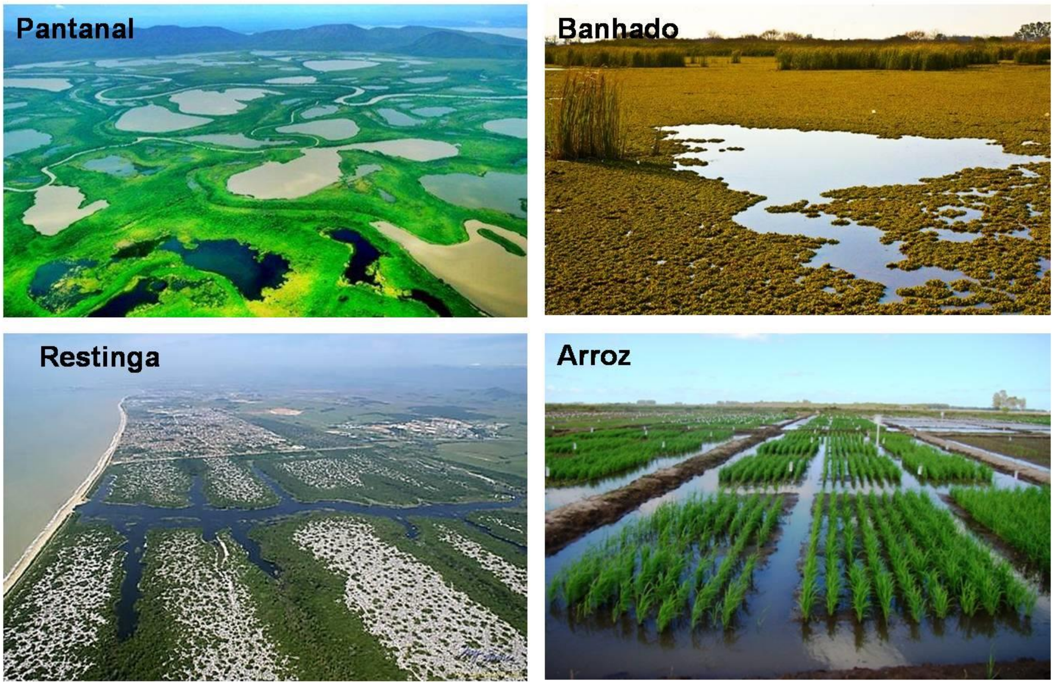


Figura 2: Exemplos de áreas úmidas interiores (áreas úmidas do pantanal e banhado), costeira (restinga) e antropogênicas (cultivos de arroz) encontradas no Brasil (modificadas do Google imagens).

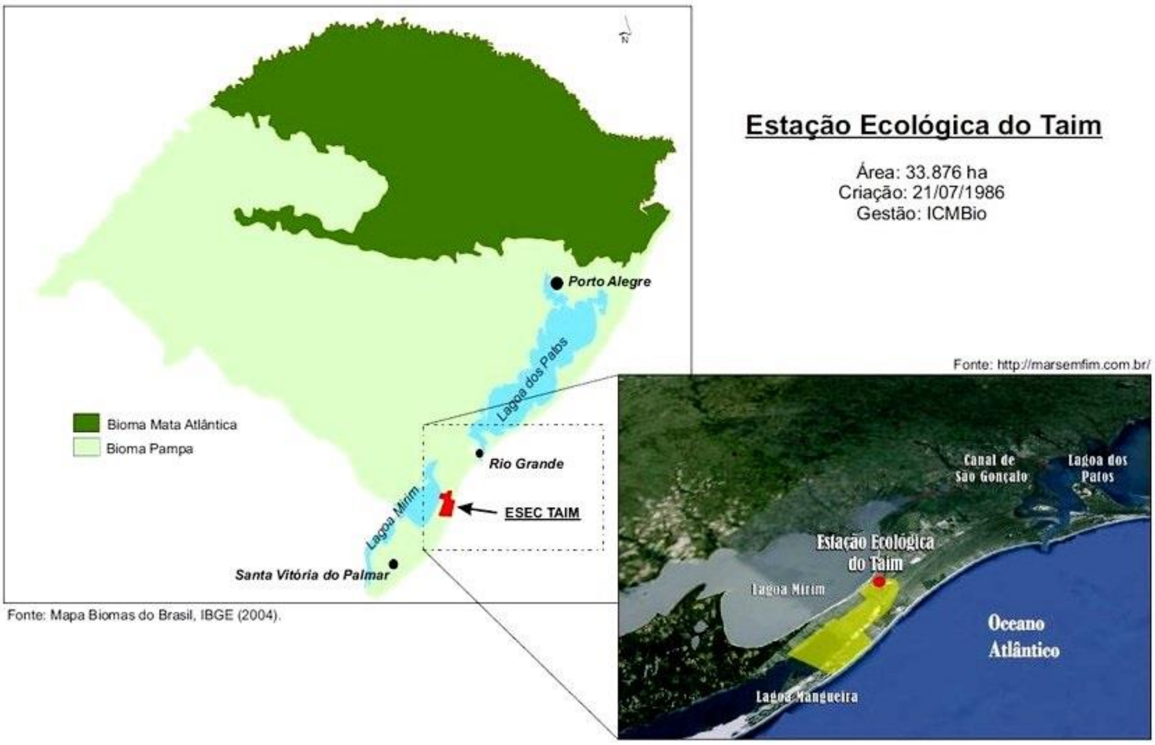
Para o Estado do Rio Grande do Sul foi registrado um total de 3.441 áreas úmidas interiores, costeiras e antropogênicas (MALTCHIK, 2003). De acordo com a permanência da água, essas áreas úmidas são categorizadas em permanentes, quando o ambiente é coberto por água ou que têm solos permanentemente saturados, e intermitentes ou temporárias que são periodicamente inundados (VAN DER VALK, 2006). Nas AUs, a variação do nível da água, ou o hidroperíodo são influenciados sazonalmente, sendo a água evaporada total ou parcialmente no verão e retomada no inverno, podendo ser abastecida por lagoas, afloramentos do lençol freático ou de precipitação pluviométrica (CARVALHO; OZORIO, 2007).

As AUs exercem inúmeras funções como recarga dos aquíferos e do lençol freático, retenção de sedimentos, purificação da água, fornecimento de água limpa, dessedentação de animais silvestres e domésticos, irrigação de lavouras, regulagem do microclima, recreação (banho, pesca, lazer), ecoturismo, manutenção da biodiversidade, estocagem de carbono e moradia para populações tradicionais (VAN DER VALK, 2006). Apesar de serem ambientes com elevada importância, as áreas úmidas estão entre os ecossistemas com maior perda entre os ecossistemas aquáticos, e estão sofrendo alterações principalmente pela urbanização e agricultura (MARQUES et al., 2000), o que tem causado intensa fragmentação destes ambientes (VAN DER VALK, 2006; MALTCHIK et al., 2010; STENERT et al., 2012). Devido à fragmentação das áreas úmidas para diferentes usos do solo, pode ocorrer modificação na estrutura e na dinâmica das comunidades aquáticas, assim como, a perda da diversidade (MARQUES et al., 2000; MALTCHIK et al., 2004; ALBERTONI et al., 2007).

A expansão urbana desordenada causa fragmentação das áreas úmidas devidas novas construções, ocorrendo também a contaminação da água e do solo por químicos e depósito de lixo urbano (MARQUES et al., 2000; MALTCHIK et al., 2004; ALBERTONI et al., 2007; CARVALHO; OZORIO, 2007). Na agricultura, a maior ameaça é a rizicultura que causa a redução das áreas naturais, através da drenagem e retirada da vegetação, a compactação e salinização do solo, variação do nível do lençol freático, erosão ou assoreamento, e contaminação da água por agrotóxicos (MARQUES et al., 2000; CARVALHO; OZORIO, 2007; MALTCHIK et al., 2010; STENERT et al., 2012).

Os cultivos de arroz irrigado têm gerado discussões interessantes, pois apesar de serem uma ameaça aos ambientes naturais, eles foram apontados como refúgios para a biodiversidade das áreas úmidas (ROLON; MALTCHIK, 2010). Os cultivos de arroz apresentam rápidas mudanças físicas e químicas, abrigando organismos com histórias de vida curtas e rápidas sucessões ecológicas (ROSSI et al., 2003). Por exemplo, já foi relatado que as lavouras podem ajudar a conservar uma importante fração da diversidade de macrófitas aquáticas, causando grande disponibilidade de habitats para invertebrados aquáticos (MALTCHIK et al., 2010). Quando verificada a riqueza de invertebrados aquáticos desses ambientes, foi possível constatar que há uma grande diversidade, tanto nos cultivos, como nos canais de irrigação (ROLON; MALTCHIK, 2010). Mesmo assim, a drenagem e retirada da vegetação, a compactação e salinização do solo, e contaminação da água por agrotóxicos, pode causar a redução da diversidade (MARQUES et al., 2000; CARVALHO; OZORIO, 2007; MALTCHIK et al., 2010; STENERT et al., 2012). Devido ao cultivo de arroz apresentar um regime hidrológico dinâmico, com variação entre fase aquática (safra) e terrestre (entressafra) por causa da irrigação (ROLON; MALTCHIK, 2010), a dinâmica das comunidades pode ser facilitada por migração das áreas úmidas circundantes (ELPHICK, 2000).

O aumento da fragmentação e a expansão dos cultivos nas áreas úmidas naturais são preocupantes, pois com o desaparecimento desses ambientes há uma influência negativa direta na biodiversidade, uma vez que ocorre a diminuição da riqueza das espécies, alterando principalmente a composição das comunidades aquáticas e os serviços ecossistêmicos que essas áreas oferecem (ROLON; MALTCHIK, 2010). Uma alternativa para a diminuição da influência antrópica e controle na perda de biodiversidade é a criação de unidades de conservação. Por exemplo, ao sul do Rio Grande do Sul encontra-se a Estação Ecológica do Taim (ESEC Taim; Figura 3), unidade de conservação federal que se constitui em um mosaico de ecossistemas, entre eles grande quantidade de áreas úmidas permanentes e intermitentes (MARQUES et al., 2000).



Fonte: http://marsemfim.com.br/

Fonte: Mapa Biomas do Brasil, IBGE (2004).

Figura 3: Localização da Estação Ecológica do Taim, na planície costeira Sul do Rio Grande do Sul (Modificado de SIMIONI; WOLLMANN, 2016).

A ESEC Taim possui áreas úmidas naturais com poucos impactos antrópicos e pode funcionar como área de referência, em comparação com áreas que sofrem contínuas alterações como as urbanas e agrícolas. Isso também possibilita a conservação tanto da biodiversidade, quanto das áreas úmidas (MARQUES et al., 2000). Após 21 anos que a Convenção de Ramsar foi incorporada no Brasil, a ESEC Taim foi regulamentada, em 2017, como um sítio Ramsar (MMA, 2020), o que indica um grande passo para a conservação das áreas úmidas do Rio Grande do Sul. Porém, mesmo com os avanços dos estudos sobre a biodiversidade, algumas lacunas sobre as comunidades aquáticas ainda faltam ser preenchidas, principalmente de áreas úmidas intermitentes dentro e fora das áreas de conservação, pois a maioria dos inventários foi realizada nas lagoas e lagunas presentes na planície costeira do Rio Grande do Sul (MARQUES et al., 2000; CARVALHO; OZORIO, 2007).

Mesmo com algumas lacunas, é perceptível que ao longo dos anos tem aumentado o interesse em conhecer a biodiversidade e a dinâmica das áreas úmidas do Rio Grande do Sul. Por exemplo, já se estudou o potencial da produção de gás carbônico no sedimento das áreas úmidas e as possíveis implicações do uso do solo para a agricultura (FURLANETTO et al., 2018), como a temperatura e o escoamento superficial afetam a comunidade de diatomáceas perifíticas e os efeitos nos grupos funcionais (SILVA et al., 2019), como grupos funcionais de macrófitas elucidam o papel relativo dos fatores ambientais e espaciais na riqueza de espécies e estrutura da assembléia (TRINDADE et al., 2018). Também foram avaliados aspectos da diversidade de macrófitas e macroinvertebrados aquáticos (MALTCHIK et al., 2010; STENERT et al., 2012; CONCEIÇÃO et al., 2020), da estrutura trófica das assembléias de anfíbios (HUCKEMBECK et al., 2020) e a distribuição e conservação de peixes anuais (VOLCAN et al., 2010). Isso demonstra que para o funcionamento das áreas úmidas, em um panorama geral, alguns componentes (e.g. produtores e consumidores secundários) já são bem conhecidos e estabelecidos nesses ambientes. Porém, ainda há a necessidade de conhecer quem são os consumidores primários e sua importância para a dinâmica das áreas úmidas (MARTINS et al., 2019; BANDEIRA et al., 2020).

Microcrustáceos: aspectos biológicos e ecológicos para colonização em áreas úmidas

Uma comunidade que tem sido pouco abordada para as áreas úmidas da planície costeira sul do Rio Grande do Sul, e que é relatada para áreas úmidas de outros países como uma das mais abundantes, é a comunidade de microcrustáceos (MARQUES et al., 2000; BOIX et al., 2001; SEMINARA et al., 2008; FRISCH et al., 2009). Os organismos que a compõe têm grande importância para as funções ecossistêmicas desses ambientes (ESTEVES, 2011), pois, apresentam variados hábitos alimentares, influenciando no ciclo de matéria, e sendo um elo importante na transferência de energia entre produtores e consumidores secundários (Figura 4; MASCLAUX et al., 2014).

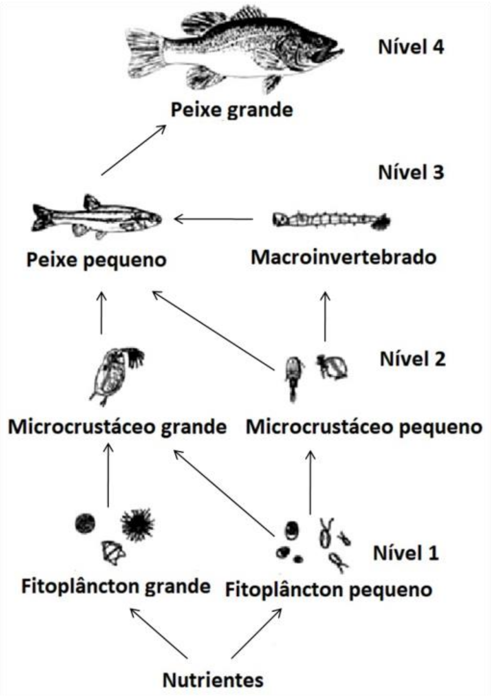


Figura 4: Exemplo de uma cadeia trófica de ambientes aquáticos, com quatro níveis de tranferência de energia entre produtores e consumidores (Modificada de FRAGOSO et al., 2009).

Os microcrustáceos (Arthropoda: Crustacea) são animais de pequeno porte (a maioria é microscópica), com ciclo de vida curto (dias ou semanas), que normalmente são encontrados em ambientes de água doce e salgada (STENERT et al., 2010; ÁVILA et al., 2015; SMITH et al., 2018; SMITH et al., 2019). Os representantes encontrados nas áreas úmidas pertecem aos grupos dos Amphipoda, Anostraca, Cladocera, Conchostraca, Copepoda e Ostracoda (Figura 5), e nesses ambientes podem ou não serem abundantes e resistentes devido às perturbações físicas e químicas (STENERT et al., 2010; ÁVILA et al., 2015; SMITH et al., 2018; SMITH et al., 2019).

Para os seis grupos de microcrustáceos há 7.697 espécies descritas em diversos ambientes naturais de água doce (BRENDONCK et al., 2008; BOXSHALL; DEFAYE, 2008; FORRÓ et al., 2008; MARTENS et al., 2008; VÄINÖLÄ et al., 2008). Essa diversidade de microcrustáceos está distribuída em 1.870 espécies de Amphipoda (VÄINÖLÄ et al., 2008), 307 espécies de Anostraca (BRENDONCK et al., 2008), 620 espécies de Cladocera (FORRÓ et al., 2008), 150 espécies de Conchostraca (BRENDONCK et al., 2008), 2.814 espécies de Copepoda (BOXSHALL; DEFAYE, 2008) e 1.936 espécies de Ostracoda (MARTENS et al., 2008).

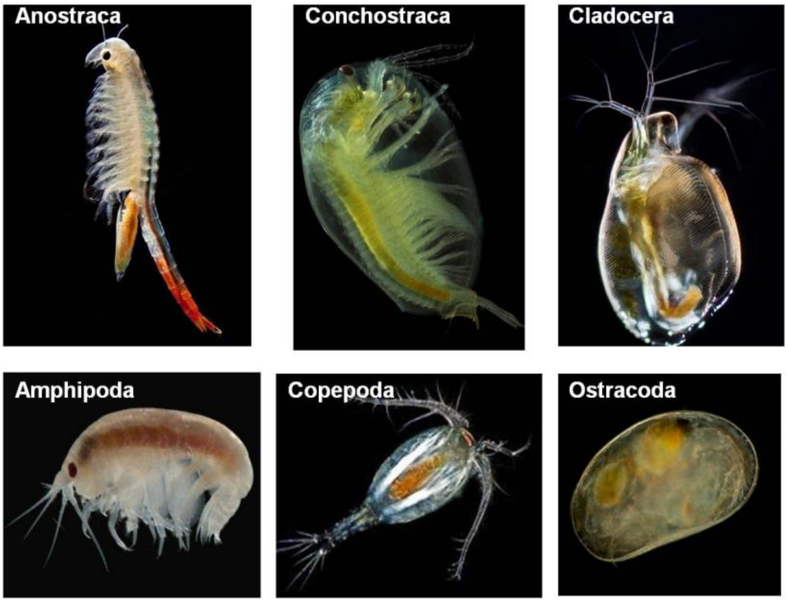


Figura 5: Grupos de microcrustáceos encontrados em áreas úmidas (Modificadas do Planeta Invertebrado Brasil: http://www.planetainvertebrados.com.br).

Amphipoda é uma ordem da classe Malacostraca, com comprimento do corpo dos organismos variando entre 2 e 40 mm. Apresentam reprodução sexuada, com machos e fêmeas no ambiente (Figura 6), e os organismos apresentam desenvolvimento direto, sem estágios larvais. A maioria das espécies são epibentônicas (colonizam substratos orgânicos vivos), bentônicas (vivem em substratos orgânicos ou inorgânicos na região de fundo) ou subterrâneas (vivem enterradas no sedimento) e vivem nos variados ambientes aquáticos (VÄINÖLÄ et al., 2008).

Figura 6: Macho e fêmea representantes de Amphipoda (Modificada de ARTAL, 2018).

Anostraca é uma ordem da classe Branchiopoda, caracterizam-se por não possuir uma carapaça e estarem constantemente nadando de costas na coluna d'água. Apresentam tamanho médio entre 6 e 25 mm, podendo atingir até 1 cm. Os organismos apresentam reprodução sexuada e estágios de desenvolvimento entre náuplius, juvenis e adultos (Figura 7). As espécies são planctônicas (vivendo na região limnética), onde a maioria são filtradoras onívoras, filtrando indiscriminadamente as partículas da coluna d'água. Todos os representantes que vivem em água doce são específicos de áreas úmidas temporárias e por isso são muito utilizados para avaliar a qualidade e a função desses ambientes (BRENDONCK et al., 2008).

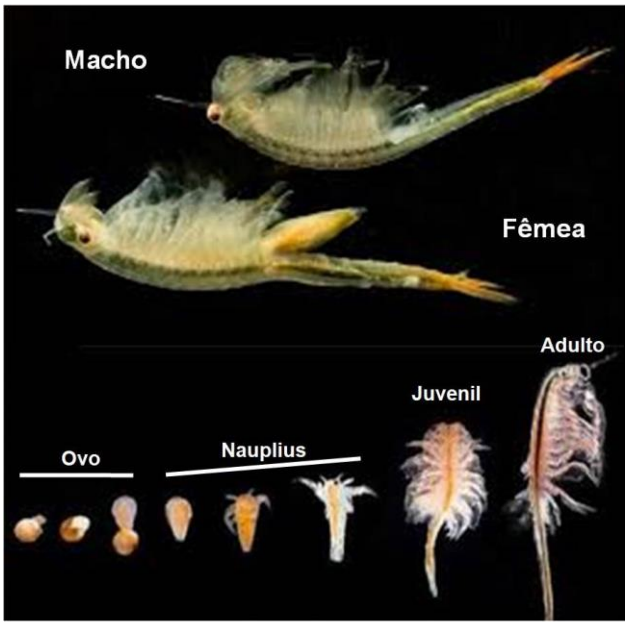


Figura 7: Macho, fêmea e estágios de desenvolvimento (ovo, nauplius, juvenil e adulto) de Anostraca (Modificada de PINTO, 2019).

Cladocera é uma subclasse da classe Branchiopoda, os organismos apresentam tamanho entre 0,2 e 18 mm. Normalmente, ocorrem somente fêmeas, e se reproduzem por partenogênese cíclica, caracterizada por apresentar principalmente uma fase assexuada, no entanto, em eventos específicos ocorre uma fase sexuada, tendo a produção de machos e fêmeas gametogênicas (Figura 8). Os organismos apresentam desenvolvimento direto, sem estágios larvais. Os representantes são encontrados nos diversos ambientes aquáticos e podem ser planctônicos, bentônicos ou epibentônicos, com a maioria das espécies sendo filtradora e pouquíssimas são predadoras (FORRÓ et al., 2008).

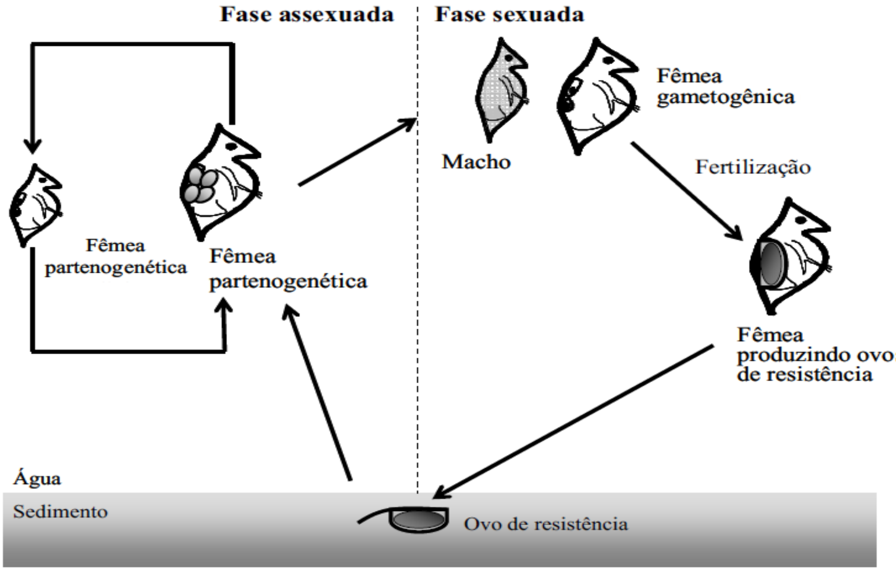


Figura 8: Reprodução de Cladocera através da partenogênese cíclica, com uma fase assexuada e outra sexuada (Modificada de SANTANGELO, 2009).

Conchostraca é uma ordem da classe Branchiopoda, os organismos apresentam tamanho entre 3,2 e 10 mm. A reprodução é essencialmente partenogênica, porém em eventos específicos ocorrem machos e fêmeas (Figura 9) nas populações e a reprodução passa a ser sexuada. Os organismos apresentam desenvolvimento direto, sem estágios larvais. Este grupo tem representantes bentônicos e epibentônicos, normalmente ficam imóveis no fundo, ou parcialmente enterrados no substrato, eles são filtradores onívoros, se alimentando de detritos, microrganismos ou algas. A maioria dos representantes desse grupo vive especificamente em áreas úmidas temporárias (BRENDONCK et al., 2008).

Figura 9: Macho, fêmea e ovos de Conchostraca (Imagens de Jean-François Cart: http://www.planetainvertebrados.com.br).

Copepoda é uma subclasse da classe Maxillopoda, e seus representantes apresentam tamanho entre 1 e 5mm. A reprodução é sexuada, e os organismos têm estágios de desenvolvimento, com náuplius, copepodito e adultos (Figura 10). Os representantes são encontrados nos variados ambientes aquáticos, onde a maioria é planctônica, uma minoria é bentônica e outra minoria é parasita de peixes e moluscos. Os de vida livre são filtradores, se alimentando de algas ou detritos suspensos (BOXSHALL; DEFAYE, 2008).

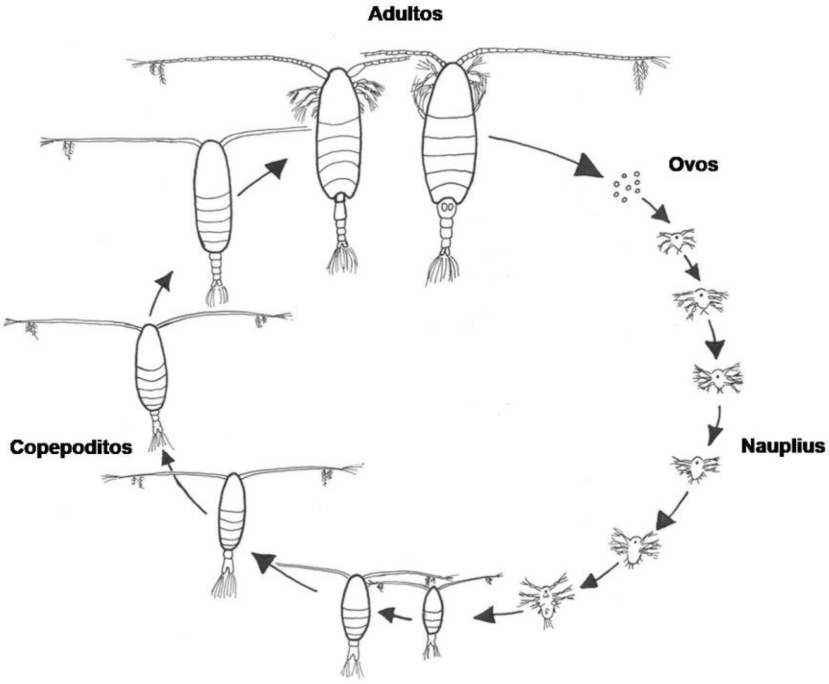


Figura 10: Estágios de desenvolvimento (ovo, nauplius, copepodito e adultos) de Copepoda (Modificada do projeto NOAA: https://www.st.nmfs.noaa.gov/copepod/about/).

Ostracoda é uma classe do subfilo Crustacea, com organismos de tamanho entre 0,1 e 32 mm. A reprodução pode ser assexuada ou sexuada, dependendo da espécie. Os organismos têm desenvolvimento direto, sem estágios larvais e tem machos e fêmeas nas populações (Figura 11). Os representantes são encontrados nos variados ambientes aquáticos e podem ser bentônicos ou epibentônicos, algumas espécies já foram registradas em ambientes terrestres vivendo dentro de plantas como bromélias. Eles podem ser filtradores onívoros, se alimentando de partículas orgânicas suspensas e detrito (MARTENS et al., 2008).

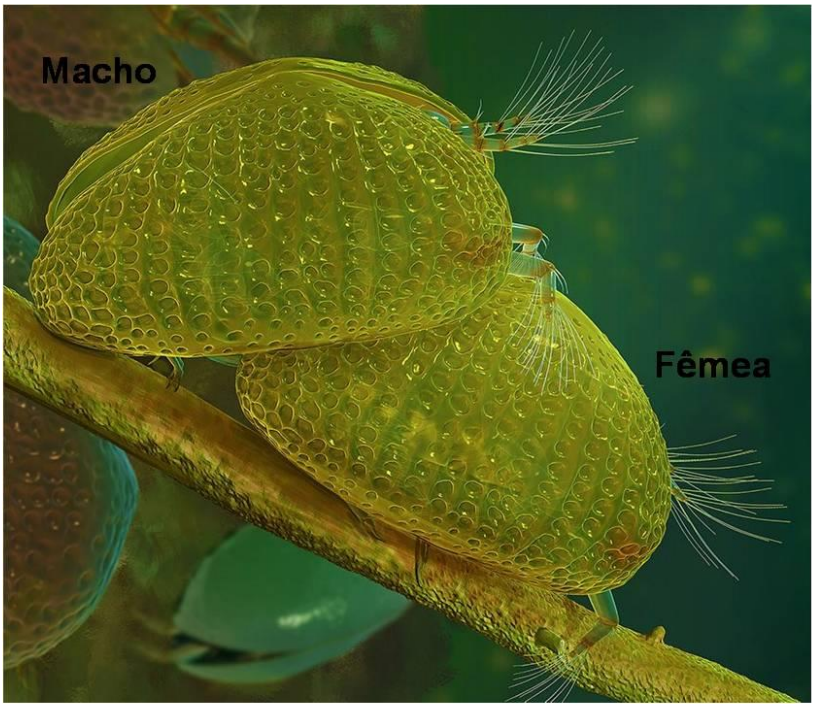


Figura 11: Macho e fêmea de Ostracoda (Imagem de Dinghua Yang: http://www.planetainvertebrados.com.br).

Os microcrustáceos têm sua história de vida influenciada por inúmeros fatores abióticos e bióticos, que podem afetar positiva ou negativamente a sobrevivência, crescimento e reprodução (SANTANGELO, 2009). Quando expostos às condições adversas (e.g. período sem água nos ambientes intermitentes), os microcrustáceos podem apresentar alterações na morfologia, no comportamento e até na história de vida, com propósito de fazer a manutenção de seus genótipos e também a persistência da comunidade no ambiente (BRENDONK; DE MEESTER, 2003). Assim, a capacidade de produzir formas dormentes é um aspecto marcante do ciclo de vida desses organismos, uma vez que permite ao indivíduo ou à sua prole sobreviver às condições muitas vezes letais às formas ativas (BRENDONK; DE MEESTER, 2003; SANTANGELO, 2009).

Nos microcrustáceos a dormência pode ocorrer através de dois mecanismos distintos, a quiescência e a diapausa (ALEKSEEV et al., 2007). A quiescência é uma forma de hibernação e é estimulada por condições ambientais desfavoráveis (e.g., super população, seca dos ambientes), onde a interrupção do desenvolvimento dos indivíduos é temporária e reversível, representantes de Copepoda Cyclopoida utilizam essa estratégia. A diapausa exige a formação de estágios específicos (ovos) tolerantes às condições desfavoráveis, chamados de ovos dormentes ou de resistência, representantes dos seis grupos de microcrustáceos utilizam essa estratégia. Quiescência e diapausa são dois processos independentes e exclusivos, ou seja, uma espécie não possui os dois mecanismos (ALEKSEEV et al., 2007).

Depois de produzidas, as formas dormentes podem flutuar na tensão superficial da água até as margens, ou decantar e se acumular no sedimento por grandes intervalos de tempo (BRENDONK; DE MEESTER, 2003; ALEKSEEV et al., 2007; SANTANGELO, 2009). Com o acúmulo no sedimento, ocorre a formação de um banco de formas dormentes, que é análogo ao banco de sementes em vegetais (DESTASIO, 1989). Esse banco é formado por inúmeras espécies, que produzem formas dormentes em diferentes momentos (BRENDONK; DE MEESTER, 2003). Dependendo da taxa de sedimentação dos ambientes aquáticos, as formas dormentes podem ser soterradas a grandes profundidades, dificultando cada vez mais a sua eclosão (DESTASIO, 1989; BRENDONK; DE MEESTER, 2003). Assim, alguns autores discutem que somente a fração superficial (3 cm) contém formas dormentes viáveis, que depois da eclosão pode liberar organismos para a coluna d'água (DESTASIO,1989; BRENDONK; DE MEESTER, 2003; ALEKSEEVet al., 2007; SANTANGELO, 2009). A dinâmica do banco de formas dormentes ocorre pela deposição de novos ovos, que aumentam sua densidade, e pela eclosão, predação, degradação e senescência, que reduzem sua densidade (DESTASIO, 1989). Além disso, a movimentação vertical do sedimento pode fazer emergir ou soterrar formas dormentes (KEARNS et al.,1996).

Desde os trabalhos pioneiros de Georg O. Sars, em 1901, as pesquisas sobre os estímulos adequados à eclosão das formas dormentes têm buscado esclarecer quais os mecanismos que desencadeiam esse processo (SARS, 1901; STROSS, 1966). Nestes, foram determinados que a temperatura e o fotoperíodo são os principais fatores que estimulam a quebra da dormência (STROSS, 1966; DE STASIO, 1989; CHARTTERJEE; GOPAL, 1998; BRENDONCK; DE MEESTER, 2003). A dormência é quebrada quando as formas dormentes são expostas a altas temperaturas e longos períodos com luz. Entretanto, a maioria desses trabalhos foi realizada para regiões temperadas, onde ocorre grande variação de temperatura e fotoperíodo, sendo registradas temperaturas abaixo de 0 °C, ocasionando congelamento dos ambientes. Para as áreas úmidas da região subtropical do hemisfério Sul, o congelamento não ocorre, sendo registrada a menor temperatura da água (~5°C) no inverno, com dias curtos de até 10 horas de luz, e as maiores temperaturas no verão (~35°C), com dias mais longos de até 14 horas com luz (COLARES et al., 2007). No entanto, embora o verão seja o período com maiores temperaturas e quantidade de luz, deve ser levado em conta que este período é coincidente com a época de déficit hídrico na região (KLEIN, 1998). Isto ocasiona a evaporação parcial ou total da água desses ambientes, ficando desfavorável para as formas ativas dos microcrustáceos (GERHARD et al., 2016). Assim, nem sempre maior exposição à luz e altas temperaturas podem ocasionar a eclosão, o que causa o questionamento de que possivelmente as condições ideais para a eclosão das formas ativas, ocorrem no inverno nas regiões subtropicais do hemisfério Sul, pois a maioria dos ambientes, como as áreas úmidas intermitentes, só aparece nesse período (VAN DER VALK, 2006).

Ambientes intermitentes como áreas úmidas temporárias e os cultivos de arroz irrigado ficam um período sem água (VAN DER VALK, 2006; ROLON; MALTCHIK, 2010), ocorrendo extinção local dos microcrustáceos na forma ativa. O banco de formas dormentes passa por um período de dessecação, mas garante a recolonização dos ambientes intermitentes depois do retorno da lâmina d'água (JAMES et al., 2008; FLORENCIO et al., 2015; SANTANGELO et al., 2015). Devido ao período de dessecação das formas dormentes, houve o questionamento se a hidratação não seria um estímulo importante para a eclosão desses organismos. Em um estudo mais recente foi verificado que a hidratação depois de um período de dessecação também pode ser um estímulo para a eclosão (BANDEIRA et al., 2020; ROSA et al., 2020).

Atualmente, a dinâmica do banco de formas dormentes tem sido investigada devido à sua importância para a resiliência das comunidades aquáticas após perturbações (e.g. super população, perda de habitat, seca dos ambientes) em ambientes permanentes (ALEKSEEV et al., 2007; PÉREZ-MARTÍNEZ et al., 2013) e intermitentes (IGLESIAS et al., 2016; ESKINAZI-SANT'ANNA; PACE, 2018; MORENO et al., 2019; VARGAS et al., 2019). Duas abordagens podem ser usadas para estudar a dinâmica do banco de formas dormentes: uma abordagem *in situ* que segue a eclosão no ambiente natural (PÉREZ-MARTÍNEZ et al., 2013) e uma abordagem *ex situ*, em que a eclosão dos ovos dormentes é acompanhada no laboratório (VAN DAMME; DUMONT, 2010; IGLESIAS et al., 2016). Normalmente, essas duas abordagens são realizadas separadamente, mas podem ser complementares. A vantagem de combinar essas duas abordagens é que podemos acompanhar como os organismos eclodem na natureza, mas também podemos testar se os mesmos padrões ocorrem de forma controlada e replicável, sem a interferência de fatores como reprodução e predação (IGLESIAS et al., 2016). No entanto, isso é necessário testar, uma vez que, os resultados de campo e experimentos nem sempre coincidem (CÁCERES; SCHWALBACH, 2001).

Alguns grupos de microcrustáceos (e.g. Anostraca e Conchostraca) ajustam seus ciclos de vida de acordo com a duração da água (hidroperíodo) das áreas úmidas intermitentes, devido a isso, acabam se tornando endêmicos desses ambientes e se adaptam a diferentes hidroperíodos (BUCKUP; BOND-BUCKUP, 1999; MARINONE et al., 2016). Esses grupos usam ovos dormentes como estratégia para sobreviver ao período sem água (BUCKUP; BOND-BUCKUP, 1999; MARINONE et al., 2016). Nas áreas úmidas temporárias do sul do Brasil, o hidroperíodo tem duração de semanas e normalmente ocorre no inverno, mas ocasionalmente ocorrem hidroperíodos curtos quando há chuva em outras estações (MALTCHIK et al., 2004). Durante esses hidroperíodos anuais, a duração da água, a variação da temperatura e a profundidade do ambiente parecem ser determinantes para o restabelecimento das populações dos organismos nos ambientes intermitentes. Esses fatores podem mudar ao longo dos anos, pois os ambientes estão sofrendo pressão antrópica, principalmente devido à urbanização (STENERT et al., 2016). Com isso, para entender a importância dos fatores ambientais e estímulos de eclosão o uso de espécies endêmicas pode ter respostas interessantes sobre a dinâmica dos ambientes intermitentes (BANDEIRA et al., 2019).

Importância da diversidade e dinâmica dos microcrustáceos em áreas úmidas

A conectividade e a proximidade são características das áreas úmidas que permitem que esses ambientes sejam excelentes modelos para se estudar a diversidade e a dinâmica da comunidade de microcrustáceos (MARTINS et al., 2019). Isso porque, os organismos apresentam mecanismos adaptativos como a produção de formas dormentes, que permitem a dispersão, a permanência e a recolonização desses ambientes (JAMES et al., 2008; FLORENCIO et al., 2015; GERHARD et al., 2016). Esse mecanismo adaptativo dos organismos permite que comunidades locais permaneçam interligadas e interagindo continuamente entre si, mantendo a diversidade, principalmente em ambientes intermitentes (LEIBOLD; MIKKELSON, 2002; LEIBOLD et al., 2004).

Conhecer a diversidade dos microcrustáceos nas áreas úmidas permite verificar o potencial dos organismos como bioindicadores. Como exemplo, foi descrito por HODKINSON; JACKSON (2005) que os microcrustáceos são sensíveis em ambientes que apresentam grandes concentrações de pesticidas e tóxicos orgânicos. Considerando o histórico da agricultura no Rio Grande do Sul (NETO; FRANTZ, 2003), seria de extrema importância uma listagem de espécies de microcrustáceos que permitisse relacionar e identificar áreas com maior ou menor incidência de contaminantes. Com isso, seria possível fazer um manejo adequado das áreas úmidas e dependendo da gravidade uma revitalização das áreas mais afetadas.

A pesquisa em estudos de biodiversidade e conservação de espécies se concentra em ambientes naturais, como lagos, sistemas fluviais e áreas úmidas (BANDEIRA et al., 2019; HERRING et al., 2019), e ambientes como cultivos de arroz, podem ser incorretamente considerados menos significativos em termos de biodiversidade porque são ambientes artificiais (KIMURA, 2005; MAIPHAE et al., 2010; SMITH et al., 2018). Estudos já demonstraram que os cultivos de arroz costumam ter uma grande diversidade de microcrustáceos (ROSSI et al., 2003; SAVATENALINTON, 2017; SMITH et al., 2018) e até costumam descrever novas espécies para esses ambientes (SAVATENALINTON, 2017; FEFILOVA; ALEKSEEV, 2018; SMITH et al., 2019). A maioria desses estudos enfoca um local e/ou grupo de animais específicos, e utiliza abordagens mais específicas, porém esses estudos são essenciais para o levantamento da biodiversidade, e contribuem para a realização de estudos globais. Uma abordagem que vem sendo bastante utilizada para fazer estudos globais são as análises cienciométricas, que tem como objetivo avaliar a produção científica de um determinado tema (LIU et al., 2017). Com isso, a cienciometria vem se tornando uma boa ferramenta para a realização de estudos globais e pode auxiliar em levantamentos de biodiversidade.

Verificar como os microcrustáceos se estruturam no espaço e no tempo possibilita o biomonitoramento das áreas úmidas (BANDEIRA et al., 2020). Como os microcrustáceos apresentam um ciclo de vida curto, eles permitem um acompanhamento detalhado de como as alterações das condições ambientais modificam a comunidade desses organismos (ALFONSO et al., 2016). Pesquisas demonstraram que muitos componentes dessa comunidade são tolerantes ao gradativo aumento de nutrientes na água (SINGH et al., 2013). Porém, outra pesquisa verificou que mesmo tendo espécies tolerantes, tanto a abundância como a biomassa diminuem com o processo de eutrofização (GAZONATO-NETO et al., 2014). Então, acompanhar a diversidade de microcrustáceos permite classificar as espécies em tolerantes e não tolerantes a alterações no ambiente e assim realizar biomonitoramentos (ALFONSO et al., 2016).

Em outra abordagem, a composição da comunidade de microcrustáceos já foi relacionada com a coexistência de peixes anuais (KEPPELER et al., 2015), uma vez que, os microcrstáceos servem de alimento para esses peixes, e que na sua maioria estão ameaçados de extinção. Além disso, os componentes da comunidade de microcrustáceos também permitem diferenciar padrões de hidroperíodos nas áreas úmidas, como visto em ALFONSO et al. (2016), no qual, eles utilizaram a presença e a ausência das espécies de microcrustáceos para identificar e diferenciar ambientes intermitentes.

Conforme mencionado anteriormente, microcrustáceos conseguem habitar ambientes intermitentes em função das estratégias de dormência (ALFONSO et al., 2016; BANDEIRA et al., 2019; BANDEIRA et al., 2020). Também foi colocada a importância dos trabalhos que investigaram os estímulos de eclosão como a temperatura, com isso, vários autores têm destacado o papel das mudanças climáticas, tanto na manutenção dos ambientes quanto nos processos de eclosão (FLORENCIO et al., 2020). Além disso, JONES; GILBERT (2016) verificaram como as mudanças climáticas estão influenciando a dinâmica das áreas úmidas e consequentemente afetando os padrões de recolonização e estruturação da comunidade de microcrustáceos em diferentes latitudes.

Como visto, já foram realizados muitos estudos relacionando direta ou indiretamente com a importância da conservação das áreas úmidas baseados na comunidade de microcrustáceos. Na sua maioria, esses estudos foram realizados em países que tem uma grande preocupação com a conservação e com a utilização adequada desses frágeis ecossistemas (ALFONSO et al., 2016; JONES; GILBERT, 2016; FLORENCIO et al., 2020). Para o Brasil, mais especificamente no Rio Grande do Sul, a maioria dos trabalhos está voltada para a proteção de uma espécie ameaçada, e não necessariamente para a proteção dos ambientes aquáticos (KEPPELER et al., 2014). Porem é notório que essa realidade está mudando, uma vez que, com a conservação das áreas úmidas é possível beneficiar tanto a biodiversidade quanto o consumo humano (ALFONSO et al., 2016).

Justificativa e perguntas da tese

Como descrito ao longo da introdução geral, a maioria dos estudos com biodiversidade enfoca um local e/ou grupo de animais específicos, e utiliza abordagens mais específicas, tendo a necessidade de reunir essas informações para estudos globais. Normalmente, os levantamentos de biodiversidade se concentram em ambientes naturais, e ambientes como cultivos de arroz, podem ser incorretamente considerados menos significativos em termos de biodiversidade, principalmente microcrustáceos porque são ambientes artificiais. Com isso, se faz necessário realizar levantamentos e quantificar a diversidade de microcrustáceos em cultivos de arroz.

Nas áreas úmidas temporárias do sul do Brasil, o hidroperíodo tem duração de semanas e normalmente ocorre no inverno, mas ocasionalmente ocorrem hidroperíodos curtos quando há chuva em outras estações. Durante esses hidroperíodos anuais, os fatores ambientais (e.g. duração da água, a variação da temperatura e a profundidade) podem mudar ao longo dos anos, pois os ambientes estão sofrendo pressão antrópica, principalmente devido à agricultura e urbanização. Para entender a importância dos fatores ambientais e estímulos de eclosão o uso de espécies endêmicas pode ter respostas interessantes sobre a dinâmica dos ambientes intermitentes. Com isso, seria interessante realizar estudos voltados para a história de vida das espécies endêmicas, uma vez que elas se especializaram a viver somente nesses ambientes.

Além disso, devido o déficit hídrico nos ambientes intermites durante as estações mais quentes, nem sempre maior exposição à luz e altas temperaturas podem ocasionar a eclosão, o que causa o questionamento de que possivelmente as condições ideais para a eclosão das formas ativas, ocorrem no inverno nas regiões subtropicais do hemisfério Sul, pois a maioria dos ambientes, como as áreas úmidas intermitentes, só aparece nesse período. Com isso, houve o questionamento se, além do fotoperíodo e da temperatura, a hidratação não seria um estímulo importante para a eclosão desses organismos, uma vez que eles passam por um período de dessecação das formas dormentes.

Com base nas informações acima, o objetivo geral da tese foi estudar a diversidade e dinâmica dos microcrustáceos em áreas úmidas intermitentes. Para isso, foram respondidas as seguintes perguntas ao longo dos capítulos: i) Qual a tendência global dos estudos com microcrustáceos em cultivos de arroz, e o potencial deste ambiente como estoque de biodiversidade; ii) Como as espécies endêmicas da região subtropical do hemisfério Sul estão respondendo aos diferentes hidroperíodos do ano; iii) Qual a influência do tempo de hidratação e da temperatura na eclosão de microcrustáceos, comparando abordagens *in situ* e *ex situ*.

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CAPÍTULO 1

Microcrustaceans in rice fields: a scientometric analysis

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Microcrustaceans in rice fields: A scientometric analysis

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ABSTRACT

We evaluated the worldwide trends in studies of the active and dormant forms of microcrustaceans in rice fields, and the potential of this environment as a stock of diversity through a scientometric analysis. The Web of Science and Scopus databases were used to compile the 77 studies published before 2019. Publications were temporally distributed over 35 years, with a positive correlation between the number of studies and the years of publication (rho = 0.34). The identified studies were from 18 countries, and 58.4% were conducted in Japan, Italy, the United States, and Spain. Most studies addressed more than two groups of microcrustaceans (37.6%), followed by those with Cladocera (27.2%) and Ostracoda (18.1%). We quantified 301 species from six groups of microcrustaceans, the majority of which were Cladocera (41.5%) and Ostracoda (39.8%). The greatest richness of microcrustaceans identified in studies were found in Italy, Thailand, Malaysia, Spain, France, Japan, and Brazil. Of the studies, 87% discussed the active forms of microcrustaceans rather than dormant forms. We found that 15.5% of the countries that grow rice have identified the richness of microcrustaceans, and even though they are artificial environments, rice fields have high potential to store a diversity of microcrustaceans.

INTRODUCTION

Irrigated rice fields cover around 167.2 million hectares across the globe, spread across 116 countries (Shahbandeh 2019). The largest rice production is concentrated in Asia, which comprises about 89% of all rice fields (Smith et al. 2018). These environments represent 15% of the wetlands of the world and function as temporary aquatic systems (Lawler 2001). They are flooded in the spring for planting seeds, during the summer the water levels are kept high for rice growth, but after harvest in autumn/winter the water level depends mainly on rainfall and agricultural management, and they can remain without water during these seasons (Lawler 2001; Stenert et al. 2010).

Rice fields are replacing natural wetland habitats, which have been lost to drainage and decreased water levels due to their use for irrigation (Stenert et al. 2010; Natuhara 2013). It was estimated that 57% of rice fields occupy areas that were previously natural wetlands (Lawler 2001). With the decline of natural wetlands, rice fields can serve as a refuge, especially during the hydroperiod, for birds (Lourenço & Piersma 2009; Herring et al. 2019), fish, crayfish (Clavero et al. 2015), amphibians (Groffen et al. 2018), and invertebrates (Maiphae et al. 2010; Savatenalinton 2017; Smith et al. 2018). Despite their function as a refuge, studies warn that it is not appropriate to convert natural wetlands into rice fields (Pires et al. 2016). The conversion of natural areas into rice fields results in many changes, such as the application of pesticides and maintenance activities (e.g. ploughing, planting, and harvesting) and can have a negative effect on their aquatic habitats, modifying the ecosystem physically and chemically, and making it difficult for animals to remain there (Sun & Yuan 2019).

Invertebrates can be sensitive to the use of pesticides and fertilizers, but even so, they are often recorded in rice fields (Reimche et al. 2014; Sun & Yuan 2019). Concerning invertebrates found in rice fields, microcrustaceans (Amphipoda, Anostraca, Cladocera, Conchostraca, Copepoda, and Ostracoda) have often been studied in these environments, as they are abundant and resistant to physical and chemical disturbances (Stenert et al. 2010; Ávila et al. 2015; Smith et al. 2018; Smith et al. 2019). These microorganisms are an important link in the trophic chains of these ecosystems, as they are the source of energy for various groups of organisms, such as fish larvae (Ali 1990; Cabral et al. 1998) and birds (Lourenço & Piersma 2009). The persistence of microcrustaceans in rice fields is due to behavioral and physiological adaptations, such as the production of a bank of dormant forms in the sediment in these environments (Stenert et al. 2010; Ávila et al. 2015).

The production of dormant forms is a common strategy for the survival and persistence of microcrustaceans in different environments, and provides not only refuge from desiccation in temporary environments, but also a way to maintain the genetic and phenotypic diversity of species and the community during periods without water (Ávila et al. 2015). Some studies suggest that the dormant forms of microcrustaceans support the dry phase and cultivation system of rice fields, enabling the hatching and maintenance of the community when the environment becomes favorable again (Stenert et al. 2010; Ávila et al. 2015). It is unknown whether dormant forms are less studied in these environments than active forms; however, active and dormant forms can be complementary for assessing the diversity of microcrustaceans in specific environments (Stenert et al. 2010). Studies have shown that rice fields often have a high diversity of microcrustaceans (Rossi et al. 2003; Savatenalinton 2017; Smith et al. 2018) and often describe new species (Savatenalinton 2017; Fefilova & Alekseev 2018; Smith et al. 2019), but most of these studies focus on a specific location and/or group of animals and use more specific approaches, which is essential for surveying biodiversity and contributes to the realization of global studies.

Research in biodiversity and species conservation studies focuses on natural environments, such as lakes, river systems, and wetlands (Bandeira et al. 2019; Herring et al. 2019), and as rice fields are artificial environments, they may be incorrectly seen as less significant in terms of biodiversity (Kimura 2005; Maiphae et al. 2010; Smith et al. 2018). Considering the global distribution of rice fields and the potential for these environments to store a high diversity of microcrustaceans, mainly because these organisms produce dormant forms that remain in the sediment, our objective was to use scientometric analysis to evaluate the global trend in studies of microcrustaceans in rice fields, and the potential of this environment as a stock of diversity. We evaluated: i) the temporal trend of studies related to microcrustaceans in rice fields from 1977 to 2019; ii) which countries have studied microcrustaceans; iii) which microcrustaceans groups are most studied in rice fields and their respective richness by groups and by countries; and iv) whether the studies focus more on active or dormant forms of microcrustaceans. Quantifying the richness of microcrustaceans in rice fields means it is possible to inform rice producers and researchers on the importance of management in cultivation, since management intensity affects diversity on rice field banks (Giuliano et al. 2018). We can also identify where the richness of microcrustaceans is being studied across the world, which could offer sustainable management solutions for meeting biodiversity requirements in these agroecosystems (Giuliano et al. 2018; Herring et al. 2019).

MATERIAL AND METHODS

The Web of Science (WoS, Clarivate Analytics) and Scopus (Elsevier) databases were used to compile studies with microcrustaceans in rice fields published since the start of the databases (WOS in 1945 and Scopus in 1960) until 2019. We started the survey in September 2019 and updated it in January 2020, and searched in the two databases for studies that contained, in the title, abstract, and keywords, acombination of the names of the main groups of microcrustaceans and the environment of interest: (*Crustacea* OR Cladocera* OR Copepoda* OR Ostracoda* OR Anostraca* OR Conchostraca* OR Amphipoda*) AND (Rice*). We accessed the databases using the Journal Portal of the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) in Brazil (https://www.periodicos.capes.gov.br/).

In the two databases, 691 studies were found. The Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA protocol; Moher et al. 2009) were used to screen those studies carried out in rice fields involving microcrustaceans (Figure 1). We excluded 614 studies with the following criteria: i) studies requested from authors, when the articles were not available in full through the databases, where there was no response until the time of writing and analyzing the data; ii) studies that were carried out in rice fields, but did not report microcrustaceans; and iii) studies that reported microcrustaceans, but were not carried out in rice fields (Figure 1). The initial compilation included a total of 193 studies in the WoS database, and 498 studies in the Scopus database (Figure 1). We removed 147 studies from the WoS database and 327 studies from Scopus after screening.

After filtering, 77 studies (46 studies from WoS and 31 from Scopus), involving microcrustaceans in rice fields, were considered suitable for scientometric analysis (see Table I in the supplementary material). We obtained the following information for each study: i) year of publication; ii) groups of microcrustaceans; iii) species of microcrustaceans (when available, n= 70 studies); iv) country where the study was developed; and v) whether the focus was on active or dormant forms of microcrustaceans (see Table II in the supplementary material).

To verify the temporal trend of studies with microcrustaceans, we performed a Spearman correlation (Best & Roberts 1975) because the range of publications over the years was low and the data did not show a normal distribution. The data were presented using descriptive statistics to verify which countries studied microcrustaceans, which groups of microcrustaceans were the most studied, and the richness of each group.

To identify possible variables that explain the number of studies carried out in different countries and the total richness of microcrustaceans found in the studies, generalized linear models (GLMs; family = Poisson; Crawley 2007) were used. Five explanatory variables were selected: i) cultivation area (in ha; FAOSTAT:http://www.fao.org/faostat/en/#data/QC); ii) rice production in countries (in tons; FAOSTAT:http://www.fao.org/faostat/en/#data/QC); iii) gross domestic product (GDP) of each country (US$ millions; World Bank:https://data.worldbank.org/indicator/NY.GDP.MKTP.CD?view=chart); iv) Human Development Index (HDI: varies between 0–1; UNDP:http://hdr.undp.org/en/composite/HDI); and v) research and development expenditure (% of GDP; World Bank:https://data.worldbank.org/indicator/GB.XPD.RSDV.GD.ZS?view=chart). Initially, Spearman's correlation was used to determine whether there was collinearity between the explanatory variables (Dormann et al. 2013). When two variables showed a high correlation (rho> 0.80), one was excluded; in this case, the cultivation area was excluded. The GLMs were compared with the Akaike Information Criterion (AIC; Burnham & Anderson 2002), using the *'MASS'* package (Venables & Ripley 2002), and considered the models that had the lowest AIC value. After selecting models, the relative importance of each variable in the models was checked using the *‘relaimpo’* package (Grömping 2006). Two explanatory variables from the 70 studies with microcrustaceans were selected to explain the total richness of microcrustaceans in the countries studied: i) use of pesticides (dummy variable, where 1 indicated presence and 0, absence); and ii) whether the study used the active or dormant form of microcrustaceans (dummy variable, where 1 indicated an active form and 0, a dormant form).

Spearman correlation was used to verify whether the total microcrustacean richness was related to the number of studies (Best & Roberts 1975). A Venn diagram was built to illustrate the number of studies with active and dormant forms of microcrustaceans (Archer 1950). The *'VennDiagram'* package (Chen 2018) was used. All analyses were performed in the R environment (R Core Team 2019).

RESULTS

Studies with microcrustaceans in rice fields had accumulated for over 35 years, with the inclusion of the first study in 1977 in the databases (Figure 2). There was a positive correlation (rho = 0.34; p = 0.041) between the number of studies and the years of publication. In the 77 studies considered, 18 countries (Figure 3a) studied microcrustaceans in rice fields. The largest number of studies (58.4% of studies) was produced in Japan, followed by Italy, the USA, and Spain. The remaining 14 countries had fewer than six studies (Figure 3a). The best model explaining the number of studies with microcrustaceans (AIC = 101.5) included the most important explanatory variables, HDI (relative importance = 0.51) and GDP (relative importance = 0.48). Most studies addressed more than two groups of microcrustaceans (37.7% of the studies), followed by those that addressed only Cladocera (27.2%) and Ostracoda (18.1%). Other groups hadless than 10 studies (Figure 3b).

The studies recorded a total richness of 301 species of microcrustaceans in 70 studies (seven studies cited only the groups) in rice fields of the 18 countries. The richness of microcrustaceans in rice fields was highest in Italy (29.5% of the species in our study), followed by Thailand (24.9%), Malaysia (19.2%), Spain (15.2%), France (13.6%), Japan

(12.2%), Brazil (11.9%), USA (3.6%), Vietnam (2.3%), and India (1.9%). The remaining eight countries registered fewer than five species (Figure 4a). The model that best explained the richness of microcrustaceans found in these countries (AIC = 591.9) included the use of pesticides in the studies as an explanatory variable. A positive correlation (rho = 0.68; p = 0.001) was also found between total microcrustacean richness and the number of studies found in these countries. Within groups, the greatest richness was Cladocera (41.5% of species), followed by Ostracoda (39.8%), and less than 20 species for Conchostraca, Anostraca, and Amphipoda (Figure 4b).

In the 77 studies, the majority involved microcrustaceans in an active form (87%), a minority in dormant forms (11.6%), and only one study used both active and dormant forms (1.2%; Figure 5). We found studies with the active forms of microcrustaceans in all 18 countries, with the dormant forms in Brazil, Spain, India, Italy, Japan, and Thailand, and with both forms only in Italy.

DISCUSSION

Agricultural activities are essential for the world’s population (Shahbandeh 2019); however, it is undeniable that these activities are very damaging to the natural environment, especially aquatic environments (Sun & Yuan 2019). Our study demonstrated the potential of rice fields as a stronghold for the biodiversity of microcrustaceans. We also demonstrated that there are still gaps in our knowledge that must be explored to define robust actions for the management of agricultural and natural systems (i.e. agroecosystems) inserted in natural/anthropogenic landscapes.

TEMPORAL TREND OF STUDIES WITH MICROCRUSTACEANS

Our results showed that there was an increase in the number of studies with microcrustaceans over 35 years in the rice fields; however, the number of studies was low compared to a previous scientometric study involving rice fields (Liu et al. 2017). This reduced number of studies may be related to less incentive for ecological research on these groups in rice fields, since general scientific research involving rice has grown by about 6.9% per year (Liu et al. 2017). These studies involvingrice fields are focused on several themes that have been summarized in scientometric studies and reviews, such as the development of cultivation technologies in Japan (Morooka et al. 2014), the importance of co-cultures with aquatic animals (Bashir et al. 2019), the effect of climate change on crops in China (Liu et al. 2019), and of fertilizers (Sun & Yuan 2019). These themes are important for understanding the practical applications of rice fields, but we realize that there is still a need for more basic ecological research, especially involving microcrustaceans, as they can helpus to understand the functions of these very unstable environments. Morooka et al. (2014), Liu et al. (2017), Bashir et al. (2019), Liu et al. (2019), and Sun andYuan (2019) demonstrated an increase in the number of studies, but used criteria different from ours to compile and filter the studies to be analyzed. We emphasize the importance of using protocols, such as PRISMA, as well as analyzing all the studies compiled to select only those that address the subject studied. This can reduce the bias of the results and enable the correct estimation of time trends for the studies.

Our initial compilation of the studies in the databases revealed that the first study involving rice fields was by Rosenberg in 1947, describing the life cycle of shrimp in crops (Rosenberg 1947). Thirty years later, in 1977, Pont (1977) published the first study with microcrustaceans in these environments that was indexed in the databases we used. However, Pont (1977) had cited previous articles involving microcrustaceans in rice fields (e.g.

Schachter & Conat 1951), showing that this area of research began well before 1977. This suggests that there may be a bias in our research, since there are more studies involving microcrustaceans in rice fields, but not all are indexed in the databases WoS and Scopus. This may contribute to the small number of studies we found, despite considering two databases. Mainly, comparing it with studies with general themes, as in the scientometric study by Liu et al. (2017), who had the minimum number of 446 studies in one year in rice fields, they used only WoS studies. We emphasize the importance of publishing studies in international databases, since the global scientific community does not always have access to regional/local journals and/or grey literature, causing language bias, since the English language is not always used and peer reviewed. Morooka et al. (2014) used different databases to compile the studies carried out only in Japan, and the smallest number of studies was found in WoS, which reinforces the idea that there may be biases in language and peer review in the databases, causing a reduction in the number of studies identified, which may not reflect the true situation. We found a positive correlation over 35 years, however, we emphasize that there is a need for more studies with microcrustaceans, as they are an important component in the function of the trophic chain of rice fields (Reimche et al. 2014).

STUDIES WITH MICROCRUSTACEANS IN RICE FIELDS

We found that 18 countries are studying microcrustaceans in rice fields, which means that only 15.5% of the 116 countries that grow rice (Shahbandeh 2019) know about the microcrustacean fauna in their fields. Of the 18 countries, eight (i.e. Japan, USA, China, Thailand, Brazil, India, Philippines, and South Korea) have already been identified as very productive in relation to the number of scientific studies on rice (Liu et al. 2017), mainly related to fertilizers in rice fields (Sun & Yuan 2019). Our results showed a different pattern, in which, most of the countries we registered had not previously stood out as conducting a high number of studies (e.g. Italy, Spain, and Malaysia), and this means that the amount of study in these countries may vary according to the approach used (Sun & Yuan 2019).

We perceived a division between the countries that have contributed the most and those that have contributed the least regarding the number of studies with microcrustaceans. We found that 58.4% of the studies were carried out in Japan, Italy, the USA, and Spain. At the level of discussion, we compared the ranking of the ten largest rice producers in the world and found that the countries that produce the most rice are not the ones that study microcrustacean fauna the most, since the USA, Japan, Italy, and Spain occupy the 11th, 13th, 31st, and 39th positions, respectively. We found that the world's largest rice producers were China, India, Vietnam, Thailand, Philippines, and Brazil, and these countries contributed only 28.5% of the studies. This does not follow the pattern found in other studies, and is the opposite of that found by Liu et al. (2017) and Sun & Yuan (2019), where the countries that produce the most rice were also those that carried out the most studies, confirming that the number of studies in countries may vary according to the approach used to define it.

We found that HDI and GDP were the main variables affecting the number of studies involving microcrustaceans in the countries found in our study. As Japan, Italy, the USA, and Spain contributed most to the number of studies, this means that more developed countries are the ones that most study microcrustaceans in rice fields. This result is not restricted to studies involving microcrustaceans in rice fields, as other scientometric studies suggest socioeconomic parameters as the main variables in the increase in the number of studies, such as the study by Coelho et al. (2014) with macroalgae as a source of raw material for biofuels, and Pereira et al. (2019) with the effect of the construction of dams on fish. With the corroboration of these studies, our results indicate that the largest number of studies are in more economically developed countries, which as Coelho et al. (2014) pointed out, have a high level of infrastructure for the development of scientific research, which has a positive effect on their high scientific productivity. May (1997), studying the scientific wealth of nations, also found that countries with the largest economies invest the most in research and development, and are consequently those with the greatest scientific production.

Most studies in our research were conducted with more than two groups of microcrustaceans. In these studies, the authors addressed topics, such as diversity, composition, and dynamics in ecological communities in rice fields (e.g., Pont 1977; Ali 1990; Martinoy et al. 2006; Chittapun et al. 2009), the effects of environmental factors on microcrustaceans (e.g., Stenert et al. 2010; Chittapun 2011), the effects of crop systems (e.g., Yamazaki et al. 2003; Reimch et al. 2014; Ávila et al. 2015), and the importance of these environments for the dissemination of invasive species and dispersion of these microorganisms (e.g., Lovas-Kiss et al. 2018). We observed an evolution in the approaches used in these studies, where, initially, the interest was in which species were present in the rice fields, since lists of species were made. Research questions evolved towards the behavioral attributes of microcrustaceans, trying to understand how these organisms react to the constant changes in environmental variables and in the cultivation process, until reaching ecological issues that have recently become more worrying, such as the effect of invasive species and the potential of these environments for the dispersion of organisms (Lovas-Kiss et al. 2018). This evolution has allowed us to note that despite finding a small number of studies, the approaches used are very relevant and are constantly updated, mainly to reflect the importance of microcrustaceans in the development and relevance of rice fields as an ecologically productive environment, although artificial (Smith et al. 2018).

We found that Cladocera and Ostracoda were the most commonly studied groups of microcrustaceans in rice fields. Studies of Cladocera focused on diversity (e.g., Maiphae et al. 2010; Sinev & Korovchinsky 2013), ecological succession throughout the cultivation cycle (e.g., Ferrari et al. 1991; Leoni et al. 1998), effect of water reuse irrigation (Grippo et al. 2016), and more widely onthe effects of pesticides and fertilizers (e.g., Zhang et al. 2016; Chen et al. 2018; Jiang et al. 2018; Içoğlu 2019; Subrero et al. 2019). For Ostracoda, the studies were focused on diversity (e.g., Rossi et al. 2003; Savatenalinton 2017; Smith et al. 2019), the effects of pesticides (e.g., Perez & Aspiras 1982; Lim& Wong 1986), species dispersion (e.g., Mckenzie & Moroni 1986), bioremediation (e.g., Grant et al. 1983; Hamdi et al. 2007), population genetics (e.g., Rossi et al. 1996; Rossi et al. 2006), and invasive species (e.g., Mesquita-Joanes et al. 2012; Valls et al. 2014). However, we found that a large contribution to the number of studies with Cladocera and Ostracoda were the result of the species *Daphnia magna* Straus, 1820 (Cladocera) and *Heterocypris incongruens* (Ramdohr), 1808 (Ostracoda), which mainly addressed the effects of pesticides and fertilizers. Diversity surveys also made a high contribution to the number of studies and, consequently, Cladocera and Ostracoda also showed the greatest richness in rice fields.

The least studied groups were Copepoda, Anostraca, Conchostraca, and Amphipoda. The studies for these groups addressed diversity (e.g., Petkovski 1997; Fefilova & Alekseev 2018), life history (e.g., Tinti & Scanabissi 1996; Plodsomboon et al. 2012), population genetics (e.g., Montoliu et al. 2015), and the effect of pesticides (e.g., Dieng et al. 2003; Chandler et al. 2004; Moore et al. 2009). Less than 20% of the studies were carried out with these four groups, and the approaches were focused on reproductive aspects and few on the survey of diversity. This suggests that these groups may be underestimated in rice crops, or that they are less present in these environments, since we also found less richness for these groups.

RICHNESS OF MICROCRUSTACEANS IN RICE FIELDS

In the six groups of microcrustaceans that we studied, 7,697 species were described in different natural freshwater environments, such as rivers, lakes, and wetlands (Brendonck et al. 2008; Boxshall & Defaye 2008; Forró et al. 2008; Martens et al. 2008; Väinölä et al. 2008). The global diversity of microcrustaceans includes 2,814 species of Copepoda (Boxshall & Defaye 2008), 1,936 species of Ostracoda (Martens et al. 2008), 1,870 of Amphipoda (Väinölä et al. 2008), 620 species of Cladocera (Forró et al. 2008), 307 species of Anostraca (Brendonck et al. 2008), and 150 species of Conchostraca (Brendonck et al. 2008). Our survey quantified a total of 301 species in rice fields in 18 countries, which represents around 4% of the global diversity of microcrustaceans. Our results showed that 63.8% of the species were registered in the rice fields of Asian countries, 59.5% in European countries, 15.6% in America, and 0.3% in Africa. Thus, we suggest that there is still high potential for recording microcrustacean biodiversity in rice fields on all continents; as mentioned previously, the countries with the highest areas and productivity are those with the lowest records of studies with microcrustaceans. Considering that only 15.5% of the countries that cultivate rice have a survey of the richness of microcrustaceans, we can assume that, despite being artificial environments, rice fields have high potential to store such diversity.

We found that more studies have investigated the use of pesticides and, therefore, found more information about the richness of microcrustaceans in the countries studied because many studies have tested the effect of insecticides (e.g., Reimche et al. 2014; Jiang et al. 2018) and fertilizers (e.g., Barceló et al. 1991; Maiphae et al. 2010) on the richness and abundance of microcrustaceans in rice fields. We observed that richness decreases with the use of pesticides in rice fields. This has been commonly noted in the literature, where Reimche et al. (2014) found that pesticides negatively affect the density of microcrustaceans in rice fields. Jiang et al. (2018) reported that pesticides negatively affect the viability of eggs, morphology of organisms, and growth and reproduction of microcrustaceans. The number of studies on fertilizer use (such as nitrogen, phosphorus, and potassium) in rice fields has continued to increase over the years (Sun & Yuan 2019). These fertilizers affect the proliferation of phytoplankton in rice fields, which serves as food for many microcrustaceans. Although high concentrations of phosphate in water can be lethal for microcrustaceans (Barceló et al. 1991), a positive correlation with phosphate and the abundance of microcrustaceans in rice fields has also been recorded (Maiphae et al. 2010).

We found that richness was positively correlated with the number of studies, indicating that the more studies that are carried out, the greater the probability of knowing the diversity of microcrustaceans in rice fields. Basic ecological studies are still needed, and we suggest that these should be mainly diversity surveys because we noted that this approach made a high contribution to the estimation of microcrustacean richness in our study, mainly for Cladocera and Ostracoda, which were the groups that presented the greatest microcrustacean richness in rice fields.

STUDIES WITH ACTIVE AND DORMANT FORMS OF MICROCRUSTACEANS

Our results showed that only 11.7% of the studies and few countries have considered the dormant forms of the groups analyzed, and 87% of the studies analyzed only the active forms of these organisms. As research has already shown, dormant form banks are the main source of active forms for the restructuring of communities in rice fields (Stenert et al. 2010; Chittapum 2011; Ávila et al. 2015; Lovas-Kiss et al. 2018). Failure to include this assessment may underestimate the potential to stock adiversity of microcrustaceans in aquatic environments formed temporarily in rice fields around the world. Thus, we suggest that the richness of dormant form banks should also be evaluated in future studies. This approach can assist in estimating the diversity of microcrustaceans in rice fields, since the dormancy structures are viable in the sediment for up to two years under desiccation, without compromising the emergence of microcrustaceans (Stenert et al. 2010). Recent research has also shown that microcrustaceans hatch at different intervals in temporary environments (Bandeira et al. 2019), which can also underestimate biodiversity in specific studies. Another factor that reinforces the need for further studies of dormant forms in irrigated rice fields is that the existence of viable dormant forms in the sediment of rice fields can help in the restoration of natural wetlands, since the diversity and the abundance of dormant form banks are also essential for the ecological success of created or restored wetlands (Stenert et al. 2010; Ávila et al. 2015).

CONCLUSIONS

Our study showed that there was an increasing trend in the number of studies and an evolution in approaches over time that assessed the diversity and behavioral and physiological responses of microcrustaceans in rice fields. The most commonly studied groups were Cladocera and Ostracoda, and the countries that produce the most rice are not the ones that most study microcrustacean fauna. Due to the low number of studies in the countries that produce the most rice, our results suggest a great underestimation of microcrustacean biodiversity. Because of this, we found a low percentage in relation to the global richness of the groups of these organisms.

We suggest that the diversity of microcrustaceans in rice fields should continue to be widely studied, especially the dormant forms. This has high potential to increase the rich knowledge of microcrustaceans in these environments and allow better understanding of communities and, consequently, the behavior of the trophic chain in rice fields. Rice fields, in conjunction with natural environments, can favor the conservation of microcrustaceans, especially in crops with less aggressive management, and this would possibly be favorable for the management of these agroecosystems.

We saw that rice fields have high potential to store a diversity of microcrustaceans, however, this study does not justify transforming natural environments into rice fields. Rice fields can be microcrustacean biodiversity shelters, and suchknowledge can serve as a basis for integrated natural wetland management programs, as a source of species that help maintain the structure and function of rice-based ecosystems.

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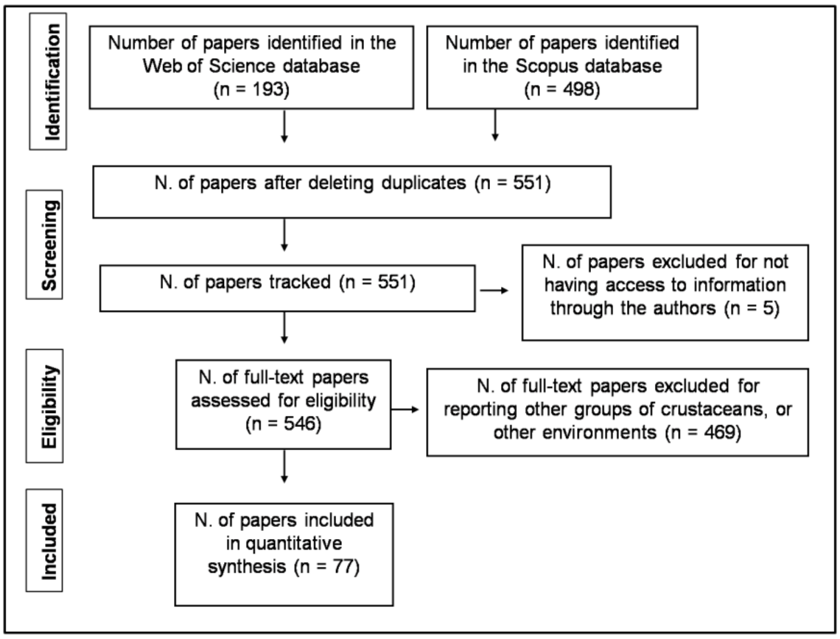
Figure 1:



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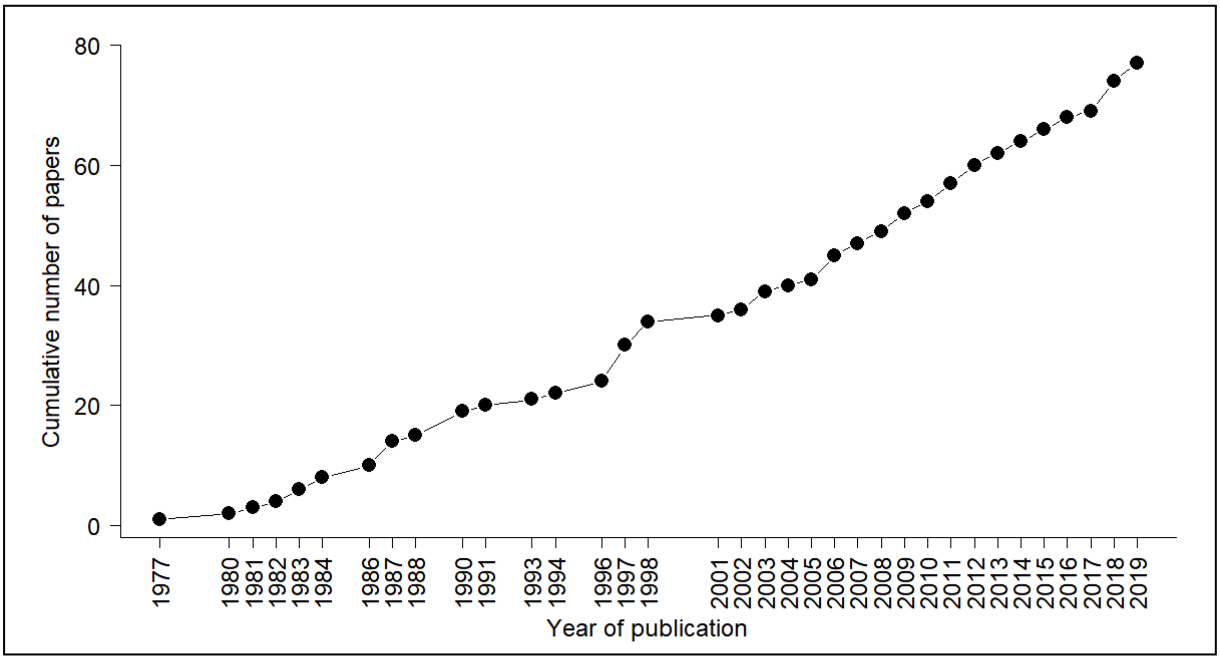

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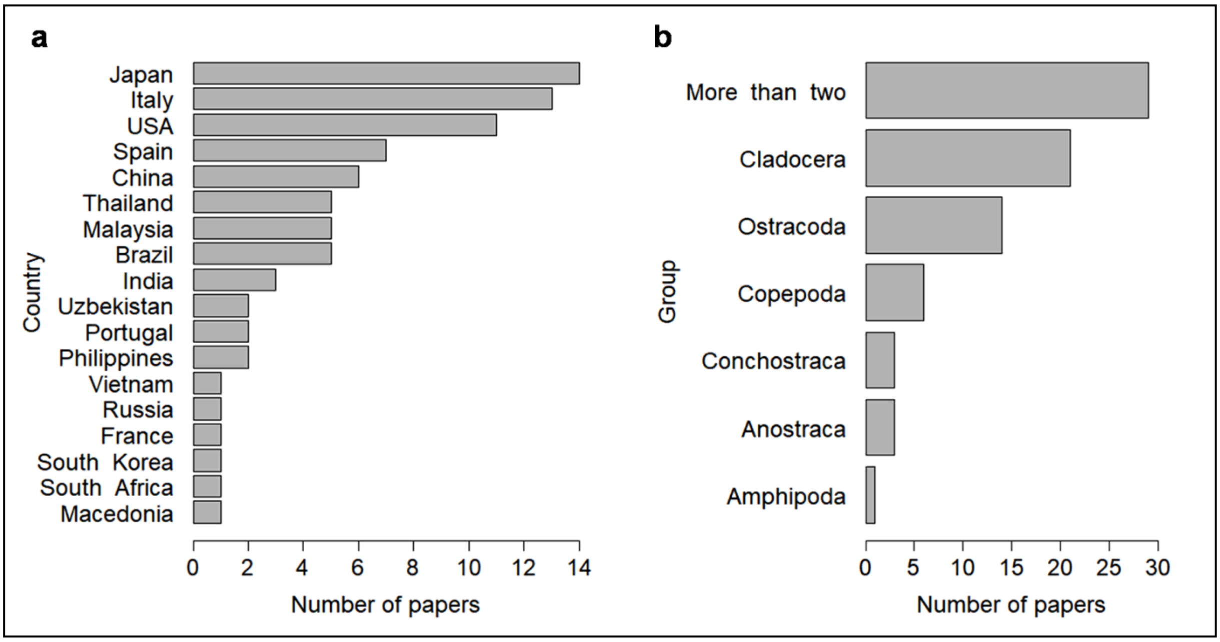

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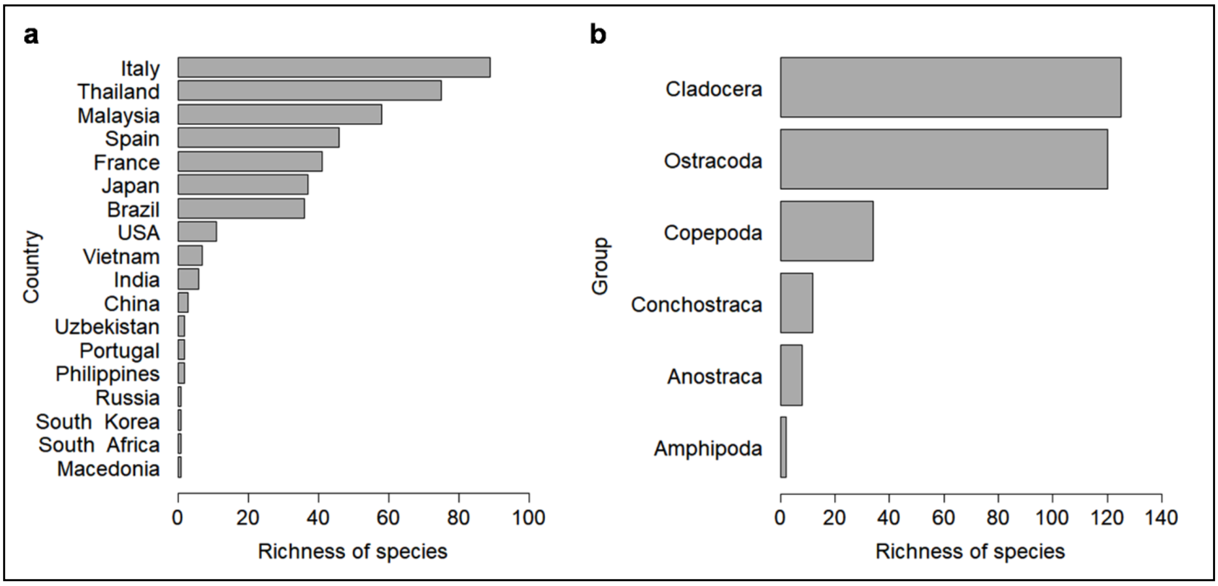

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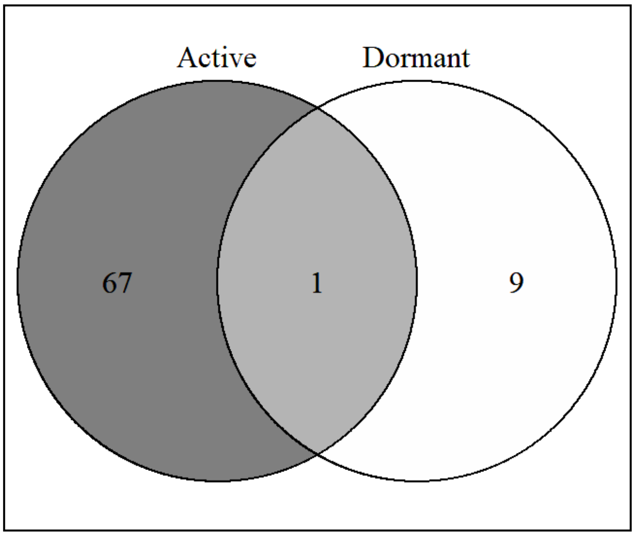

Figure 5 - Venn diagram with the number of studies showing the active (dark grey), dormant (white), and the two (light grey) forms of microcrustaceans in the rice fields.

Supplementary material

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Table I – Description of the 77 studies with microcrustaceans in rice fields found in the Web of Science (WOS) and Scopus databases between the years 1977 and 2019.

	Database	Year	Authors	Title	Journal	Volume	Pages/ article number	Doi
1	WOS/ Scopus	2019	Smith et al.	*Ilyocypris* (Crustacea: Ostracoda) species in North East Asian rice fields; description of one new species, and redescriptions of *Ilyocypris dentifera* Sars, 1903 and *Ilyocypris japonica* Okubo, 1990	Zootaxa	4652	56-92	10.11646/zootaxa.4652.1.2
2	WOS/ Scopus	2019	Subrero et al.	Exposure to anti-mosquito insecticides utilized in rice fields affects survival of two non-target species, *Ischnura elegans* and *Daphnia magna*	Paddy and Water Environment	17	1-11	10.1007/s10333-018-0678-3
3	Scopus	2019	Içoğlu	Acute and chronic effects of thifluzamide on *Daphnia magna*	Turkish Journal of Zoology	43	554-559	10.3906/zoo-1909-8
4	WOS/ Scopus	2018	Chen et al.	Effects of straw leachates from Cry1C-expressing transgenic rice on the development and reproduction of *Daphnia magna*	Ecotoxicology and Environmental Safety	165	630-636	10.1016/j.ecoenv.2018.09.045
5	WOS/ Scopus	2018	Jiang et al.	Ecotoxicity of the nonsteroidal ecdysone mimic RH-5849 to *Daphnia magna*	Environmental Science and Pollution Research	25	10730-10739	10.1007/s11356-018-1275-0
6	WOS/ Scopus	2018	Chen et al.	Safety of Bacillus thuringiensis Cry1C protein for *Daphnia magna* based on different functional traits	Ecotoxicology and Environmental Safety	147	631-636	10.1016/j.ecoenv.2017.08.065
7	Scopus	2018	Lovas-Kiss et al.	Crayfish invasion facilitates dispersal of plants and invertebrates by gulls	Freshwater Biology	63	392-404	10.1111/fwb.13080
8	Scopus	2018	Fefilova and Alekseev	A new species and new records of harpacticoids (Crustacea: Copepoda: Harpacticoida) from North-Eastern Borneo	Zoosystematica Rossica	27	205-217	10.31610/zsr/2018.27.2.205
9	WOS/ Scopus	2017	Savatenalinton	Species diversity of ostracods (Crustacea: Ostracoda) from rice fields in Northeast Thailand, with the description of a new *Tanycypris* species	Zootaxa	4362	499-516	10.11646/zootaxa.4362.4.2

10	Scopus	2016	Zhang et al.	Genetically modified rice Bt-Shanyou63 expressing Cry1Ab/c protein does not harm *Daphnia magna*	Ecotoxicology and Environmental Safety	132	196-201	10.1016/j.ecoenv.2016.06.011
11	Scopus	2016	Grippo et al.	Unexpected Increases in Fecundity of *Ceriodaphnia dubia* Exposed to Reused Rice Irrigation Water	Bulletin of Environmental Contamination and Toxicology	96	720-724	10.1007/s00128-016-1818-3
12	WOS/ Scopus	2015	Avila et al.	The effects of different rice cultivation systems and ages on resting stages of wetland invertebrates in southern Brazil	Marine and Freshwater Research	66	276-285	10.1071/MF14048
13	WOS/ Scopus	2015	Montoliu et al.	Using DNA Barcodes to detect non-indigenous species: The case of the asian copepod *Mesocyclops pehpeiensis* Hu, 1943 (Cyclopidae) in two regions of the world	Crustaceana	88	1323-1338	10.1163/15685403-00003500
14	WOS/ Scopus	2014	Valls et al.	Rice fields as facilitators of freshwater invasions in protected wetlands: the case of Ostracoda (Crustacea) in the Albufera Natural Park (E Spain)	Zoological Studies	53	68	10.1186/s40555-014-0068-5
15	WOS/ Scopus	2014	Reimche et al.	Zooplankton community responses to the mixture of imazethapyr with imazapic and bispyribac-sodium herbicides under rice paddy water conditions	Ciência Rural	44	1392-1397	10.1590/0103-8478cr6151
16	WOS/ Scopus	2013	Wang et al.	Field and laboratory studies on the impact of two Bt rice lines expressing a fusion protein Cry1Ab/1Ac on aquatic organisms	Ecotoxicology and Environmental Safety	92	87-93	10.1016/j.ecoenv.2013.02.018
17	WOS/ Scopus	2013	Sinev and Korovchinsky	Cladocera (Crustacea: Branchiopoda) of Cat Tien National Park, South Vietnam	Journal of Limnology	72	125-141	10.4081/jlimnol.2013.s2.e8
18	WOS/ Scopus	2012	Plodsomboon et al.	Reproductive cycle and genitalia of the fairy shrimp *Branchinella thailandensis* (Branchiopoda: Anostraca)	Journal of Crustacean Biology	32	711-726	10.1163/193724012X638509
19	WOS/ Scopus	2012	Hayasaka et al.	Differences in susceptibility of five cladoceran species to two systemic insecticides, imidacloprid and fipronil	Ecotoxicology	21	421-427	10.1007/s10646-011-0802-2
20	Scopus	2012	Mesquita-Joanes et al.	Global distribution of *Fabaeformiscandona subacuta*: An exotic invasive ostracoda on the Iberian Peninsula?	Journal of Crustacean Biology	32	949-961	10.1163/1937240X-00002096
21	WOS/ Scopus	2011	Chittapun	Fire and recovery of resting egg bank: an experimental study in paddy fields in Pathum Thani province, Thailand	Hydrobiologia	662	163-170	10.1007/s10750-010-0492-4
22	Scopus	2011	Bahaar and Bhat	Taxocoenosis and distribution of nektonic fauna in the rice fields of Kashmir (J and K) India	Pakistan Journal of Biological Sciences	14	483-489	10.3923/pjbs.2011.483.489
23	Scopus	2011	Marques et al.	*In situ* aquatic bioassessment of pesticides applied on rice fields using a microalga and daphnids	Science of the Total Environment	409	3375-3385	10.1016/j.scitotenv.2011.05.025
24	WOS/ Scopus	2010	Maiphae et al.	The Cladocera (Ctenopoda and Anomopoda) in rice fields during a crop cycle at Nakhon Si Thammarat Province, Southern Thailand	Crustaceana	83	1469-1482	10.1163/001121610X539489

25	WOS/ Scopus	2010	Stenert et al.	Do Hydrologic Regimes Used in Rice Fields Compromise the Viability of Resting Stages of Aquatic Invertebrates?	Wetlands	30	989-996	10.1007/s13157-010-0083-1
26	Scopus	2009	Chittapun et al.	Diversity and composition of zooplankton in rice fields during a crop cycle at Pathum Thani province, Thailand	Songklanakarin Journal of Science and Technology	31	261-267	
27	Scopus	2009	Selvarani	Effect of feed on cyst hatching performance of fairy strimp *Streptocephalus dichotomus* Baird (Crustacea: Anostraca)	Ecology Environment and Conservation	15	535-538	
28	Scopus	2009	Moore et al.	Efficiency of experimental rice (*Oryza sativa* L.) fields in mitigating diazinon runoff toxicity to *Hyalella azteca*	Bulletin of Environmental Contamination and Toxicology	82	777-780	10.1007/s00128-009-9696-6
29	WOS/ Scopus	2008	Reimche et al.	Water persistence and influence of herbicides utilized in rice paddy about zooplankton community of Cladocers Copepods and Rotifers	Ciência Rural	38	7-13	10.1590/S0103-84782008000100002
30	Scopus	2008	Golombieski et al.	Cladocers, Copepods and Rotifers in rice-fish culture handled with metsulfuron-methyl and azimsulfuron herbicides and carbofuran insecticide	Ciência Rural	38	2097-2102	10.1590/S0103-84782008000800001
31	Scopus	2007	Hamdi et al.	Bioaugmentation and biostimulation effects on PAH dissipation and soil ecotoxicity under controlled conditions	Soil Biology and Biochemistry	39	1926-1935	10.1016/j.soilbio.2007.02.008
32	Scopus	2007	Barata et al.	Combined use of biomarkers and *in situ* bioassays in *Daphnia magna* to monitor environmental hazards of pesticides in the Field	Environmental Toxicology and Chemistry	26	370-379	10.1897/06-209R.1
33	WOS/ Scopus	2006	Sánchez-Bayo and Goka	Influence of light in acute toxicity bioassays of imidacloprid and zinc pyrithione to zooplankton crustaceans	Aquatic Toxicology	78	262-271	10.1016/j.aquatox.2006.03.009
34	WOS/ Scopus	2006	Rossi et al.	Clonal diversity of *Heterocypris incongruens* (Crustacea : Ostracoda) in Northern Italian ricefields	Archiv Fur Hydrobiologie	166	225-240	10.1127/0003-9136/2006/0166-0225
35	Scopus	2006	Martinoy et al.	Crustacean and aquatic insect assemblages in the Mediterranean coastal ecosystems of Empordà wetlands (NE Iberian peninsula)	Limnetica	25	665-682	
36	Scopus	2006	Sánchez-Bayo and Goka	Ecological effects of the insecticide imidacloprid and a pollutant from antidandruff shampoo in experimental rice fields	Environmental Toxicology and Chemistry	25	1677-1687	10.1897/05-404R.1
37	Scopus	2005	Konwick et al.	Acute enantioselective toxicity of fipronil and its desulfinyl photoproduct to *Ceriodaphnia dubia*	Environmental Toxicology and Chemistry	24	2350-2355	10.1897/04-459R.1
38	Scopus	2004	Chandler et al.	Fipronil effects on estuarine copepod (*Amphiascus tenuiremis*) development, fertility, and reproduction: A rapid life-cycle assay in 96-well	Environmental Toxicology and Chemistry	23	117-124	10.1897/03-124

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39	WOS/ Scopus	2003	Dieng et al.	Life history effects of prey choice by copepods: Implications for biocontrol of vector mosquitoes	Journal of the American Mosquito Control Association	19	67-73	
40	WOS/ Scopus	2003	Yamazaki et al.	Changes in the community structure of aquatic organisms after midseason drainage in the floodwater of Japanese paddy fields	Soil Science and Plant Nutrition	49	125-135	10.1080/00380768.2003.10409987
41	Scopus	2003	Rossi et al.	Ostracoda of the Italian ricefields thirty years on: New synthesis and hypothesis	Journal of Limnology	62	1-8	10.4081/jlimnol.2003.1
42	WOS/ Scopus	2002	Grygier et al.	Distributional survey of large branchiopods of rice paddies in Shiga Prefecture, Japan: a Lake Biwa Museum project based on lay amateur participation	Hydrobiologia	486	133-146	10.1023/A:1021342500327
43	WOS/ Scopus	2001	Yamazaki et al.	Seasonal variations in the community structure of aquatic organisms in a paddy field under a long-term fertilizer trial	Soil Science and Plant Nutrition	47	587-599	10.1080/00380768.2001.10408422
44	WOS	1998	Schoenly et al.	Analysis of invertebrate biodiversity in a Philippine farmer's irrigated rice field	Environmental Entomology	27	1125-1136	10.1093/ee/27.5.1125
45	WOS/ Scopus	1998	Leoni et al.	Seasonal succession of Cladocerans in a ricefield in Italy	Hydrobiologia	391	241-248	
46	WOS	1998	Mirabdullayev	*Moina mukhamedievi* n. sp. (Crustacea, Cladocera) from ricefields of Uzbekistan (central Asia)	Hydrobiologia	385	11-16	10.1023/A:1003436930510
47	WOS/ Scopus	1998	Cabral et al.	Environmental and biological factors influence the relationship between a predator fish, *Gambusia holbrooki*, and its main prey in rice fields of the Lower Mondego River Valley (Portugal)	Hydrobiologia	382	41-51	10.1023/A:1003480920168
48	WOS/ Scopus	1997	Mirabdullayev	Redescription of *Microcyclops rechtyae* Lindberg, 1960 (Crustacea, Copepoda)	Hydrobiologia	362	217-221	10.1023/A:1003178400061
49	WOS	1997	Petkovski	On the presence of the genus *Branchipus Schaeffer*, 1766 (Crustacea: Anostraca) in Macedonia	Hydrobiologia	359	37-44	10.1023/A:1003198400634
50	WOS	1997	Taniguchi et al.	Epibiotic bacteria associated with microcrustaceans in the overlying water of paddy fields	Soil Science and Plant Nutrition	43	633-641	10.1080/00380768.1997.10414789
51	WOS	1997	Taniguchi et al.	Seasonal variation of microcrustaceans and microbial flora on their surface in the overlying water of a Japanese paddy Field	Soil Science and Plant Nutrition	43	651-664	10.1080/00380768.1997.10414791
52	WOS/ Scopus	1997	Moore and Farris	Acute and chronic toxicity of the herbicide Stam (R)M-4 in field and laboratory exposures	Archives of Environmental Contamination and Toxicology	33	199-202	10.1007/s002449900243
53	WOS/ Scopus	1997	Scanabissi and Tommasini	Occurrence of *Limnadia lenticularis* (Linnaeus, 1761) (Conchostraca, Limnadiidae) in Emilia-Romagna, Italy	Crustaceana	70	206-213	10.1163/156854097X00843
54	WOS/ Scopus	1996	Tinti and Scanabissi	Reproduction and genetic variation in clam shrimps (Crustacea, Branchiopoda, Conchostraca)	Canadian Journal of Zoology (Revue	74	824-832	10.1139/z96-095

					Canadienne de Zoologie)			
55	WOS/ Scopus	1996	Rossi et al.	Egg diapause and clonal structure in parthenogenetic populations of *Heterocypris incongruens* (Ostracoda)	Hydrobiologia	320	45-54	10.1007/BF00016803
56	WOS/ Scopus	1994	Rayner	Tropodiaptomus-zambeziensis, T-Bhangazii and T-Capriviensis, 3 new species of *Tropodiaptomus* (Copepoda, Calanoida) from Southern Africa	Hydrobiologia	293	97-104	
57	WOS	1993	Rossi and Menozzi	The clonal ecology of *Heterocypris incongruens* (Ostracoda) - life-history traits and photoperiod	Functional Ecology	7	177-182	10.2307/2389884
58	WOS/ Scopus	1991	Ferrari et al.	Succession of Cladocerans in a Northern Italian ricefield	Hydrobiologia	225	309-318	10.1007/BF00028409
59	WOS/ Scopus	1990	Ali	Seasonal dynamics of microcrustacean and rotifer communities in Malaysian rice fields used for rice-fish farming	Hydrobiologia	206	139-148	10.1007/BF00018640
60	WOS/ Scopus	1990	Grigarick et al.	Effect of pesticide treatments on nontarget organisms in California rice paddies. 1. Impact of Triphenyltin Hydroxide. 2. Impact of Diflubenzuron and Triflumuron	Hilgardia	58	1-36	
61	Scopus	1990	Blaustein	Evidence for predatory flatworms as organizers of zooplankton and mosquito community structure in rice fields	Hydrobiologia	199	179-191	10.1007/BF00006351
62	Scopus	1990	Rossi and Menozzi	The clonal ecology of *Heterocypris incongruens* (Ostracoda)	Oikos	57	388-398	10.2307/3565969
63	Scopus	1988	Fores and Comin	Action of malathion plus lindane pesticide on crustacean populations	Ecotoxicology and Environmental Safety	15	180-185	10.1016/0147-6513(88)90070-X
64	WOS	1987	Vidrine et al.	*Eulimnadia texana* Packard (Conchostraca, Limnadiidae) in rice fields in Southwestern Louisiana	Southwestern Naturalist	32	1-4	10.2307/3672002
65	Scopus	1987	Hudec	*Moina oryzae* n. sp. (Cladocera, Moinidae) from Tamil Nadu (South India)	Hydrobiologia	145	147-150	10.1007/BF02530274
66	Scopus	1987	Margaritora et al.	A Far East *Moina*, M. *weismanni* Ishikawa, 1896 found in an Italian ricefield	Hydrobiologia	145	93-103	10.1007/BF02530269
67	Scopus	1987	Taira	Species Composition of Phyto and Zooplankton Communities in Fertilized and Non-fertilized Paddy Fields	Japanese Journal of Limnology (Rikusuigaku Zasshi)	48	77-83	10.3739/rikusui.48.77
68	WOS/ Scopus	1986	Lim and Wong	The effect of pesticides on the population-dynamics and production of *Stenocypris major* Baird (Ostracoda) in ricefields	Archiv fur Hydrobiologie	106	421-427	
69	WOS	1986	Mckenzie and Moroni	Man as an agent of crustacean passive dispersal via useful plants - exemplified by Ostracoda *Ospiti esteri* of the Italian ricefields ecosystem - and implications arising therefrom	Journal of Crustacean Biology	6	181-198	10.2307/1547979

70	WOS/ Scopus	1984	Lim et al.	Ecological-studies of Cladocera in the ricefields of Tanjung Karang, Malaysia, subjected to pesticide treatment	Hydrobiologia	113	99-103	10.1007/BF00026596
71	Scopus	1984	Ferrari	Use of theoretical models in an experimental research on a ricefield ecosystem	Atti dei Convegni Lincei - Accademia Nazionale dei Lincei	62	175-196	
72	Scopus	1983	Ishibashi et al.	Effects of application of certain herbicides on soil nematodes and aquatic invertebrates in rice paddy fields in Japan	Crop Protection	2	289-304	10.1016/0261-2194(83)90003-0
73	Scopus	1983	Grant et al..	Regulation of invertebrate grazers as a means to enhance biomass and nitrogen fixation of Cyanophyceae in wetland rice fields	Soil Science Society of America Journal	47	669-675	10.2136/sssaj1983.03615995004700040013x
74	WOS	1982	Perez and Aspiras	The ricefield ostracods (Crustacea) and their predation on blue-green-algae as affected by pesticides	Kalikasan the Philippine Journal of Biology	11	373-373	
75	Scopus	1981	Idris and Fernando	Cladocera of Malaysia and Singapore with new records, redescriptions, and remarks on some species	Hydrobiologia	77	233-256	10.1007/BF00019671
76	Scopus	1980	Wilson et al.	Effect of microcrustaceans on blue-green algae in flooded soil	Soil Biology and Biochemistry	12	237-240	10.1016/0038-0717(80)90067-X
77	Scopus	1977	Pont	Structure and seasonal changes of populations of Copepoda, Cladocera and Ostracoda in the rice fields of the Camargue	Annales de Limnologie	13	15-28	10.1051/limn/1977011

Table II – Information used for the quantitative data of 77 studies with microcrustaceans from rice fields, from the Web of Science and Scopus databases between the years 1977 to 2019.

	Study	Groups	Species	Coutries	Form ative	Form dorment	Ative and dorment
1	Smith et al. 2019	Ostracoda	*Ilyocypris dentifera; Ilyocypris japonica; Ilyocypris incus*	Japan	Yes		
2	Subrero et al. 2019	Cladocera	*Daphnia magna*	Italy		Yes	
3	Içoğlu 2019	Cladocera	*Daphnia magna*	USA	Yes		
4	Chen et al. 2018a	Cladocera	*Daphnia magna*	China	Yes		
5	Jiang et al. 2018	Cladocera	*Daphnia magna*	China	Yes		
6	Chen et al. 2018b	Cladocera	*Daphnia magna*	China	Yes		
7	Lovas-Kiss et al. 2018	[1]Anostraca; [2]Cladocera; Conchostraca; Ostracoda	[1]*(Artemia* sp.; *Streptocephalus* cf. *torvicornis)* [2] *(Alona* sp.; *Daphnia pulex; Leydigia acanthocercoides; Moina* sp.; *Ceriodaphnia* cf. *quadrangula)*	Spain		Yes	
8	Fefilova and Alekseev 2018	Copepoda	*Elaphoidella bidens; Elaphoidella grandidieri*	Malaysia	Yes		
9	Savatenalinton 2017	Ostracoda	*Astenocypris papyracea; Bradleystrandesia weberi; Bradleytriebella decorata; Bradleytriebella lineata; Bradleytriebella tuberculata; Candona* sp.; *Candonopsis* sp.; *Chrissia formosa; Chrissia humilis indica; Chrissia* sp.; *Cypretta* sp.; *Cypridopsis spp.; Cyprinotus uenoi; Cypris subglobosa; Dentocypria aequiloba; Dentocypria smithi; Dentocypria chantaranothaii; Dolerocypris fasciata; Dolerocypris sisaketensis; Hemicypris exigua; Hemicypris mizunoi; Hemicypris ovata; Hemicypris reticulata; Ilyocypris sp.; Limnocythere stationis; Metacypris srisumonae; Notodromas sinensis; Pseudocypretta maculata; Pseudostrandesia calapanensis; Pseudostrandesia gaetani; Pseudostrandesia mamarilorum; Pseudostrandesia ovata; Pseudostrandesia phetchabunensis; Pseudostrandesia striatoreticulata; Pseudostrandesia thailandensis; Pseudostrandesia* cf. *phetchabunensis; Stenocypris derupta; Stenocypris major; Stenocypris malayica; Stenocypris orientalis; Strandesia hornei; Strandesia kraepelini; Strandesia perakensis; Strandesia sexpunctata; Strandesia* cf. *kraepelini; Tanycypris eugenkempf; Vestalenula boteai*	Thailand	Yes		
10	Zhang et al. 2016	Cladocera	*Daphnia magna*	China	Yes		
11	Grippo et al. 2016	Cladocera	*Ceriodaphnia dubia*	USA	Yes		
12	Ávila et al. 2015	[1]Cladocera; [2]Copepoda; [3]Ostracoda	[1] *(Alona dentifera; Alona glabra; Ceriodaphnia cornuta* fa. *Rigaudi; Dunhevedia colombiensis; Ephemeroporus hybridus; Ephemeroporus tridentatus; Ilyocryptus spinifer; Karualona muelleri; Latonopsis*	Brazil		Yes	

			australis; Leydigia striata; Leydigiopsis ornata; Macrothrix paulensis; Macrothrix spinosa; Macrothrix elegans; Moina minuta; Parvalona parva) ^{2}*(Argyrodiaptomus furcatus)* ^{3}*(Stenocypris major; Cypretta* sp.; *Cypridopsis vidua; Strandesia obtusata; Strandesia bicuspis)*			
13	Montoliu et al. 2015	Copepoda	*Mesocyclops pehpeiensis*	Spain	Yes	
14	Valls et al. 2014	Ostracoda	*Candonocypris novaezelandiae; Stenocypris macedonica; Cypris subglobosa; Hemicypris barbadensis; Hemicypris Salina; Dolerocypris sinensis; Trajancypris clavata; Fabaeformiscandona subacuta; Ilyocypris gibba*	Spain	Yes	
15	Reimche et al. 2014	Cladocera; Copepoda	-	Brazil	Yes	
16	Wang et al. 2013	Cladocera; Copepoda	*Daphnia hyalina*	China	Yes	
17	Sinev and Korovchinsky 2013	Cladocera	*Ceriodaphnia cornuta; Moina micrura; Macrothrix spinosa; Ilyocryptus spinifer; Alona cambouei; Karualona karua; Leydigia ciliata*	South Vietnam	Yes	
18	Plodsomboon et al. 2012	Anostraca	*Branchinella thailandensis*	Thailand		Yes
19	Hayasaka et al. 2012	Cladocera	*Ceriodaphnia dubia; Ceriodaphnia reticulata; Daphnia magna; Daphnia pulex; Moina macrocopa*	Japan	Yes	
20	Mesquita-Joanes et al. 2012	Ostracoda	*Fabaeformiscandona subacuta*	Spain; Russia; Japan; China; South Korea	Yes	
21	Chittapun 2011	^{1}Cladocera; Copepoda; Ostracoda	^{1}*(Guernella raphalis; Macrothrix spinosa; Moinodaphnia macleayi)*	Thailand		Yes
22	Bahaar and Bhat 2011	^{1}Conchostraca; ^{2}Anostraca; ^{3}Amphipoda	^{1}*(Cyzicus* sp.; *Eulimnadia* sp.*)* ^{2}*(Branchinecta acanthopenes)* ^{3}*(Gammarus pulex)*	India	Yes	
23	Marques et al. 2011	Cladocera	*Daphnia longispina; Daphnia magna*	Portugal	Yes	
24	Maiphae et al. 2010	Cladocera	*Bosmina* sp.; *Bosminopsis deitersi; Alona* cf. *cambouei; Alona monacantha; Alona verrucosa; Alona pulchella; Dadaya macrops; Ephemeroporus barroisi; Karualona iberica; Karualona karua; Oxyurella singalensis; Ceriodaphnia cornuta; Scapholeberis kingi; Ilyocryptus* sp.; *Guernella raphaelis; Macrothrix spinosa; Macrothrix triserialis; Moina micrura; Moinodaphnia macleayi; Diaphanosoma excisum; Pseudosida bidentata*	Thailand	Yes	
25	Stenert et al. 2010	^{1}Cladocera; ^{2}Ostracoda; ^{3}Copepoda; Conchostraca	^{1}*(Ilyocryptus verrucosus; Ilyocryptus sordidus; Macrothrix laticornis; Macrothrix mira; Moina micrura; Ephemeroporus barroisi)* ^{2}*(Chlamydotheca incisa;Cypridopsis vidua)* ^{3}*(Metacyclops leptopus leptopus)*	Brazil		Yes

26	Chittapun et al. 2009	^{1}Cladocera; ^{2}Copepoda	^{1}*(Alona costata; Alona puchella; Ceriodaphnia cornuta; Diaphanosoma excisum; Euryalona orientalis; Guernella raphalis; Kurzia longirostris; Ilyocryptus spinifer; Macrothrix spinosa; Moinodaphnia macleayii; Scapholeberis kingi)* ^{2}*(Phyllodiaptomus praedictus; Mesocyclops thermocyclopoides; Thermocyclop decipiens)*	Thailand	Yes	
27	Selvarani 2009	Anostraca	*Streptocephalus dichotomus*	India		Yes
28	Moore et al. 2009	Amphipoda	*Hyalella azteca*	USA	Yes	
29	Reimche et al. 2008	Cladocera; Copepoda	-	Brazil	Yes	
30	Golombieski et al. 2008	^{1}Cladocera; Copepoda	^{1}*(Daphnia magna; Daphnia pulex; Daphnia ambigua; Daphnia longiremis; Ceriodaphnia* sp.; *Scapholebris* sp.*)*	Brazil	Yes	
31	Hamdi et al. 2007	Ostracoda	*Heterocypris incongruens*	Japan	Yes	
32	Barata et al. 2007	Cladocera	*Daphnia magna*	Spain	Yes	
33	Sánchez-Bayo and Goka 2006	^{1}Ostracoda; ^{2}Cladocera	^{1}*(Ilyocypris dentifera; Cypridopsis vidua; Cyretta seurati)* ^{2}*(Chydorus sphaericus; Daphnia magna)*	Japan	Yes	
34	Rossi et al. 2006	Ostracoda	*Heterocypris incongruens*	Italy	Yes	
35	Martinoy et al. 2006	^{1}Cladocera; ^{2}Copepoda; ^{3}Ostracoda	^{1}*(Simocephalus exspinosus; Ceriodaphnia reticulata; Ceriodaphnia quadrangula; Megafenestra aurita; Moina macrocopus; Macrothrix hirsuticornis; Wlassicsia pannonica; Chydorus sphaericus; Alona rectangula; Alona costata; Alona guttata; Camptocercus rectirostris; Oxyurella tenuicaudis; Tretocephala ambigua)* ^{2}*(Calanipeda aquaedulcis; Macrocyclops albidus; Tropocyclops prasinus; Acanthocyclops* sp.; *Microcyclops varicans; Thermocyclops dybowskii)* ^{3}*(Ilyocypris gibba; Heterocypris incongruens; Heterocypris salina; Herpetocypris chevreuxi; Cypris bispinosa; Cypretta seurati)*	Spain	Yes	
36	Sánchez-Bayo and Goka 2006	Ostracoda; Cladocera; Copepoda; Conchostraca	-	Japan	Yes	
37	Konwick et al. 2005	Cladocera	*Ceriodaphnia dubia*	USA	Yes	
38	Chandler et al. 2004	Copepoda	*Amphiascus tenuiremis*	USA	Yes	
39	Dieng et al. 2003	Copepoda	*Macrocyclops distinctus; Megacyclops viridis; Mesocyclops pehpeiensis*	Japan	Yes	
40	Yamazaki et al. 2003	^{1}Cladocera; ^{2}Ostracoda; ^{3}Copepoda	^{1}*(Moina* sp.; *Scapholeheris* sp.*)* ^{2}*(Jlyocypris; Heterocypris)* ^{3}(Harpacticoida; Cyclopoida; Calanoida)	Japan	Yes	
41	Rossi et al. 2003	Ostracoda	*Limnocythere inopinata; Limnocythere* cf. *stationis; Ilyocypris inermis; Ilyocypris australiensis; Ilyocypris biplicata; Ilyocypris decipiens;*	Italy	Yes	

			Ilyocypris monstrifica; Ilyocypris gibba; Candona candida; Candona neglecta; Fabaeformiscandona fabaeformis; Fabaeformiscandona fragilis; Pseudocandona albicans; Paracandona euplectella; Notodromas persica; Chlamydotheca incisa; Chrissia sp.; *Cypretta dubia; Cypretta globulus; Cypretta seurati; Cypretta turgida; Bradleystrandesia fuscata; Cypris pubera; Dolerocypris fasciata; Dolerocypris sinensis; Eucypris ornata; Eucypris virens; Hemicypris dentatomarginata; Herpetocypris reptans; Heterocypris incongruens; Heterocypris salina; Ilyodromus viridulus; Isocypris beauchampi cicatricosa; Psychrodromus olivaceus; Stenocypris major; Strandesia caudata; Strandesia spinulosa; Strandesia tonolli; Tanycypris pellucida; Trajancypris clavata; Prionocypris zenkeri; Cypridopsis elongata; Cypridopsis hartwigi; Cypridopsis helvetica; Cypridopsis obesa; Cypridopsis parva; Cypridopsis vidua; Plesiocypridopsis newtoni; Potamocypris arcuata; Potamocypris fulva; Potamocypris smaragdina; Potamocypris villosa*			
42	Grygier et al. 2002	^{1}Anostraca; ^{2}Conchostraca	^{1}*(Branchinella kugenumaensis)* ^{2}*(Caenestheriella gifuensis; Leptestheria kawachiensis; Eulimnadia braueriana; Eulimnadia packardiana; Eulimnadia* sp.; *Lynceus biformis)*	Japan	Yes	
43	Yamazaki et al. 2001	^{1}Anostraca; ^{2}Cladocera; ^{3}Ostracoda; ^{4}Copepoda	^{1}*(Branchinella* sp.*)* ^{2}*(Moina* sp.; *Scapholeberis* sp.; *Bosmina* sp.*)* ^{3}*(Ilyocypris* sp.; *Heterocypris* sp.*)* ^{4}(Harpacticoida; Cyclopoida)	Japan	Yes	
44	Schoenly et al. 1998	^{1}Ostracoda; ^{2}Copepoda	^{1}*(Heterocypris luzonensis)* ^{2}*(Eucyclops serrulatus)*	Philippines	Yes	
45	Leoni et al. 1998	Cladocera	*Daphnia galeata; Eubosmina coregoni; Bosmina longirostri; Ceriodaphnia reticulata; Ceriodaphnia laticaudata; Scapholeberis rammneri; Simocephalus vetulus; Simocephalus serrulatus; Macrothrix rosea; Macrothrix laticornis; Wlassicsia pannonica; Alona rectangula; Alonella excisa; Chydorus sphaericus; Moina affinis; Moina micrura*	Italy	Yes	
46	Mirabdullayev 1998	Cladocera	*Moina mukhamedievi*	Uzbekistan	Yes	
47	Cabral et al. 1998	Cladocera; Copepoda	-	Portugal	Yes	
48	Mirabdullayev 1997	Copepoda	*Microcyclops rechtyae*	Uzbekistan	Yes	
49	Petkovski 1997	Anostraca	*Branchipus schaefferi*	Macedonia	Yes	
50	Taniguchi et al. 1997	^{1}Cladocera; ^{2}Copepoda; ^{3}Ostracoda	^{1}*(Moina macrocopa)* ^{2}*(Cyclopidae)* ^{3}*(Cypretta* sp.; *Tanycypris* sp.*)*	Japan		Yes
51	Taniguchi et al. 1997	^{1}Cladocera; ^{2}Copepoda; ^{3}Ostracoda	^{1}*(Moina* sp.; *Chydoridae* sp.; *Simocephalus* sp.; *Macrothrix* sp.*)* ^{2}*(Cyclopidae)* ^{3}*(Cypris maculosa; Ilycypris* sp.; *Cypridopsis* sp.; *Candonidae* sp.*)*	Japan	Yes	

52	Moore and Farris 1997	Cladocera	*Ceriodaphnia dubia*	USA	Yes		
53	Scanabissi and Tommasini 1997	Conchostraca	*Limnadia lenticularis*	Italy	Yes		
54	Tinti and Scanabissi 1996	Conchostraca	*Eoleptestheria ticinensis; Leptestheria dahalacensis; Limnadia lenticularis*	Italy	Yes		
55	Rossi et al. 1996	Ostracoda	*Heterocypris incongruens*	Italy			Yes
56	Rayner 1994	Copepoda	*Tropodiaptomus zambeziensis*	South Africa	Yes		
57	Rossi and Menozzi 1993	Ostracoda	*Heterocypris incongruens*	Italy		Yes	
58	Ferrari et al. 1991	Cladocera	*Diaphanosoma brachyurum; Latonopsis australis; Bosmina longirostris; Ceriodaphnia reticulata; Ceriodaphnia laticaudata; Ceriodaphnia megops; Scapholeberis rammneri; Simocephalus vetulus; Simocephalus serrulatus; Daphnia curvirostris; Moina affinis; Moina weismanni; Moina brachiata; Moina micrura; Ilyocryptus agilis; Echinisca rosea; Pleuroxus aduncus; Pleuroxus denticulatus; Dunhevedia crassa; Chydorus sphaericus; Kurzia latissima; Alona rectangula; Alona guttata; Alona diaphana; Oxyurella tenuicaudis; Tretocephala ambigua*	Italy	Yes		
59	Ali 1990	^{1}Copepoda; ^{2}Cladocera	^{1}*(Mesocyclops thermocylopoides; Tropodiaptomous vicinus)* ^{2}*(Alona davidi; Alona costata; Alona dentifera; Alona karau; Alona quadrangularis; Alona* sp. *Alonella excisum; Alonella* sp.*; Bosminopsis deitersi; Ceriodaphnia cornuta; Chydorus eurynotus; Chydorus reticulatus; Chydorus ventricosus; Diaphanosoma excisum; Diaphanosoma sarsi; Dunhevedia serrata; Ephemeroporus barroisi; Euryalona orientalis; Guernella raphalis; Macrothix spinosa; Macrothix triserealis; Moina micrura; Moinodaphnia macleayii; Pseudosida bidentata; Scapholeberis kingii; Simocephalus latirostris)*	Malaysia	Yes		
60	Grigarick et al. 1990	^{1}Conchostraca; ^{2}Ostracoda; ^{3}Cladocera	^{1}*(Caenestberiella sp.)* ^{2}*(Cypricerus* sp.; *Cypris* sp.; *Candona* sp.*)* ^{3}*(Ilyocryptus spinifer)*	USA	Yes		
61	Blaustein 1990	^{1}Cladocera; Copepoda; Ostracoda	^{1}*Moina micrura*	USA	Yes		
62	Rossi and Menozzi 1990	Ostracoda	*Heterocypris incongruens*	Italy	Yes		
63	Fores and Comin 1988	^{1}Cladocera; ^{2}Copepoda	^{1}*(Moina brachiata; Moina micrura; Bosmina longirostris)* ^{2}*(Acanthocyclops vernalis)*	Spain	Yes		
64	Vidrine et al. 1987	Conchostraca	*Eulimnadia texana*	USA	Yes		
65	Hudec 1987	Cladocera	*Moina oryzae*	India	Yes		
66	Margaritora et al. 1987	Cladocera	*Moina weismanni; Moina brachiata; Moina affinis; Moina micrura*	Italy	Yes		
67	Taira 1987	^{1}Cladocera; ^{2}Ostracoda;	^{1}*(Moina macrocopa)* ^{2}*(Cypridopsis* sp.*)*	Japan	Yes		

		^{3}Copepoda	^{3}*(Tropocyclops prasinus)*		
68	Lim and Wong 1986	Ostracoda	*Stenocypris* sp.	Malaysia	Yes
69	Mckenzie and Moroni 1986	Ostracoda	*Ospiti Esteri*	Italy	Yes
70	Lim et al. 1984	Cladocera	*Diaphanosoma excisum; Diaphanosoma sarsi; Pseudosida bidentata; Scapholeberis kingi; Moina micrura; Macrothrix spinosa; Acroperus harpae; Alona guttata; Alonella excisa; Chyorus barriosi; Chyorus* cf. *sphaericus;*	Malaysia	Yes
71	Ferrari 1984	Cladocera; Copepoda	-	Italy	Yes
72	Ishibashi et al. 1983	^{1}Copepoda; ^{2}Cladocera	^{1}*(Cyclops strenuus)* ^{2}*(Moina macrocopa; Bosmina* sp.*)*	Japan	Yes
73	Grant et al. 1983	Ostracoda	-	USA	Yes
74	Perez and Aspiras 1982	Ostracoda	-	Philippines	Yes
75	Idris and Fernando 1981	Cladocera	*Diaphanosoma excisum; Diaphanosoma sarsi; Pseudosida bidentata; Latonopsis australis; Ceriodaphnia cornuta; Scapholeberis kingi; Simocephalus serrulatus; Simocephalus latirostris; Moinadaphnia macleayi; Moina micrura; Bosminopsis deitersi; Ilyocryptus spinifer; Grimaldina brazzai; Gurnella raphalis; Streblocercus pygmaeus; Macrothrix spinosa; Macrothrix capensis-monodi; Macrothrix triserialis; Alonella nana; Alonella excisa; Chydorus barroisi; Chydorus ventricosus; Chydorus parvus; Chydorus eurynotus; Chydorus pubescens; Chydorus reticulatus; Pseudochydorus globosus; Dunhevedia crassa; Dunhevedia serrata; Dadaya macrops; Leydigia acanthocercoides; Alona quadrangularis; Alona eximia; Alona affinis; Alona macronyx; Alona davidi; Alona sarasinorum; Alona costata; Alona guttata; Alona pulchella; Alona karua; Alona monacantha; Alona verrucosa; Kurzia longirostris; Acroperus harpae; Oxyurella sinhalensis; Euryalona orientalis; Indialona globulosa*	Malaysia	Yes
76	Wilson et al. 1980	^{1}Ostracoda; ^{2}Cladocera	^{1}*(Cypris* sp.*)* ^{2}*(Daphnia magna)*	USA	Yes
77	Pont 1977	^{1}Cladocera; ^{2}Copepoda; ^{3}Ostracoda	^{1}*(Daphnia similis; Ceriodaphnia reticulata; Ceriodaphnia pulchella; Simocephalus exspinosus; Simocephalus vetulus; Scapholeberis mucronata; Scapholeberis aurita; Moina brachiata; Moina macrocopa; Bosmina longirostis; Ilyocryptus agilis; Macrothrix rosea; Macrothrix laticornis; Acroperus harpae; Alona quadrangularis; Alona costata; Alonella exigua; Chydorus sphaericus)* ^{2}*(Eudiaptomus gracilis; Macrocyclops albidus; Macrocyclops fuscus; Eucyclops serrulatus; Paracyclops fimbriatus; Cyclops strenuus; Cyclops furcifer; Diacyclops bisetosus; Acanthocyclops vernalis; Acanthocyclops robustus; Megacyclops viridis viridis; Megacyclops gigas; Thermacyclops crassus; Metacyclops minutus; Mesocyclops*	France	Yes

leukarti; Crytocyclops bicolor)
[3]*(Strandesia bicuspis bicuspis; Strandesia reticulata; Cypridopsis parva; Cyprinotus capensis; Dolcrocypris sinensis; Stenocypris malcomsoni; Iliocypris bradyi)*

CAPÍTULO 2

Strategy for the hatching of microcrustaceans endemic to intermittent environments along hydroperiods

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ESTRATÉGIA DE ECLOSÃO DE MICROCRUSTÁCEOS ENDÊMICOS DE AMBIENTES INTERMITENTES AO LONGO DOS HIDROPERÍODOS

STRATEGY FOR THE HATCHING OF MICROCRUSTACEANS ENDEMIC TO INTERMITTENT ENVIRONMENTS ALONG HYDROPERIODS

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RESUMO: Nós acompanhamos a estratégia de eclosão de *Branchinecta iheringi* e *Eulimnadia pampa*, em diferentes hidroperíodos do ano. Para isso: i) verificamos as estratégias de eclosões das duas espécies; ii) caracterizamos o tempo de desenvolvimento e reprodução das duas espécies; iii) analisamos a relevância dos fatores ambientais (hidroperíodo, temperatura e profundidade) para a eclosão e restabelecimento das duas espécies. Durante um ano acompanhamos quatro hidroperíodos consecutivos em três áreas úmidas intermitentes, três curtos (SH1: primavera; SH2: verão; e SH3: outono), e um longo (LH: inverno). *Branchinecta iheringi* eclodiu em todos os hidroperíodos do ano (SH1: 4 ± 6,9 org; SH2: 7 ± 4,3 org; SH3: 7 ± 5,1 org; LH: 35,3 ± 43,3 org). Por outro lado, *E. pampa* eclodiu somente no hidroperíodo longo (LH: 51,6 ± 61,2 org). A resposta de eclosão e ciclo de vida das duas espécies foi diferente. O tempo de permanência da água e a variação de temperatura tiveram efeito significativo no restabelecimento das espécies. Através do acompanhamento das estratégias de eclosão das duas espécies podemos destacar que elas apresentaram diferentes respostas aos hidroperíodos anuais. *Branchinecta iheringi* respondeu de imediato aos estímulos de eclosão enquanto *E. pampa* precisou de um tempo maior para iniciar as eclosões.

PALAVRAS-CHAVE: Anostraca, Diplostraca, dormência, ambientes temporários

ABSTRACT: We followed the hatching strategy of *Branchinecta iheringi* and *Eulimnadia pampa* in different hydroperiods of the year: i) we verified the hatching strategies of the species, ii) we characterized the time of development and reproduction of the species, and iii) we analyzed the relevance of environmental factors (hydroperiod, temperature, and depth) for hatching and reestablishment of the species. We followed four consecutive hydroperiods in three intermittent wetlands over one year; three short (SH1, SH2, and SH3), and one long (LH). *Branchinecta iheringi* hatched in all hydroperiods of the year (SH1: 4 ± 6.9 org; SH2: 7 ± 4.3 org; SH3: 7 ± 5.1 org; LH: 35.3 ± 43.3 org). *E. pampa*, however, hatched only in the long hydroperiod (LH: 51.6 ± 61.2 org). The hatching responses and life cycles of the two species were different. The water retention time and the temperature variation had a significant effect on the reestablishment of the species. Monitoring the hatching strategies of the two species allows us todemonstrate that they presented different responses to the annual hydroperiods. *Branchinecta iheringi* responded immediately to the hatching stimuli while *E. pampa* needed a longer time to initiate hatching.

KEYWORDS: Anostraca; Diplostraca; dormancy; temporary ponds

1. INTRODUCTION

The main characteristic of intermittent wetlands is the presence of water for a period of time during the year (Maltchik *et al.*, 2004). This is called a hydroperiod (van der Valk, 2006). Aquatic organisms have developed adaptive mechanisms to remain in these ephemeral environments even after a period without water (Blaustein& Schwartz, 2001). A dormancy strategy is one of the main mechanisms for resilience in temporary environments, used by many groups of invertebrates (Brendonck, 1996) and vertebrates (Thompson & Ort, 2016).

The main stimuli for the hatching of dormant eggs is variation in the temperature and light intensity between the seasons (Alekseev *et al.,* 2007), but the effect is dependent on the hydration of the dormant eggs after a period without water (Brendonck, 1996). In the subtropical region, the hydroperiod is a marked seasonal variation in the duration of the flooded phase (Maltchik*et al.*, 2004), altering the length of hydration for dormant eggs. The southern winter (June to September) corresponds to the period of greatest rainfall in southern Brazil (Alvares*et al.*, 2014), resulting in longer hydroperiods lasting weeks or months (Maltchik*et al.*, 2004). Precipitation is reduced in other seasons, but occasionally occurs, and water remains for a few days. The difference in the duration of hydroperiods may affect the frequency and intensity of species hatching throughout the year, since hatching stimuli may also vary (Stenert*et al.*, 2017). The long photoperiod stimuli and high temperatures that occur in the warmer months are related to the volume of precipitation, which can result in long periods without water in the summer months (Alvares*et al.*, 2014).

In addition to the stimuli required for hatching, the depth of the intermittent environments is also important for the process of species reestablishment (Buckup& Bond-

Buckup, 1999; Marinone *et al.*, 2016). Environments are more ephemeral in warmer seasons, with reduced water volume through evaporation, and thus less depth (Maltchik*et al.*, 2004; van der Valk, 2006). The variation in depth over time may affect the time of permanence of the species (Marinone*et al.*, 2016).

Some groups of organisms adjust their lifecycles according to the duration of the water in the environment, such as the microcrustaceans *Branchinecta iheringi*Lilljeborg, 1889 (Branchiopoda: Anostraca) and *Eulimnadia pampa* Marinone, Urcula & Rabet, 2016 (Branchiopoda: Diplostraca), which are endemic to intermittent environments and have adapted to different hydroperiods (Buckup & Bond-Buckup, 1999; Marinone *et al.*, 2016). The two species use dormant eggs as a strategy to survive the waterless period (Buckup & Bond-Buckup, 1999; Marinone *et al.,* 2016). *Branchinecta iheringi* was described with examples of intermittent areas in the state of Rio Grande do Sul (Southern Brazil), and was recorded only in that state (César, 1990; Young, 1999), but its distribution extends to Argentina and Uruguay (César, 1990; Cohen, 1995). The literature on this species is focused on taxonomic resolution (César, 1990; Cohen, 1993; Cohen, 1995; Belk & Brtek, 1995; Young, 1999; Rogers, 2013), with reduced information on the life cycle and ecology. Information about *Eulimnadia pampa* is even more scarce, since there is only one work describing this species in the intermittent wetlands of Argentina (Marinone *et al.*, 2016).

In the temporary wetlands of southern Brazil the hydroperiod has a duration of weeks and normally occurs in winter, but there are occasionally short hydroperiods when there is rain in other seasons (Maltchik *et al.*, 2004). During these annual hydroperiods, the duration of the water, the temperature variation and the depth of the environment seem to be determinant of the reestablishment of *B. iheringi* and *E. pampa* populations in the intermittent environments. These factors may change over the years, as the environments are suffering from anthropogenic pressure, mainly due to urbanization (Stenert *et al.*, 2017). The objective of this study was therefore to monitor how these species are responding to the different hydroperiods in the year, in intermittent wetlands in southern Brazil. For this: i) we verified the hatching strategies of the two species in the different hydroperiods; ii) we analyzed the environmental factors for hatching and the reestablishment of the two species; iii) we characterized the time of development and reproduction of the two species.

2. MATERIALS AND METHODS

2.1 Sampling procedures

The study was conducted in three intermittent urban wetlands (area of 464 ± 276 m^2), located in the city of Rio Grande, RS, Brazil (32 ° 04 '38.3 "S, 052 ° 10' 09.1" W). We followed four consecutive hydroperiods between 2016 and 2017. The first three were short hydroperiods (SHs), of up to five days in duration.We sampled only once in each short hydroperiod, four days after the precipitation. The first hydroperiod (SH1) occurred in spring (sampling on October 18, 2016), the second (SH2) in summer (sampling on March 13, 2017), and the third (SH3) in autumn (sampling on May 15, 2017). The fourth hydroperiod was longer (LH), in late fall and early winter (between May 22 and June 23, 2017). This hydroperiod had a duration of 34 days and we made collections every two days.

We examined biological (species) and abiotic (water temperature and depth) data to monitor how species respond to the four different hydroperiods of the year and analyzed the environmental factors. Composite sampling of organisms was used, with three subsamples.We collected60 L of water (20 L/ sub-sample), which was filtered in a plankton net with 68 μm diameter mesh netting. The samples were fixed with alcohol (concentration of 80%) and transferred to the Laboratory of the Limnology of Federal University of Rio Grande (FURG). In the laboratory, the samples were stained with Bengal Rose to assist with screening and subsequent identification. The temperature was measured with a multiparameter probe (U-5000/ Horiba) and depth with a graduated ruler.

We quantified the organisms hatching and the different stages of development in each hydroperiod to characterize the time for the development and reproduction of the two species. The organisms were counted using a stereomicroscope (P45BI/ Precision), and identified with an optical microscope (CX41/ Olympus), and specialized literature (Buckup & Bond-Buckup,1999; Marinone *et al.*, 2016).

2.2 Data analysis

We tracked the two species throughthe hydroperiods, and analyzed the long hydroperiod separately from the short ones to identify the relevance of environmental factors in the hatching and reestablishment of the species. We performed a factorial ANOVA for the short hydroperiods (Crawley, 2007), and compared the abundance of organisms (variable response) in the different hydroperiods (Factor 1), with their respective temperatures (Factor

2) and depths (Factor 3). A linear Pearson correlation was performed to verify whether there was a correlation between temperature and depth.

Three Covariance Analyses (ANCOVA) were performed in the long hydroperiod, comparing abundances of species in the hydroperiod and the effect of the environmental conditions. The species were used as a factor in all ANCOVAs, and the hydroperiod time, temperature and depth were used as covariates (Crawley, 2007). The abundance data (log +1) was transformed for the analysesin order to reach the normality assumption. All analyses were performed in Environment R, version 3.5.1 (R Core Team, 2018).

3. RESULTS

The two species responded differently to the duration of the water. *Branchinecta iheringi* hatched in both short and long hydroperiods, while *Eulimnadia pampa* hatched only in the long hydroperiod. There was a significant correlation between temperature and depth (R = 0.76) in the short hydroperiod (SH). The highest temperatures and the lowest depths were recorded in SH2, corresponding to summer, followed by SH3 (autumn) and SH1 (spring) (Table 1). In short hydroperiods (SH1, SH2, and SH3) we only recorded the presence of *Branchinecta iheringi* in the larvae stage (Figure 1). There was no significant difference in larval abundance among the SHs (Table 2, Figure 1).

Table 1: Temperature and depth data (mean ± standard deviation) for the short hydroperiods of spring (SH1), summer (SH2) and autumn (SH3).

	Temperature (°C)	Depth (cm)
SH1 (Spring)	15 ± 0.13	30 ± 4.7
SH2 (Summer)	27 ± 1.67	21 ± 7.3
SH3 (Autumn)	16 ± 0.97	25 ± 21

During the long hydroperiod (LH) the temperature reached a maximum of 23 ± 1.7 °C on the fourth day and a minimum of 11 ± 0.6 °C on the thirtieth day (Figure 2). The depth varied as a function of the precipitation in the hydroperiod, to a maximum of 38 ± 0.03 cm on the sixth day, and a minimum of 11 ± 0.05 cm on the thirty-fourth day (Figure 3). The temperature was significantlycorrelated with depth (R = 0.72). The two species co-occurred during LH and the responses in terms of predominance were different (Figure 4). *Branchinecta iheringi* predominated at the beginning of the hydroperiod until the tenth day, and then *E. pampa* predominated until the environments completely dried up (Figure 4).

Table 2: Results of factorial ANOVA for *Branchinecta iheringi* abundance in the short hydroperiods, and of the three ANCOVAS for the abundance of *Branchinecta iheringi* and *Eulimnadia pampa* and the environmental conditions in the long hydroperiod. The abundance of *B. iheringi* in the three short hydroperiods was considered in the ANOVA. In ANCOVA 1 the two species were considered as factors and the hydroperiod time as a covariate. In ANCOVA 2 the two species were considered as factors and temperature as a covariate. In ANCOVA 3 the two species were considered as factors and depth as a covariate.Indicator of statistical data significative (*).

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
ANOVA					
Hidroperiods	2	18.00	9.00	0.200	0.827
Temperature	1	6.47	6.47	0.144	0.724
Depth	1	1.35	1.35	0.030	0.871
Residuals	4	180.18	45.04		
ANCOVA 1					
Species	1	3.16	3.155	4.310	**0.0405***
Time of hidroperiod	1	7.96	7.962	10.875	**0.0013***
Species : time of hidroperiod	1	4.02	4.016	5.485	**0.0212***
Residuals	98	71.75	0.732		
ANCOVA 2					
Species	1	3.16	3.155	4.514	**0.0361***
Temperature	1	15.07	15.074	21.564	**<0.001***
Species : temperature	1	0.15	0.146	0.209	0.6484
Residuals	98	68.50	0.699		
ANCOVA 3					
Species	1	3.16	3.1551	3.877	0.0518
Depht	1	1.81	1.8060	2.219	0.1395
Species : depth	1	2.16	2.1641	2.659	0.1062
Residuals	98	79.75	0.8138		
TukeyHSD (Species)		diff	lwr	upr	p adj
B.iheringi – E.pampa		0.3517	0.0077	0.7112	0.055

When we evaluated the relevance of environmental conditions to the abundance of species in the LH, we observed a significant effect on the interaction of the species and hydroperiod duration (Table 2, ANCOVA 1: F$_{1-98}$ = 5.485, p = 0.0212). There was a significant effect on abundance in relation to temperature variation (Table 2, ANCOVA 2: F$_{1-98}$ = 21.564, p <0.001, Figure 2). There was no significant effect of depth on species abundance (Table 2, ANCOVA 3: F$_{1-98}$ = 2.219, p = 0.1395, Figure 3). When comparing the abundance of the species in the hydroperiod we found that there was no significant difference between them (Table 2, Tukey HSD: p = 0.055).

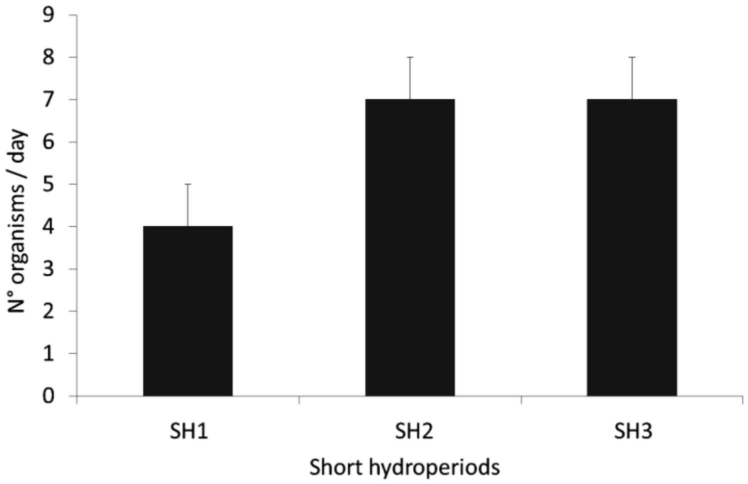

Figure 1: Number of *Branchinecta iheringi* organisms (mean ± standard error) by sampling in short spring (SH1), summer (SH2) and autumn (SH3) hydroperiods.

We characterized the time of development and reproduction for the two species and recorded the stages of development of *B. iheringi* and *E. pampa*. The larvae of *B. iheringi* were recorded from the second to the tenth day of the hydroperiod (Figure 5). The young of *B. iheringi* were recorded on the fourth and eighth day, the males on the twelfth and fourteenth day, and the females with eggs on the twelfth, eighteenth and twenty-sixth days (Figure 5). Only the young and female adults were recorded for *E. pampa*. The young were recorded from the fourth to the twenty-fourth day of the hydroperiod (Figure 5). Females were recorded from the tenth day until the end of the hydroperiod, and the first females with eggs were found from the twenty-second day (Figure 5).

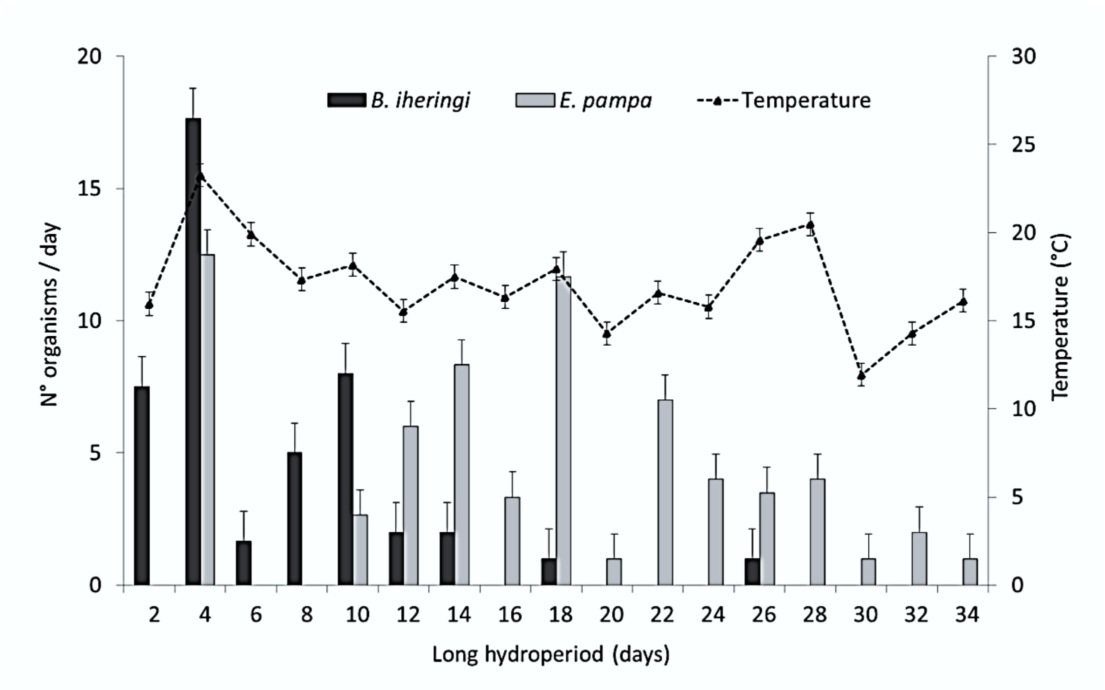

Figure 2: Variation in the temperature and number of organisms of *Branchinecta iheringi* and *Eulimnadia pampa* in the winter hydroperiod (mean ± standard error).

4. DISCUSSION

4.1 Strategies for species hatching in different hydroperiods

Both *Branchinecta iheringi* and *Eulimnadia pampa* were resilient regarding the recolonization of temporary environments after a period of desiccation, indicating the importance of dormant eggs for the reestablishment of organisms during the hydroperiods. The two species responded differently to the duration of the water, as *B. iheringi* hatched in all hydroperiods of the year and *E. pampa* only in the long hydroperiod.

The long hydroperiod was fundamental to verifying the recolonization process of the two species. It was possible to see that there was a difference in species permanence in the hydroperiod, since *B. iheringi* was predominant at the beginning and only afterward *E. pampa* predominated. Many authors describe the importance of this variation in the permanence of the species for equilibrium in the reestablishment of communities of intermittent environments (Brendonck, 1996; Wang *et al.*, 2012; Pinceel *et al.*, 2017; Stenert *et al.*, 2017). This variation can be affected by competition for food or space for reproduction. Establishing themselves at different times minimizes competition for food and enables the success of organisms throughout hydroperiods. This was demonstrated by Wang *et al.* (2012), who recognized that large branchiopods synchronize their life cycles and use space at different times to reduce competitive pressure in intermittent environments.

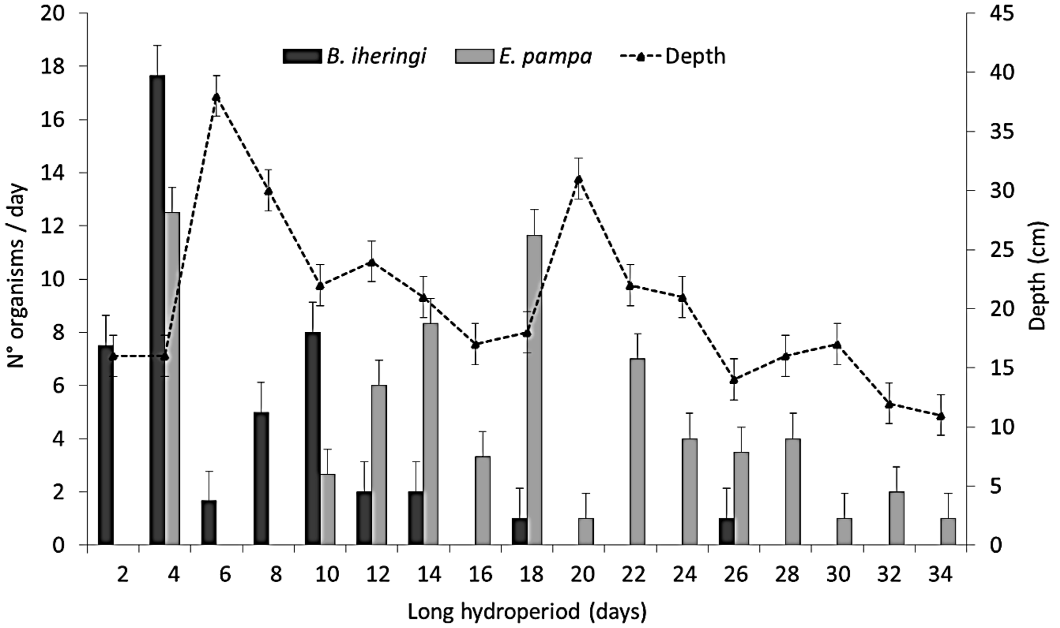

Figure 3: Variation in the depth and number of organisms of *Branchinecta iheringi* and *Eulimnadia pampa* in the winter hydroperiod (mean ± standard error).

4.2 The relevance of environmental factors for hatching and reestablishment of the species

The *B. iheringi* species showed a rapid response to hatching stimuli in all the hydroperiods monitored. The temperature appeared to be of little relevance in the hatching process of this species because there was great temperature variation during the year which did not significantly affect the hatching abundance of the organisms in the short hydroperiods. Hatching in the long hydroperiod started when the temperature was around 15 °C, however, but the highest hatching number was recorded when the temperature increased to 24 °C. The optimum temperature for egg hatching for other species of the same genus as those evaluated in our study is reported as 15 °C for *Branchinecta lindahli* and 20 °C for *Limnadia stanleyana* (Brendonk, 1996). Similarly, *Branchinecta sandiegonensis* will hatch in the range of 10 to 20 °C (Hathaway & Simovich, 1996). This may indicate that an increase in temperature accelerates the hatching process, but is not necessarily the main stimulus for *B. iheringi*. This observation has already been noted for other groups, such as in Paes *et al.* (2016), who worked with the hatching stimuli of dormant *Daphnia* eggs and found that other factors such as the absence of light can affect the hatching process.

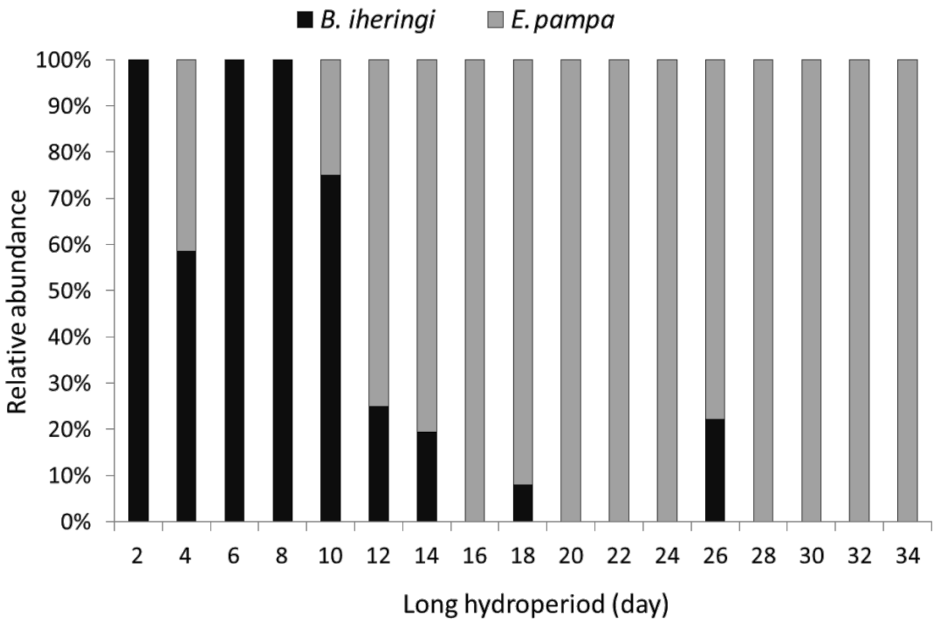

Figure 4: Relative abundance of the species *Branchinecta iheringi* and *Eulimnadia pampa* over the 34 days of the winter hydroperiod.

As well as the temperature, the duration of the water was also a significant factor in the long hydroperiod. *B. iheringi* dormant eggs hatch soon after they are hydrated, regardless of the temperature to which they are exposed. This may suggest that hydration time is more important than temperature for *B. iheringi* hatching, because hatching occurred in all the hydroperiods of the year, regardless of the duration of the water (short or long period), or the temperature that was recorded. The duration of the water was also an important factor in the reestablishment of other crustaceans, such as Cladocera (Florencio *et al.*, 2015; Stenert *et al.*, 2017) and Copepoda (Florencio *et al.*, 2015) in intermittent environments. Different adaptive responses by large branchiopods, regarding the duration of the water have been demonstrated for several species of fairy shrimps: for example, in experiments with three species, Dararat *et al.* (2011) demonstrated that *Branchinella* and *Streptocephalus* hatch after three to four days of egg hydration.

For *E. pampa*, the response was the reverse as that recorded for the first species, as it seems that the temperature is as important as the duration of the water since hatching only occurred in the long winter hydroperiod. The temperature increase caused hatching on the fourth day of the hydroperiod for this species, indicating that this great increase is necessary for the dormancy of *E. pampa* eggs. This increase may act as an initial trigger for the hatching, because even when the temperature was reduced the hatching continued. The need for a specific temperature as the initial trigger in hatching is very common in cladocerans (Alekseev *et al.*, 2007; Paes *et al.*, 2016), and it may be that this strategy is also adopted by *E. pampa*. Marcus & Weeks (1997) tested the effect of the duration of the water in *Eulimnadia texana* and recorded that high temperatures can affect the onset of hatchings.

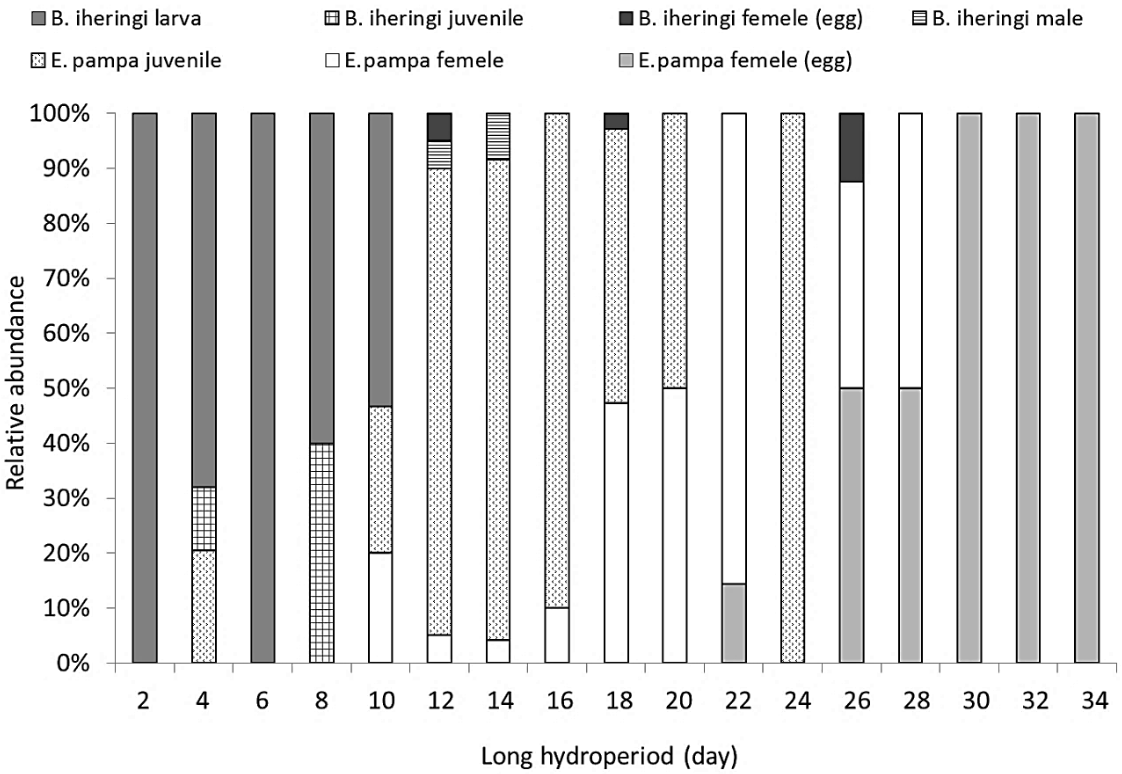

Figure 5: Relative abundance of the stages of development of *Branchinecta iheringi* and *Eulimnadia pampa* in the long winter hydroperiod.

4.3 Characterization of the time of development and reproduction of the species

Observation of the time of development and reproduction for the two species demonstrated that, even though *B. iheringi* had more stages of life (egg, larva, young and adult), the development of these stages was faster, with a 12-day interval between larval hatching and recording of adult males and females with eggs. This *B. iheringi* cycle occurred at the beginning of the hydroperiod when instability in the water temperature was recorded. *Eulimnadia pampa* has direct development, hatching on the fourth day of the hydroperiod, and predominated only after temperature stability, and there was an interval of 18 days between the hatching of dormant eggs and the recording of females with eggs. The maturation time of *E. pampa* appears to be somewhat slower than *B. iheringi* since we recorded adult females on the tenth day of the hydroperiod, but only observed females with eggs after 12 days. Marcus & Weeks (1997) observed that the duration of the water altered the maturation time of *Eulimnadia texana*, where shorter hydroperiods accelerated the maturation time. Brendonk (1996) reported that in other subtropical regions the difference in maturation time for *Branchinecta* and *Eulimnadia* species favors the maintenance and viability of the dormant egg bank.

Depth and temperature were important for the beginning of production of the *E. pampa* eggs since we registered females with eggs from the twenty-second day. There was an increase in the temperature and a reduction in the depth of the environment, causing acceleration in the production of the eggs. This may be indicative of the timing of the species in realizing that the environment is becoming unfavorable, and egg production is a response to the final hydroperiod condition. This is also well documented for Cladocera, in which species can perceive environmental stimuli, and produce dormant eggs to ensure the next generation in the next hydroperiod (Alekseev *et al.*, 2007). Although the two species predominate at different times in the hydroperiod, we observed that after the beginning of the production of both eggs, there was no record of larvae or newborns. This may suggest that in intermittent environments these organisms are investing primarily in the production of dormant eggs. This finding emphasizes the importance of duration of the water of these environments, to maintain the dormant egg bank in the sediment.

5. CONCLUSION

In conclusion, monitoring the hatching strategies of the dormant eggs of the two species, allows us to demonstrate that they presented different responses to the annual hydroperiods of the intermittent wetlands. *Branchinecta iheringi* responds immediately to hatching stimuli, and *E. pampa* needs a trigger to initiate hatching. Both species have a different maturation time and this may be an indication that there is no competitive pressure between them. Even when they appear in the same hydroperiod, each predominates at different times of the duration of the water. In intermittent environments, these species are apparently investing mainly in the production of dormant eggs, strengthening egg bank maintenance, which proves to be fundamental for the recolonization and dynamics of these aquatic environments.

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CAPÍTULO 3

Hydration time influences microcrustacean hatching in intermittent wetlands: *in situ* and *ex situ* approaches

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Hydration time influences microcrustacean hatching in intermittent wetlands: *in situ* and *ex situ* approaches

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Abstract

Organisms living in intermittent wetlands present adaptations to cope with the inundation-desiccationprocess. Microcrustaceans are commonly found in intermittent wetlands because they present reproductive strategies able to synchronize with the hydroperiod. To know the dynamic of the microcrustaceans that inhabit these wetlands of the subtropical coastal plain, which predominate the Pampas biome in Brazil, we analyzed the influence of hydration time and temperature on the hatching of microcrustaceans, comparing *in situ* and *ex situ* approaches. We followed hatching 34 days after *in situ* flooding and tested three temperatures (10, 15, and 20°C) 30 days after laboratory flooding. In both approaches, we classified the hydration time as the beginning, middle, and end of the hydroperiod. We recorded a total of 41 taxa distributed in Cladocera (26 taxa), Ostracoda (8), Copepoda (3), Anostraca (1), and Conchostraca (1). We observed that *in situ* hydration time was the most important factor for hatching. *Ex situ* hydration time was also important, but the increase in temperature positively affected the hatching of organisms. We also found that in both approaches, the beginning of hydration time is the most important period for the hatching of microcrustaceans.

Keywords: dormancy; hatching stimuli; hydration time; resilience; zooplankton

Introduction

Intermittent wetlands are shallow aquatic environments that mainly depend on the climatic conditions (e.g., rainfall) to the permanence of water in the inundation-desiccationprocess, which results in seasonal and interannual periodicity (Maltchiket al., 2004). Intermittent environments are characterized by distinct water periods, alternating the presence (wet phase or hydroperiod) and absence (dry phase) of water (Batzer & Boix, 2016). During the dry phase, local extinctions and/or the migration of organisms occur (Sim et al., 2013; Chaparro et al., 2016). Some organisms that cannot migrate in their active form survive through reproductive adaptations that adjust to these strong variations of inundation-desiccation in wetlands (James et al., 2008; Waterkeyn et al., 2010). In the zooplankton community, microcrustaceans are among the best-adapted organisms to these intermittent environments (James et al., 2008; Waterkeyn et al., 2010).

Microcrustaceans include groups (e.g., Anostraca, Cladocera, Copepoda, Conchostraca and Ostracoda) with different sexual or asexual reproduction and different life cycles (Batzer & Boix, 2016). Microcrustaceans have adaptations that allow them to survive in the environment during the dry phase (Gray & Arnott, 2012; Moreno et al., 2019), and torecolonize when the hydroperiod returns (James et al., 2008; Florencio et al., 2016; Gerhard et al., 2017). The ability to produce dormant forms (quiescent or diapausic) and remain in the sediment (forming a dormant egg bank) ensures the survival of these organisms in intermittent environments (Brendonck & De Meester, 2003; Moreno et al., 2019). Dormant forms are highly resistant and can tolerate conditions unfavorable to the active forms, such as extreme temperatures (Cáceres et al., 2007; Paes et al., 2016), high salinity (Waterkeyn et al., 2010), water with low levels of dissolved oxygen, and desiccation (De Stasio, 1989; Brendonck & De Meester, 2003).

Ricci (2001) described three patterns for dormant egg banks in relation to unfavorable environmental conditions and demonstrated that when environmental conditions are unpredictable (e.g., momentary changes), the active community (active organisms) remains in the environment and can produce dormant eggs at a low but continuous rate (polyphasic pattern). When the environment becomes unfavorable, the active community decreases in numbers of individuals and produces dormant eggs at a high ratein a single event (monophasic pattern). In temporarily unfavorable conditions, the active community becomes locally extinct, but the environment is recolonized from the bank of dormant eggs when favorable environmental conditions return (“bang-bang” pattern). The “bang-bang” pattern may occur in intermittent environments because of the local extinction of the active community in periods of dry phase, and when the hydroperiod returns, the community can reestablish (Ricci, 2001; James et al., 2008). Currently, the dynamics of dormant egg banks have been investigated because of their importance to the resilience of aquatic communities after disturbance in permanent (Alekseev et al., 2007; Pérez-Martínez et al., 2013) and intermittent environments (Iglesias et al., 2016; Eskinazi-Sant'Anna & Pace, 2018; Moreno et al., 2019; Vargas et al., 2019).

Two methods can be used to study the dormant forms: an *in situ* approach that follows hatching in the natural environment (Pérez-Martínez et al., 2013) and an *ex situ* approach, in which the hatching of the dormant eggs is studied in the laboratory (Van Damme & Dumont, 2010; Iglesias et al., 2016). Typically, these two approaches are performed separately, but they may be complementary. The advantage of combining these two approaches is that we can track how organisms hatch in the wild but can also test whether the same patterns occur in a controlled and replicable way, without the interference of factors such as breeding and predation (Iglesias et al., 2016).However, it is necessary to test because field and experimental results do not always match (Cáceres & Schwalbach, 2001).

For microcrustaceans to hatch, the environment must have adequate environmental conditions for the organisms to survive, and there are many factors (e.g. pH, oxygen, and food availability) that indicate that the environment may be favorable to hatching (Iglesias et al., 2016). However, before the hatching process, it is necessary to break the dormancy of the microcrustaceans (Alekseev et al., 2007). The main factors that stimulate the breakdown of dormancy are high temperatures, photoperiod, and light intensity (Brendonck & De Meester, 2003; Alekseev et al., 2007; Iglesias et al., 2016). In the southern hemisphere subtropical region, these conditions coincide with the summer, which is a dry phase in the wetlands (Alvares et al., 2014), leading to local extinction of the active community rather than the emergence of dormant forms (Paes et al., 2016). For the intermittent wetlands of the subtropical regions of the eastern coast of South America, the hydroperiod normally occurs in winter (Alvares et al., 2014). In this season there is higher precipitation and water remains in the environment without evaporating due to the low temperatures; therefore, the stimuli for breaking dormancy and hatching occur in this period in intermittent wetlands (Maltchik, 2003; Freiry et al., 2020).

Many studies support a positive relationship between the hydroperiod and the dynamics of the active zooplankton community in intermittent wetlands. For example, the length of the hydroperiod influences the seasonal and spatial patterns of the community

(Chaparro et al., 2016; Florencio et al., 2016); it is one of the factors determining community structuring in different types of wetlands (Nhiwatiwa et al., 2017; Chaparro et al., 2018). In addition, the hydroperiod influences the viability and hatching patterns of zooplanktonic organisms from the dormant egg bank (Ricci, 2001; Iglesias et al., 2016; Vargas et al., 2019). Thus, in addition to temperature and photoperiod, we are proposing that the hydration time of dormant forms is an important factor for the emergence of microcrustaceans from intermittent environments. How the bank of dormant forms goes through periods of desiccation and hatching of microcrustaceans is dependent of the hydration of the dormant forms (Iglesias et al., 2016); it is possible that the beginning of hydroperiod occurs as soon as the dormant forms are hydrated, which may be the period with the greatest influence after desiccation.

Therefore, our objective was to analyze the influence of hydration time and temperature on the hatching of microcrustaceans, comparing *in situ* and *ex situ* approaches. We tested the hypotheses that: (i) due to desiccation of the bank of dormant forms after the dry phase, microcrustacean hatching is determined by hydration along the hydroperiod rather than by temperature in the *in situ* and *ex situ* approaches; (ii) in both approaches, the hatching of all groups of microcrustaceans is higher at the beginning than in the middle or end of the hydroperiod. We expected this because the primary stimulus for hatches is the hydration of dormant forms.

Materials and methods

Study area

The municipality of Rio Grande is located on the coastal plain of the state of Rio Grande do Sul (32° 04' 38.3" S; 52° 10' 09.1" W), southern Brazil, bordering the Atlantic Ocean (Martins et al., 2019). The southern part of the coastal plain, where the municipality is located, has a predominance of the Pampas biome, which is characterized by the absence of large rivers and the presence of shallow lagoons and large expanses of flooded land (Maltchik, 2003). The climate is subtropical humid, with mean annual temperatures varying between 17 and 19°C and annual rainfall between 1200 and 1500 mm (Alvares et al. 2014). The municipality has a complex of wetlands typical of the coastal plain of southern Brazil, including intermittent wetlands. These environments form in periods of the highest precipitation (i.e., in winter) and generally present deficits in spring and summer (Albertoni et al., 2014).

For our study, we sampled three intermittent wetlands, approximately 10m apart. These wetlands have sandy soil rich in organic matter, the hydroperiod usually occurs in winter, remaining with water for 30 to 40 days; however, a short hydroperiod of five days of precipitation may occur in other seasons (Bandeira et al., 2019). The area of the wetlands varied from 289 to 783 m^2 (464 ± 276 m^2). The three study sites present similar microcrustacean species composition (Martins et al., 2019).

In situ approach

For the *in situ* approach, we monitored the hatching of microcrustaceans without interfering with priority effects, predation, among other possible biotic interactions. We followed the precipitation data from the National Institute of Meteorology (INMET) at Pelotas Station (WMO: 83985), Rio Grande do Sul, Brazil (31° 52' 00" S; 52° 21' 24" W), about 60 km from the sampled wetlands. We started to monitor the wetlands when the water remained with precipitation after a complete desiccation. The monitoring took place during a complete hydroperiod of 34 days, starting on May 20 and drying on June 24, 2017. Since the dormant forms went through a drying period, we assumed that they were dehydrated, so the start of the hydroperiod corresponds to the start of the hydration time of the dormant forms. We collected samples from the wetlands every two days, totaling 17 sampled days. This interval allowed for the development of the necessary structures for reliable identification of Cladocera, Ostracoda, and Conchostraca; furthermore, the direct development and the taxonomic list that already exist for the study area allowed reliable taxonomic identification using juveniles (Buckup & Bond-Buckup, 1999; Bandeira et al., 2019; Martins et al., 2019). When organisms did not develop structures for reliable identification (e.g., the post-abdomen in the Cladocerans and the fifth leg in the Copepods), we maintained the level of genera or order. For Copepoda and Anostraca, we also considered the larval stages to quantify abundance, which was used in statistical analysis.

To characterize the wetlands, on each collection date we checked the maximum depth with a graduated ruler (with 0.5 cm intervals). We measured the water temperature, pH, conductivity, turbidity, and dissolved oxygen with a multiparameter probe (U-5000/ Horiba®). All parameters were measured in the central region and near the wetland's sediment. For the microcrustacean sampling, we made a composite sample, based on three points equidistant in each wet area. Because they are shallow wetlands, we used a millimeter bucket to collect 20 L of water at each point and then filtered the water in plankton nets of 68-

µm mesh, totaling 60 L in each wetland. After filtration, the samples were fixed with 80% Ethanol and taken to the laboratory, where the organisms were counted and identified. We added 1% Bengal Rose to perform screening of the microcrustaceans. We identified the organisms to the lowest possible taxonomic level using a stereomicroscope (P45BI/Precision®), optical microscope (CX41/Olympus®), and specialized literature (Korovchinsky, 1992; Smirnov, 1996; Elmoor-Loureiro, 1997; Buckup & Bond-Buckup, 1999; Fernando, 2002; Marinone et al., 2016).

Ex situ approach

In the *ex situ* approach, we specifically analyzed the hatching period by interfering with the priority effects, predation, and other possible biotic interactions. The sediment was collected on January 10, 2017 in the dry phase preceding the hydroperiod and in the same wetlands that we performed *in situ* monitoring. We collected the surface 5 cm of the sediment with a cutting blade at three random points in the wetlands. In the laboratory, we conditioned the sediment in dark plastic bags to reduce contact with light and stored atambient temperature untilthe experiment (Iglesias et al., 2016). We homogenized the sediment from each site manually and placed 100 g of sediment into three 100-mL Bequer cups (300 g per wetland).

We conducted the experiment in three incubation chambers (BOD regulated) with a photoperiod of 10:14h (light: dark), which is the condition found in winter in southern Brazil. The temperatures used were 10, 15, and 20°C, which correspond to the minimum, mean, and maximum historical averages for the periods of flooding of the wetlands (Albertoni et al., 2014). We put three replicates per wetland at each temperature (3 wetlands x 3 Bequer cups x 3 temperatures = 27sampling units). Next, we hydrated the sediment with distilled water to reduce the effects of other environmental variables (e.g., pH and conductivity) (Van Damme & Dumont, 2010). We monitored the three temperatures simultaneously for 30 days, totaling 15 days sampled in the 27 sampling units. Every two days, all water from the Bequer cups was filtered in a 68-µm mesh to observethe hatching, then the containers were hydrated with the same water (when necessary, the amount of water was supplemented with new water) and returned to the incubators. The organisms were fixed, counted, and identified at the lowest possible taxonomic level, with the same methodology and literature described previously. As in the *in situ* approach, microcrustaceans were categorized at the lowest possible taxonomic level (genera, family or order), and we also considered the larval stages for Copepoda and Anostraca to quantify the abundance and use in statistical analysis.

Data analysis

We performed a curve of species accumulation to monitor the total hatching of microcrustaceans along the hydration time (Supplementary Material 1). We classified the hydration time (explanatory variables) in three periods to perform the analyses, corresponding to the beginning (day 2 to 12), the middle (day 14 to 24), and the end (day 26 to 34) of the hydroperiod *in situ*. For the *ex situ* approach, we performed the same categorization, but with different time intervals: the beginning corresponded to the first ten days, the middle was day 11 to day 20, and the end was the last ten days. We used the average of richness and abundance (response variables) of the three wetlands for each period (beginning, middle, and end) of the hydration time to perform the analyses.

To test the influence of hydration time and temperature (explanatory variables) on microcrustacean hatching, we applied Generalized Linear Models (GLMs). These analyses allow model fitting, providing a predictor description and a description of the error distribution for each specified family (Crawley, 2007). Initially, we used the Poisson family for GLM models because our response variables (richness and abundance) were count data, which may have a Poisson distribution. However, when we tested the assumptions, the data showed overdispersion so we used the negative binomial as an alternative to the Poisson family (Venables & Ripley, 2002).

We performed GLMs (negative binomial family) for the total richness and abundance data combined, and also separately for the richness (when applicablebecause some groups presented only one species) and abundance data of each microcrustacean group in both approaches. In each analysis, we tested the significance of the proposed model with a null model including no variables (e.g. richness ~ 1), using a two-way ANOVA with a Chi-square test (Crawley, 2007).

As a posterior test of GLMs, we used an Orthogonal Contrast Analysis to check which factor level had the biggest difference (e.g. in the beginning, middle, and end levels of the hydration time factor) (Crawley, 2007). All analyses were performed in the R environment (R Core Team, 2018). We used the ‘vegan’ package for the species accumulation curve (Oksanenet al., 2018). We used the ‘MASS’ package for GLMs (negative binomial)

(Venables & Ripley, 2002). The 'RT4Bio' package was used for the Orthogonal Contrast Analysis (Reis et al., 2013).

Results

In situ approach

In the *in situ* approach, the wetland depth ranged from 7 to 42 cm, and the water temperature ranged from 11 to 25°C (Figure 1a). The pH ranged from 5.5 to 7.6 (min and max), conductivity was 0.07 ± 0.01 µS.L^{-1}, turbidity was 27.2 ± 18.5 NTU, and dissolved oxygen was 16.3 ± 8.6 mg.L^{-1} (all values are mean ± sd).

We recorded a total of 35 microcrustacean taxa (Table 1), and the species accumulation curve increased until the end of the hydroperiod (Supplementary Material 1). At the beginning of the hydroperiod, representatives of five groups of microcrustacean emerged; Cladocera had 11 taxa, Copepoda had three taxa (and copepodites and nauplii), and Ostracoda had two taxa. Anostraca and Conchostraca each was represented by a single species. Not all representatives of the groups emerged as soon as the hydroperiod began. We recorded taxa that only emerged in the middle and at the end of the hydroperiod. Ten Cladocera taxa and three Ostracoda taxa emerged exclusively in the middle of the hydroperiod, and two Ostracoda taxa emerged exclusively at the end of the hydroperiod (Table 1).

Of the hatching stimuli examined in this study, only hydration time had a significant effect on both the total richness and abundance of the microcrustaceans ($p < 0.001$ and $p = 0.044$, respectively; Table 2). Analyzing each group, we observed that the abundance of Anostraca was influenced by the hydration time and temperature (both with $p < 0.001$). For the abundance of Conchostraca, we observed that the interaction between temperature and hydration time showed a significant effect ($p = 0.002$). For Cladocera, Copepoda, and Ostracoda, we observed an effect of hydration time on richness and abundance (Table 2).

The total richness of microcrustaceans was higher in the middle and at the end of the hydration time (Table 2, Figure 1b); total abundance was higher in the middle of the hydration time (Table 2, Figure 1b). For Anostraca, abundance was higher at the beginning of the hydration time (Table 2, Figure 1c). For Conchostraca, the greatest abundance was in the middle of the hydration time (Table 2, Figure 1c). We recorded the highest Cladocera richness in the middle and at the end of the hydration period, and abundance increased with hydration time (Table 2, Figure 1d). For Copepoda, the richness was highest at the beginning, while abundance was higher at the beginning and middle of the hydration time (Table 2, Figure 1e). For Ostracoda, richness and abundance were highest at the end of the hydration time (Table 2, Figure 1f).

Ex situ approach

In the laboratory experiments, we recorded the highest microcrustacean richness at 15°C and 20°C, with the hatching of 13 taxa at both temperatures; 10 taxa hatched at 10°C (Table 3). For the three temperatures, the species accumulation curve increased until the end of the hydroperiod (Supplementary Material 1). At each temperature, we recorded the hatching of Anostraca, Cladocera, Copepoda, and Ostracoda taxa.

Of the hatching stimuli, only the hydration time had a significant effect on the total richness of microcrustaceans ($p < 0.001$, Table 4). However, both hydration time and temperature affected the total abundance of microcrustaceans ($p < 0.001$ and $p = 0.018$, respectively, Table 4). Hydration time affected the abundance of Anostraca ($p < 0.001$, Table 4). For Cladocera, hydration time affected the abundance of organisms ($p = 0.021$), but not the richness. For Copepoda, hydration time affected richness and abundance ($p < 0.001$ for both, Table 4). For Ostracoda, hydration time affected richness ($p = 0.007$, Table 4), while abundance was influenced by temperature-mediated hydration time ($p = 0.024$, Table 4).

At each temperature, the total richness and abundance were greater at the beginning of the hydration time (Table 4, Figures 2a and 3a). However, the total abundance was greater at 20°C, compared with other temperatures (Figure 3a). For Cladocera, richness was low over the hydration time (Figure 2b). For Copepoda and Ostracoda, the greatest richness was at the beginning of hydration time (Figures 2c, 2d). We also observed the greatest abundance of the four groups at the beginning of the hydration time (Figure 3b, 3c, and 3d).

Discussion

In situ microcrustacean hatching

Hydration time was the most important environmental factor that affected the total richness and abundance of microcrustaceans and, specifically, Cladocera, Copepoda, and Ostracoda. These three groups contributed the most to the total emergence richness and abundance; they also rapidly responded to the hydration time. This pattern has been supported in the literature for the wetlands of Spain (Antón-Pardo et al., 2016; Florencio et al., 2016) and Canada (Jones & Gilbert, 2016). On the other hand, the abundance of Anostraca and Conchostraca was influenced by hydration time and temperature, showing that temperature can be important for hatching, primarily influencing the number of organisms to emerge (Paes et al., 2016). The large branchiopods *Branchinecta iheringi* Lilljeborg, 1889 and *Eulimnadia pampa* Marinone, 2016 are endemic to the wetlands of subtropical South America (Bandeira et al., 2019) and their presence can indicate the excellent status of conservation to the wetlands. The large branchiopods have high sensitivity to multiple stressors, mainly habitat modification and loss (Brendonck et al., 2007). However, with the change in habitat, the diversity of these organisms is lost, which has caused relevant concerns since many branchiopods are on the IUCN list of threatened species (García-de-Lomas et al., 2017; Bird et al., 2018; Rogers et al., 2019).

In this study, we observed that microcrustacean hatching varied during the hydration period, demonstrating that the community seems to be resilient to recover after inundation through the species emergence from the egg bank and is heterogeneously structured over the hydroperiod. Figure 4 represents a conceptual model based on the greatest richness and abundance for the hatching behavior of different groups of microcrustaceans in the studied wetlands. Although it does not account for the different stressors in the community, we believe that it expresses the adaptive strategies for survival and reproduction that structure communities in intermittent subtropical wetlands. For the total richness of microcrustaceans, the highest values were found during the middle and end of the hydration time; for the total abundance, the highest values were in the middle of the hydration time (Figures 4a, b). Considering that we cannot control all environmental factors affecting the community for *in situ* conditions, our results reflected the community dynamics in the three wetlands (Ricci, 2001). At the beginning of the hydration time, the dormant eggs hatch, and during the hydration time, the microcrustaceans reproduce and remain in the community until the end of their life cycles or the end of the hydroperiod (Sim et al., 2013). In addition, the total abundance of microcrustaceans in the middle of the hydroperiod was the productof hatching and reproduction. The drop in abundance occurs at the end of the hydroperiod when organisms have completed their life cycle.

The species that hatched at the beginning of the hydration time remained along the hydroperiod, so more species were present at the middle and end of the hydroperiod. Since physical variables and biotic processes (e.g., competition and priority effects) could influence the abundance and richness of crustaceans in the first days after inundation (Antón-Pardo et al., 2016). Each group has different dormancy (diapause eggs or quiescence of other developmental stages) and different reproduction (sexual or asexual) strategies (Alekseev et al., 2007). These differences may explain the temporal variations in the abundance of each group. In addition, there are biotic interactions among the different groups, such as competition between filter-feeders or predation. Indeed, many cyclopid and calanoid species could be predators of small cladocerans (Waterkeyn et al., 2010).

When we observed the microcrustacean groups separately, we found that the five groups of the community established at different times of the hydroperiod (Figure 4b). Anostraca and Copepoda predominated at the beginning, Conchostraca and Cladocera predominated in the middle, and Ostracoda predominated at the end of the hydroperiod. We found a high abundance of nauplii and juveniles mostly from Copepoda with fewer from Anostraca at the beginning of the hydroperiod; of the groups we recorded, Copepoda and Anostraca are the only groups that go through several developmental stages (César, 1990; Dussart & Defaye, 2001). Therefore, the hatching of these two groups and their presence from the beginning of the hydroperiod may be a response to ensure that development and reproduction occur before the dry phase of the intermittent wetland begins. Our results corroborate those of Florencio et al. (2016) from intermittent wetlands of Spain, who found that Anostraca and Copepoda erupted early in the hydroperiod.

The presence of Conchostraca and Cladocera in the middle of the hydroperiod may be due to their similar developmental strategies, as they show direct development, without larval stages (Buckup & Bond-Buckup, 1999). Conchostraca emergence occurred at the beginning and predominated in the middle of the hydroperiod. This result is similar to that found for Conchostraca by Sabnis et al. (2017), hatching occurred as soon as the hydroperiod began and continued for about five days, and mature adults were observed for 10 days and survived for up to 16 days. This can indicate that Conchostraca needs a longer hydration time to emerge in the community over the hydroperiod.

Cladocera hatching also occurred from the beginning of the hydroperiod but predominated from the middle to the end, with abundance increasing over the hydration period. This increasing abundance may be related to this group’s method of reproduction and the hatching of dormant eggs (Santangelo, 2009). Normally, dormant Cladocera eggs hatch parthenogenetic females that can reproduce after two days, laying 10 to 40 eggs at a time (Elmoor-Loureiro, 1997). Thus, the increasing abundance we encountered is consistent with the recruitment of egg bank organisms, coupled with the production of new organisms after hatching.

The prevalence of Ostracoda at the end of the hydration time may be due to the accumulation of species hatching along the hydroperiod. Ostracoda (*Chlamydotheca mangueirensis* Kotzian, 1974 and *Chlamydotheca* sp.) was the only group that hatched exclusively at the end of the hydration time. Ostracoda is one of the most resistant to desiccation (Bird et al., 2018), suggesting that some representatives require a greater hydration time for emergence to occur. In addition, the abundance of Ostracoda has been positively correlated with the pH of the water (Allen & Dodson, 2011; Perçin-Paçal, 2019). Other possibilities could affect such patterns, such as a reduction of predators, a reduction in the water level, or an increase in organic matter to decompose as the food of ostracods (Allen & Dodson, 2011).

Ex situ microcrustacean hatching

The *ex situ* approach and isolation of the hatching stimuli showed that hydration time and temperature influenced the hatching of microcrustaceans. We observed that total abundance was most strongly influenced by the abundance of Ostracoda. Thus, in addition to the hydration time, Ostracoda abundance was induced by the higher temperature. The increase in abundance was recorded at 20°C indicating that temperature accelerated the cessation of organism dormancy, but the temperature did not influence the abundance of specific taxa. Previous research has demonstrated that an increase in temperature positively affects hatching abundance (Alekseev et al., 2007).

In a review by Iglesias et al. (2016), a survey of the methodological approaches used to study the structure and dynamics of the microcrustacean egg bank in South America was conducted, in which they emphasized that some groups need specific temperatures for hatching. When we tested *ex situ* factors, we did not find specific groups hatching at each temperature, but we observed that hatching of specific groups occurred at different times of the hydration period. This indicates that, for intermittent wetlands, the hydration time may have a greater influence on microcrustacean hatching than temperature. In addition, there were a set of species that hatched in the experiment and did not appear in the field [e.g., *Ceriodaphnia quadrangular* (O. F. Müller, 1785), *Leydigia ciliate* Bergamin, 1939, *Ovalona glabra* (Sars, 1901), and *Darwinula* sp.]; this was probably a result of different temperatures, minor roles of biotic interactions, or rare species that were not detected in the field. Also, the conditions in the cups may have been different from the ones observed in the field (e.g., oxygen concentration) which may have contributed to this difference (Jones & Gilbert, 2016).

Recent information has thrown some doubts on the actual hatching of species of *Cytheridella* and *Darwinula* from dried mud, so these results have to be taken with caution (Martens, personal communication).

Through this experiment, it was possible to evaluate the impact of temperature and hydration time on hatching, but more species hatched *in situ* than *ex situ*. This is an indication that other important factors (e.g., oxygen concentration) related to hatching could be considered in the experiment. Oxygen depletion is normal in these experiments, especially when the volumes are small (Jones & Gilbert, 2016), but because our interest was focused on hatching and we removed the organisms every two days, this factor was not controlled in the experimental cups.

The experimental temperatures were lower than the temperatures recorded in the field sampling, but, we used historical average temperatures, and this may have also contributed to the set of species that hatched in the experiment and did not appear in the field. The finding that the dormant egg bank is a biodiversity stock is already well accepted in the literature (Moreno et al., 2019; Vargas et al., 2019; Florencio et al. 2020). Moreover, our results can contribute to the information that there is a temporal distribution in the hatching of microcrustaceans, as described by Jones & Gilbert (2016).

We found that microcrustacean hatching was higher at the beginning of the hydration periodin the *ex situ* approach (Figures 4c, 4d). At all experimental temperatures, the richness and abundance of the microcrustacean groups were higher at the beginning of the hydration time (except Cladocera richness). Since organisms were removed from the experiment every two days, there was no time for reproduction, so all the registered organisms hatched from the bank of dormant eggs. In an *ex situ* approach, Paes et al. (2016) compared the influence of different temperature and light conditions on Cladocera hatching and also found the highest values at the beginning of the experiment. However, in an *ex situ* approach verifying the potential for dormant eggs to restore the zooplankton community, Eskinazi-Sant’Anna &Pace (2018) recorded that abundance increased throughout the hydration time.

The richness of Cladocera was very low in the *ex situ* approach. In addition, there was no hatching of Conchostraca, but the species accumulation curves increased at the end of hydration time at each temperature. This suggests that the amount of sediment used for the experiments was insufficient for the comparison of microcrustaceans from the wetlands. Therefore, we suggest that infuture experiments, researchers analyze larger volumes of sediment.

In our study, we found that the *in situ* and *ex situ* approaches complement each other. The results of the experiment could contribute to understanding the community without considering the biotic interactions and the high number of species recorded *in situ*. When we summarized the richness of the two approaches, we found that the number of taxa recorded in the three wetlands was high, even compared to studies that used a greater number of environments and examined the cumulative richness for longer than one month. In nine wetlands of Australia, five microcrustacean taxa were found (Sim et al., 2013). In eight wetlands of the Albufera National Park in Spain, 26 microcrustacean taxawere recorded (Antón-Pardo et al., 2016). In 19 wetlands in the Doñana Biological Reserve in Spain, 78 microcrustacean taxa were recorded (Florencio et al., 2016; Florencio et al., 2020), and 18 taxa of microcrustaceans were registered in 25 wetlands in Canada (Jones & Gilbert, 2016). Our results highlight the importance of intermittent wetlands as biodiversity hotspots for microcrustaceans.

Our results showed a coupling of total microcrustacean richness and abundance during the beginning phase, followed by their decoupling until the abundance sharply rose during the final desiccation phase of the hydroperiod *in situ*. The final desiccation process is often found in other works, but the initial phase where richness and abundance were coupled could be a general feature that previous research might have missed because they lacked the intensity of sampling/identification effort on the whole microcrustacean community. These results were due to high identification effort, done on the whole microcrustacean community with numerous samples along the hydroperiod; the combination with laboratory hatching experiments contributes to the knowledge of the ecology of these groups in intermittent subtropical wetlands.

Conclusion

Our results explore some general mechanisms of the hatching process which can apply to intermittent wetlands in subtropical regions, where daily light and temperature variation is less acute than water availability. Our study demonstrated that for the *in situ* approach, the hydration time was the most important factor for microcrustacean hatching, and we verified that the community is resilient but heterogeneously structured throughout the hydration period. In the *ex situ* approach, the hydration time was the most important factor for microcrustacean hatching, but the increase in temperature positively influenced the number of hatchings. In addition, the hydroperiod influenced the hatching of microcrustaceans, especially at the beginning of the hydration time, and the temperature mainly influenced the abundance of hatching in the intermittent wetlands. This demonstrates that these organisms are resilient. Our registration of 41 taxa in three wetlands reinforces the importance of further studies and the conservation of intermittent wetlands in subtropical regions. These wetlands are often threatened by agriculture and urbanization, which reduce these environments on the southern coastal plain of Brazil. In addition, changes in the global climate can affect hatching stimuli and negatively affect the emergence of microcrustaceans in intermittent wetlands, especially for species that need a longer hydration time to emerge. This demonstrates the importance of the dormant egg bank in the recovery of the community during the hydroperiod and ensures the functioning of the wetlands.

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Table 1 Abundance (mean±sd) of taxa hatching in the *in situ* approach over a 34-day hydroperiod in intermittent environments in southern Brazil.

Taxa		***In situ***	
	Beginning	**Middle**	**End**
ANOSTRACA			
Branchinecta iheringi Lilljeborg, 1889	34±41	1±1.7	0.3±0.5
CLADOCERA			
Daphnia sp.		6.6±9.0	0.3±0.5
Ceriodaphnia sp.	0.3±0.5		
Ceriodaphnia reticulata (Jurine, 1820)	0.3±0.5	43±40	227.3±284.8
Scapholeberis spinifera (Nicolet, 1849)		13.3±12.5	145±116
Simocephalus latirostris Stingelin, 1906	0.3±0.5	33.6±56.5	98.3±167.7
Pseudosida bidentata Herrick, 1884	0.6±1.1	20±31	36±47
Pseudosida ramosa (Daday, 1904)	0.3±0.5		
Sarsilatona serricauda (Sars, 1901)		0.6±1.1	0.3±0.5
Macrothrix spinosa King, 1853	0.3±0.5		
Chydorus sp.		28±25	199.3±288.3
Chydorus eurynotus Sars, 1901	0.3±0.5		
Chydorus cf. *sphaericus* (O.F. Müller, 1785)	0.3±0.5	1±1.7	0.3±0.5
Chydorus parvireticulatus Frey, 1987		0.3±0.5	
Chydorus pubescens Sars, 1901	3.6±3.5	4.6±5.6	0.6±1.1
Dunhevedia odontoplax Sars, 1901		3.6±1.1	6.3±5.0
Euryalona brasiliensis Brehm & Thomsen, 1936		0.3±0.5	
Kurzia sp.		0.6±0.5	0.3±0.5
Leberis davidi (Richard, 1895)		11.6±20.2	8.3±12.7
Picripleuroxus denticulatus (Birge, 1879)	0.3±0.5	12.3±21.3	184.3±185.0

Pleuroxus aduncus (Jurine, 1820)	0.3±0.5		
Pleuroxus similis Vavra, 1900		2±3	0.6±1.1
CONCHOSTRACA			
Eulimnadia pampa Marinone, 2016	17±22	29.6±31.2	5±7.8
COPEPODA			
Calanoida	208.3±271.7	682.6±581.4	390±101
Cyclopoida	567.6±468.7	1381±1308	19±29.5
Harpacticoida	13±17.4	4.3±6.6	1.3±1.5
Copepodito	201.3±157.3		75±129
Nauplius	2395±1374	3026±1849	33.6±52.3
OSTRACODA			
Candonopsis brasiliensis Sars, 1901	1.3±2.3	3±1.7	531±415.5
Chlamydotheca sp.			1±1.7
Chlamydotheca mangueirensis Kotzian, 1974			27±8.8
Cytheridella sp.		35.6±47.2	136.3±226.6
Cypridopsis vidua (O. F. Müller, 1776)	354±467	407±197	144±106
Limnocythere sp.		3±3	1±1.7
Strandesia sp.		3.3±5.7	1±1.7
Total richness	**20**	**27**	**28**
Total abundance	**3,243**	**4,351**	**6,435**

Table 2 GLM results for richness and abundance for the *in situ* approach with hydration time (Time) and temperature as explanatory variables. The (*) indicates significant values. B = beginning, M = middle, and E = end of hydroperiod.

	df	Deviance	Resid. df	Resid. dev	P value (>Chi)	Contrast Analysis
Richness *in situ*						
Total						
Null			50	61.273		
Time	2	14.206	48	47.066	**<0.001***	B< (M=E)
Temperature	1	0.333	47	46.733	0.563	
Time: temperature	2	1.064	45	45.668	0.587	
Cladocera						
Null			50	98.190		
Time	2	31.319	48	66.870	**<0.001***	B < (M = E)
Temperature	1	0.000	47	66.870	0.9864	
Time: temperature	2	1.232	45	65.637	0.5399	
Copepoda						
Null			50	26.633		
Time	2	8.980	48	17.652	**0.011***	B > (M = E)
Temperature	1	0.043	47	17.608	0.834	
Time: temperature	2	0.701	45	16.907	0.704	
Ostracoda						
Null			50	31.060		
Time	2	13.436	48	17.624	**0.001***	E > (B = M)
Temperature	1	0.070	47	17.553	0.790	
Time:	2	1.491	45	16.062	0.474	

temperature						
Abundance *in situ*						
Total						
Null			50	64.407		
Time	2	6.217	48	58.189	**0.044***	M > (B = E)
Temperature	1	0.113	47	58.075	0.735	
Time: temperature	2	1.077	45	56.998	0.583	
Anostraca						
Null			50	93.020		
Time	2	51.06	48	41.959	**<0.001***	B > (M = E)
Temperature	1	11.91	47	30.044	**<0.001***	
Time: temperature	2	4.539	45	25.504	0.103	
Cladocera						
Null			50	216.110		
Time	2	150.620	48	65.485	**<0.001***	B < M < E
Temperature	1	0.00	47	65.485	0.982	
Time: temperature	2	4.54	45	60.945	0.103	
Conchostraca						
Null			50	83.062		
Time	2	9.461	48	73.600	**0.008***	M > (B = E)
Temperature	1	13.407	47	60.193	**<0.001***	
Time: temperature	2	12.136	45	48.056	**0.002***	

Copepoda						
Null			50	85.180		
Time	2	26.015	48	59.164	**<0.001***	E < (B = M)
Temperature	1	0.358	47	58.806	0.549	
Time: temperature	2	0.048	45	58.757	0.975	
Ostracoda						
Null			50	76.075		
Time	2	9.580	48	66.495	**0.008***	E > (B = M)
Temperature	1	2.541	47	63.953	0.110	
Time: temperature	2	3.813	45	60.139	0.148	

Table 3 Abundance (mean±sd) of taxa hatching in the *ex situ* approach from the bank of dormant eggs of intermittent environments along the 30-days hydroperiod at 10, 15, and 20°C. B = beginning, M = middle, and E = end of hydroperiod.

	10 °C			**15 °C**			**20 °C**		
Taxa	**B**	**M**	**E**	**B**	**M**	**E**	**B**	**M**	**E**
ANOSTRACA									
Branchinecta iheringi Lilljeborg, 1889	1±1	0.3±0.5	0.3±0.5	1.3±2.3	1.6±2.0		5.6±9.8	0.3±0.5	
CLADOCERA									
Ceriodaphnia quadrangula (O.F. Müller, 1785)	0.3±0.5	0.3±0.5			0.3±0.5		1.3±1.5		
*Pseudosida*sp.				0.3±0.5					
Chydoridaesp.	0.6±1.1			0.3±0.5			0.3±0.5		
Leydigia ciliate Bergamin, 1939						0.3±0.5		0.3±0.5	
Leberis davidi (Richard, 1895)					0.3±0.5		0.6±1.1	0.3±0.5	
Ovalona glabra (Sars, 1901)	0.3±0.5	0.3±0.5				0.3±0.5		0.3±0.5	
COPEPODA									
Cyclopoida	0.6±0.5	0.3±0.5		3±2.6	0.3±0.5	0.3±0.5	5±2.6	0.6±0.5	
Harpacticoida	0.3±0.5		0.3±0.5	0.3±0.5	1±1.7	0.6±1.1	0.3±0.5	0.3±0.5	0.3±0.5
Nauplius	2.6±3.7			7±7			4.3±7.5		
OSTRACODA									
Candonopsis brasiliensis Sars, 1901		0.3±0.5			0.3±0.5	0.3±0.5		1±1.7	0.6±1.1
*Cytheridella*sp.						0.3±0.5			1±0
Cypridopsis vidua (O. F. Müller, 1776)	8.6±1.1	1.3±0.5	0.6±1.1	11.6±10.7	0.3±0.5	0.6±1.1	8.3±6.0	4±2.6	1±1
*Darwinula*sp.			0.5±0.7					0.6±1.1	
Total richness		**10**			**13**			**13**	
Total abundance		**58**			**95**			**111**	

Table 4 GLM results forrichness and abundance in the *ex situ*approachwith hydration time (Time) and temperature as explanatory variables. The (*) indicates significant values. B = beginning, M = middle, and E = end of hydroperiod.

	df	Deviance	Resid. df	Resid. dev	P value (>Chi)	Contrast Analysis
Richness *ex situ*						
Total						
Null			134	156.75		
Time	2	34.477	132	122.28	**<0.001***	B> (M = E)
Temperature	2	4.964	130	117.31	0.083	
Time: temperature	4	2.145	126	115.17	0.709	
Cladocera						
Null			134	74.017		
Time	2	5.863	132	68.154	0.053	
Temperature	2	2.357	130	65.796	0.307	
Time: temperature	4	7.584	126	58.212	0.108	
Copepoda						
Null			134	109.018		
Time	2	19.624	132	89.393	**<0.001***	B > (M = E)
Temperature	2	3.464	130	85.929	0.176	
Time: temperature	4	1.450	126	84.479	0.835	
Ostracoda						
Null			134	101.571		
Time	2	9.723	132	91.848	**0.007***	B > (M = E)
Temperature	2	3.476	130	88.371	0.175	
Time: temperature	4	7.539	126	80.832	0.109	

Abundance *ex situ*						
Total						
Null			134	228.92		
Time	2	90.010	132	138.91	**<0.001***	B> (M = E)
Temperature	2	7.995	130	130.91	**0.018***	20°C > (10°C =15°C)
Time: temperature	4	1.265	126	129.65	0.867	
Anostraca						
Null			134	72.848		
Time	2	16.808	132	56.040	**<0.001***	B> (M = E)
Temperature	2	1.977	130	54.062	0.372	
Time: temperature	4	7.866	126	46.196	0.096	
Cladocera						
Null			134	72.353		
Time	2	7.658	132	64.694	**0.021***	B> (M = E)
Temperature	2	0.889	130	63.805	0.641	
Time: temperature	4	5.750	126	58.054	0.218	
Copepoda						
Null			134	121.604		
Time	2	39.980	132	81.623	**<0.001***	B> (M = E)
Temperature	2	4.722	130	76.901	0.094	
Time: temperature	4	0.670	126	76.231	0.954	
Ostracoda						
Null			134	175.72		
Time	2	43.643	132	132.07	**<0.001***	B> (M = E)
Temperature	2	3.826	130	128.25	0.147	
Time: temperature	4	11.153	126	117.09	**0.024***	

Figure 1

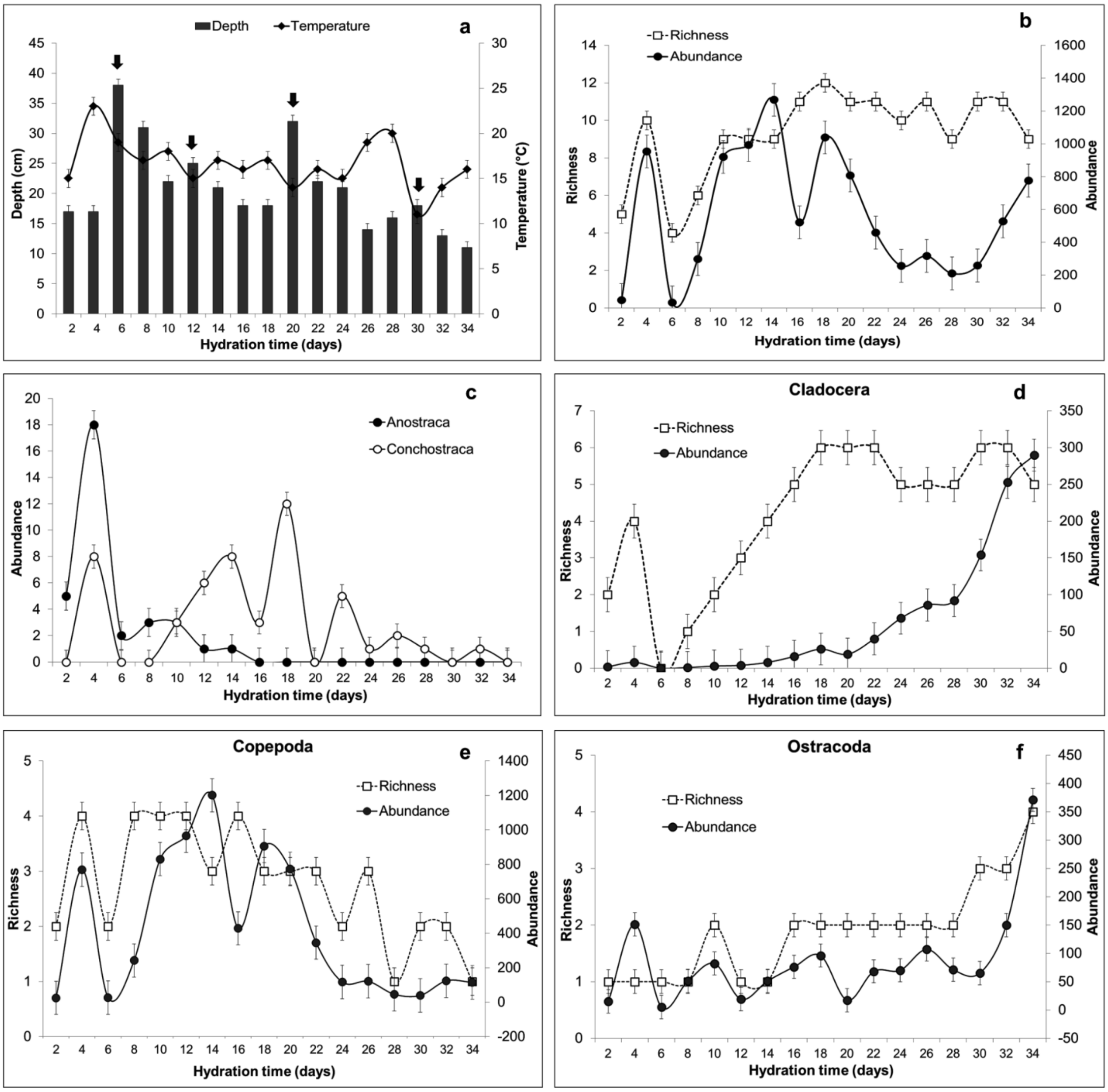

Fig. 1 Variation (mean/se) in the depth, temperature, and hatching of microcrustaceans in the *in situ* approach along the 34-day hydroperiod. **(a)** Variation in the depth and temperature along the hydroperiod; the arrows indicate the precipitation along the hydroperiod in the wetlands. **(b)** Variation in total richness (n° of species.L^{-1}) and abundance (ind.L^{-1}) of microcrustaceans over 34 days of hydroperiod. Variation in the abundance of **(c)** Anostraca and Conchostraca, **(d)** Cladocera, **(e)** Copepoda, and **(f)** Ostracoda over 34 days of hydration.

Figure 2

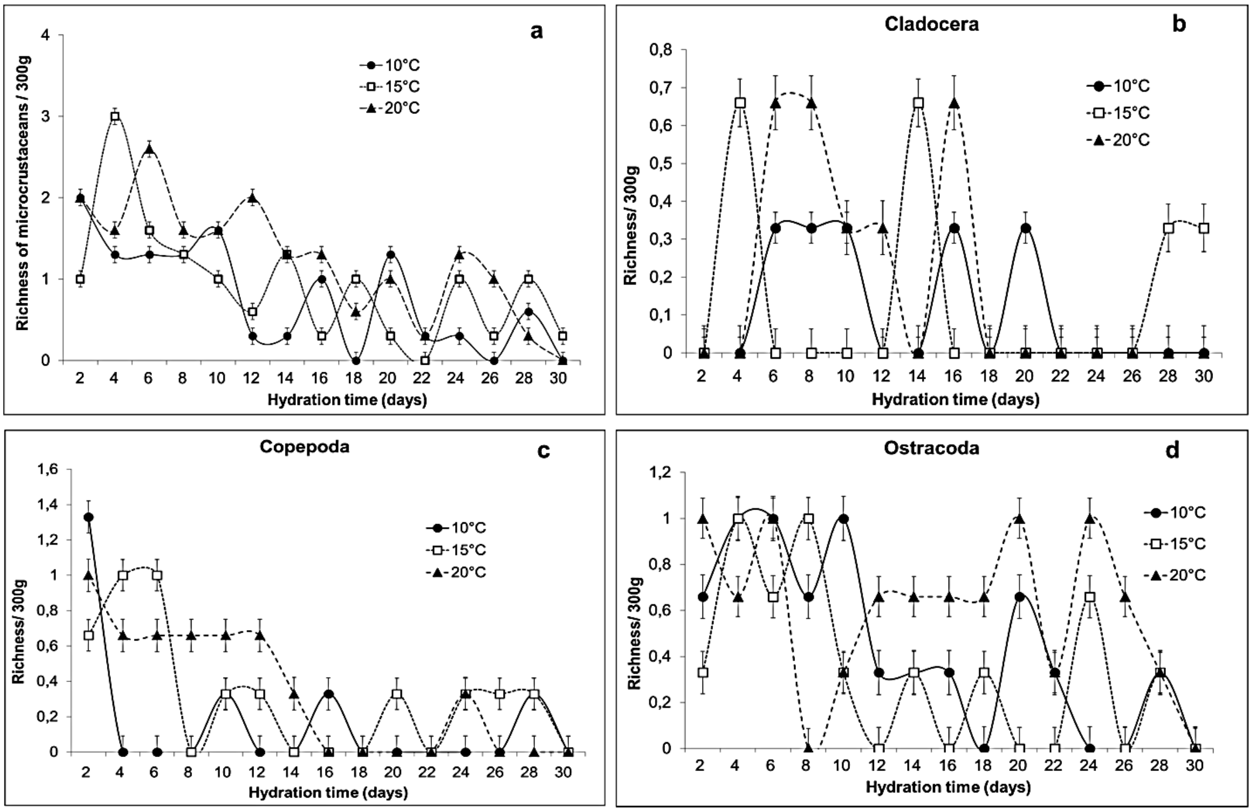

Fig. 2 Variation (mean/se) in microcrustacean richness in the *ex situ* approach at water temperatures of 10, 15, and 20°C. **(a)** Variation in the total richness (n° of species.L^{-1}) over 30 days ateach temperature. Variation in richness of **(b)** Cladocera, **(c)** Copepoda, and **(d)** Ostracoda richness over 30 days at each temperature.

Figure 3

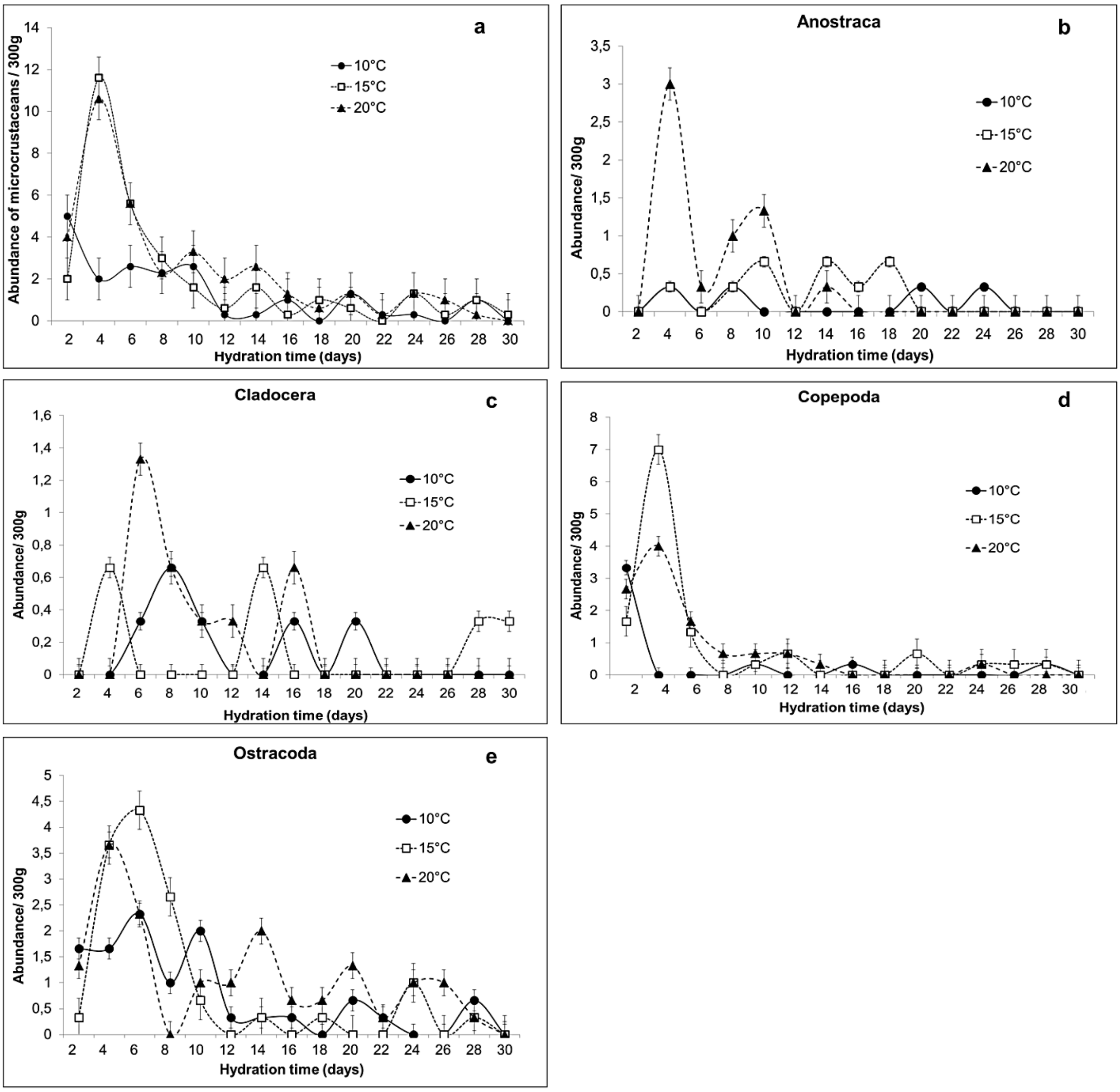

Fig. 3 Variation (mean/se) in the abundance of microcrustaceans for the *ex situ* approach at temperatures of 10, 15, and 20°C. **(a)** Variation in total abundance (ind.L^{-1}) over 30 days at each temperature. Variation in the abundance of **(b)** Anostraca, **(c)** Cladocera, **(d)** Copepoda, and **(e)** Ostracoda over 30 days at each temperature.

Figure 4

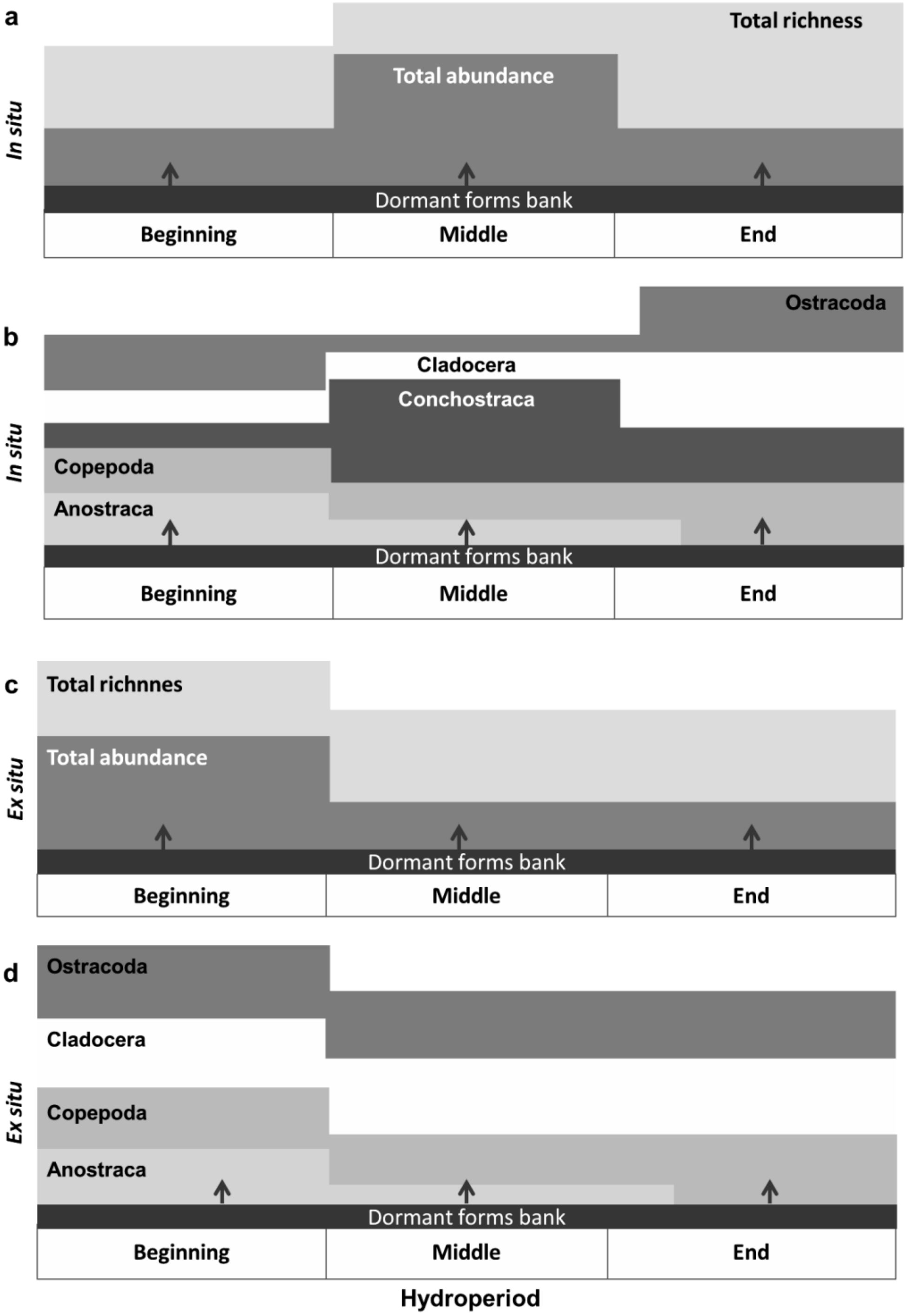

Fig. 4 Structuring of microcrustaceans along the hydroperiod after hatching of dormant forms for *in situ* and *ex situ* approaches. **(a)** The permanence of the total richness in the middle and at the end of the hydroperiod and of the total abundance in the middle period for the *in situ* approach. **(b)** The heterogeneous hatching and permanence of the five groups of microcrustacean along the hydroperiod for the *in situ* approach. **(c)** The highest values of richness and total abundance at the beginning of the hydroperiod for the *ex situ* approach. **(d)** The highest hatching values of the four groups of microcrustaceans at the beginning of the hydroperiod for the *ex situ* approach. The arrows indicate the hatching from the bank of dormant eggs in the two approaches

Supplemetary material

Hydration time influences microcrustacean hatching in intermittent wetlands: *in situ* and *ex situ* approaches

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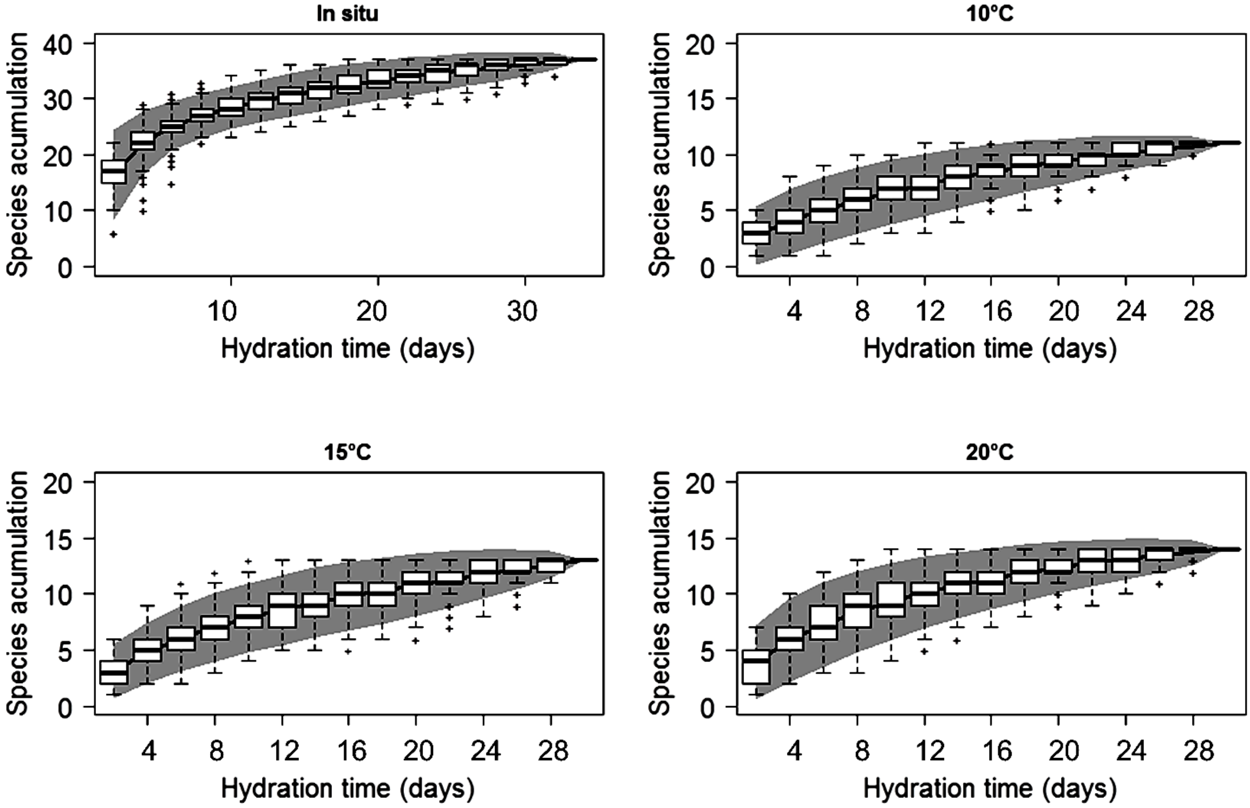

Supplementary Material 1 Curves of species accumulation over time of hydration in the **(a)** *in situ* approach and at water temperatures of **(b)** 10°C, **(c)** 15°C, and **(d)** 20°Cin the *ex situ* approach.

CONSIDERAÇÕES FINAIS E PERSPECTIVAS

A proposta da tese foi estudar a diversidade e dinâmica dos microcrustáceos em áreas úmidas intermitentes. A partir dos resultados obtidos com a análise apresentada no capítulo 1, podemos afirmar que, embora com poucos estudos pode-se estimar a alta potencialidade desses ambientes como locais de conservação da comunidade de microcrustáceoas. Quando fizemos um levantamento global sobre a diversidade de microcrustáceos em cultivos de arroz, nosso estudo mostrou que 4% da diversidade global são encontrados nesses ambientes. Isso nos possibilitou demonstrar que além deles funcionarem como refúgio (ROLON; MALTCHIK, 2010), esses ambientes também tem potencialidade de estocar biodiversidade. Além disso, vimos que os países que mais produzem arroz não são os que mais estudam a fauna de microcrustáceos. Se os países grandes produtores de arroz também investirem nos estudos voltados para a conservação da biodiversidade, possivelmente reduziria a subestimativa dos levantamentos e aumentaria a potencialidade de proteção e até manejo desses ambientes (LIU et al., 2017). Isso porque, os cultivos de arroz, em conjunto com ambientes naturais, podem favorecer a conservação de microcrustáceos, principalmente em lavouras com manejo menos agressivo (ÁVILA et al., 2015). Voltamos a ressaltar que, mesmo que os cultivos de arroz possuem alto potencial para armazenar a diversidade de microcrustáceos, nós não aconselhamos a transformação de ambientes naturais em rizicultura.

Nós vimos que para os estudos ecológicos relacionados a estratégia de eclosão e respostas adaptativas das espécies endêmicas *Branchinecta iheringi* e *Eulimnadia pampa*, com os nossos dados do Capítulo 2 houve um grande avanço no entendimento dos padrões e respostas adaptativas desses organismos. Até nosso conhecimento, esse é o primeiro trabalho a abordar esses aspectos para esses organismos. Quando nós acompanhamos a estratégia de eclosão dessas espécies, nós demonstramos que elas apresentaram respostas diferentes aos hidroperíodos anuais. Antes do nosso estudo, todo o conhecimento que havia dessas espécies, era voltado para a resolução taxonômica (BUCKUP; BOND-BUCKUP, 1999; MARINONE et al., 2016), então, nossos resultados podem contribuir para o conhecimento de como as espécies endêmicas se estabelecem em ambientes tão instáveis. O levantamento de dados de história de vida de espécies endêmicas permite o avanço nos estudos com biomonitoramento, além de estudos ecotoxicológicos (HODKINSON; JACKSON, 2005), uma vez que, é possível utilizar esses organismos que vivem nas condições locais e podem refletir melhor as alterações ambientais. Além disso, nos ambientes intermitentes, essas espécies endêmicas aparentemente estão investindo principalmente na produção de ovos dormentes, indicando que, elas se adaptaram as alterações do ambiente, garantindo novas gerações nos hidroperíodos seguintes, permitindo a recolonização e dinâmica desses ambientes (ALFONSO et al., 2016).

No Capítulo 3, quando testamos um novo estímulo de eclosão (hidratação), além dos que estão registrados na literatura (temperatura e fotoperíodo), acompanhados *in situ* e testados em laboratório, nosso estudo demonstrou que o tempo de hidratação foi o fator mais importante na eclosão dos microcrustáceos. Isso indica que, a dormência é um mecanismo adaptativo intrigante e com alto potencial para mais estudos, pois tem grande importância para a dinâmica dos microcrustáceos (JAMES et al., 2008), que são organismos fundamentais para o funcionamento das áreas úmidas intermitentes (GERHARD et al., 2016). Ainda mais porque, encontramos que as formas dormentes permitem a resiliência dos microcrustáceos, principalmente para que a comunidade se estruture de forma heterogênea ao longo do hidroperíodo, reduzindo a pressão competitiva e garantindo que os organismos mantenham suas funções no ambiente (MASCLAUX et al., 2014). Nosso registro de 41 táxons em três áreas úmidas reforça a importância de mais estudos e da conservação de áreas úmidas intermitentes em regiões subtropicais. Ainda mais porque, essas áreas úmidas são frequentemente ameaçadas pela agricultura e urbanização, que reduzem esses ambientes no litoral sul planície do Brasil (NETO; FRANTZ, 2003). Além disso, mudanças no clima global (principalmente temperatura e precipitação) podem afetar os estímulos de eclosão e afetar negativamente o surgimento de microcrustáceos em áreas úmidas intermitentes, especialmente para as espécies que precisam de um tempo de hidratação maior para emergir.

Além das questões respondidas nesta tese, e das propostas em cada capítulo, outras questões seriam interessantes para perspectivas futuras de estudos com áreas úmidas do Rio Grande do Sul. Como por exemplo, conhecer a diversidade de microcrustáceos em áreas úmidas permanentes e em cultivos de arroz dessa região. Ainda, como está distribuída essa diversidade, tentando entender a estruturação, desde a diversidade gama (diversidade regional), alfa (diversidade local) e as partições (*turnover* e aninhamento) da diversidade beta (mudança de espécies ao longo de um gradiente), assim como, os mecanismos e fatores que atuam nesses processos. Além disso, estudar a estruturação de metacomunidade usando as áreas úmidas como modelo, seria uma bordagem muito interessante, uma vez que, esses ambientes podem ter conectividade e proximidade, facilitando a dispersão das espécies. E os microcrustáceos devido a produção das formas dormentes, apresentam uma alta capacidade de dispersão podendo acrescentar muitas respostas a essa teoria.

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ANEXOS

Anexo 1: Artigo publicado como coautora durante o Doutorado em 2019.

Tropical Diversity (2019) 1(2): 32-47.
ISSN: 2596-2388.

RESEARCH ARTICLE

Does predation by planktonic organisms influence the size structure of phytoplanktonic algae in a black water lake in the Amazon?

Predação por organismos planctônicos influencia a estrutura de tamanho das algas fitoplanctônicas em um lago de água preta na Amazônia?

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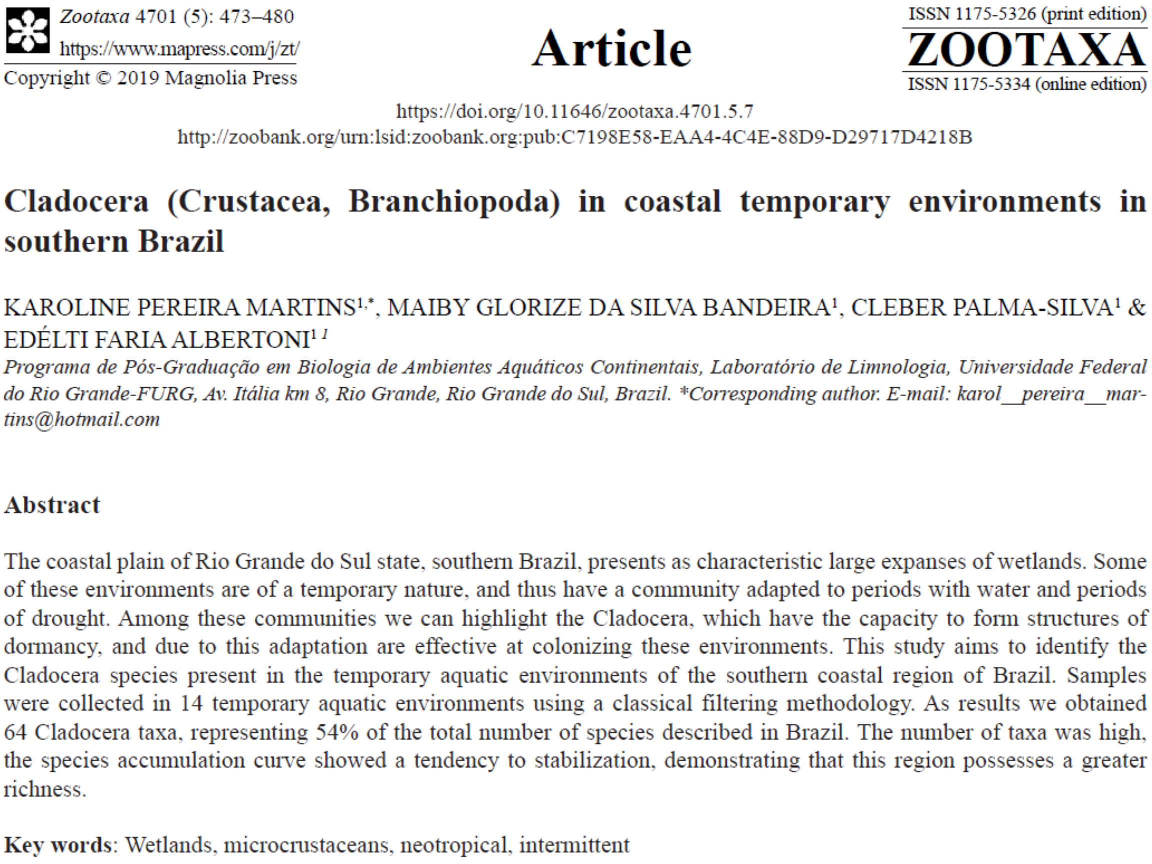
Resumo Organismos do fitoplâncton podem pertencer às categorias de tamanho pico, nano e microplâncton e organismos do zooplâncton ao micro, meso e macroplâncton. Por terem tamanhos diferentes, os organismos zooplanctônicos podem se alimentar de diferentes tamanhos do fitoplâncton. O objetivo foi avaliar se microcrustáceos e rotíferos planctônicos consomem o pico, nano e microfitoplâncton de forma homogênea nos períodos de seca enchente do lago Tupé. Um experimento foi colocado durante 24 horas no período de seca e enchente no lago Tupé. Amostras de zooplâncton e fitoplâncton foram coletadas com um tubo de PVC de 4 m de comprimento e os organismos zooplanctônicos foram contados e medidos. A amostra de fitoplâncton foi fracionada em pico, nano e microfitoplâncton para ser medida a biomassa de cada fração. No período de seca, a biomassa inicial total foi 1,92µg/L, especificamente pico 0,82, nano 0,55 e micro 0,55µg/L, sendo o valor da biomassa final 1,09µg/L correspondente ao pico 0,55, nano 0,27 e micro 0,27µg/L. No período de enchente, a biomassa inicial foi 2,91µg/L, especificamente pico igual a zero, nano 0,54 µg/L e micro 2,37 µg/L, sendo o valor da biomassa final 0,81 µg/L correspondente apenas ao picoplâncton. A maior densidade de organismos foi encontrada no experimento do período de seca. Concluímos que a pressão de predação do zooplâncton não influencia a estrutura de tamanho do fitoplâncton no ambiente estudado, uma vez que atua de forma similar sobre as diferentes classes.

Palavras-Chave: Fitoplâncton, nanoplâncton, microplâncton, mesocosmo, biomassa.

Abstract Phytoplanktonic organisms may be categorized as pico, nano and microplankton, and zooplanktonic organisms as micro, meso and macroplankton. Because they are different sizes, zooplanktonic organisms can feed on varying sizes of phytoplankton. The study objective was to test whether microcrustaceans and planktonic rotifers consumed pico-, nano- and microphyoplankton non-selectively during low- and high-water periods in Lake Tupé, Amazonian Brazil. An experiment was carried out across 24 hours in the low- and high-water periods, with zooplankton and phytoplankton samples collected from the lake with a PVC tube 4 m in length. Zooplankton were counted and measured, while the phytoplankton sample was divided into pico-, nano- and microphytoplankton and the biomass of each fraction measured. During low water, total initial biomass was 1.92 µg/L and, by fraction, contained pico 0.82, nano 0.55 and microphytoplankton 0.55 µg/L. Total biomass was1.09 µg/L, corresponding to pico- 0.55, nano- 0.27 and microphytoplankton 0.27 µg/L. During high water, total initial biomass was 2,91µg/L and by fraction, contained pico- equal to zero, nano- 0.54µg/L and micro- 2.37 µg/L. Total biomass was 0.81µg/L corresponding only to picophytoplankton. The highest density of organisms occurred in the low-water sample. We conclude that predation pressure from zooplankton does not influence phytoplankton size structure in the studied environment, since it impacts the different size classes equally.

Keywords: Picoplankton; Nanoplankton; Microplankton; Mesocosm; Biomass.

Anexo 2: Artigo publicado como coautora durante o Doutorado em 2019.



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Article

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Cladocera (Crustacea, Branchiopoda) in coastal temporary environments in southern Brazil

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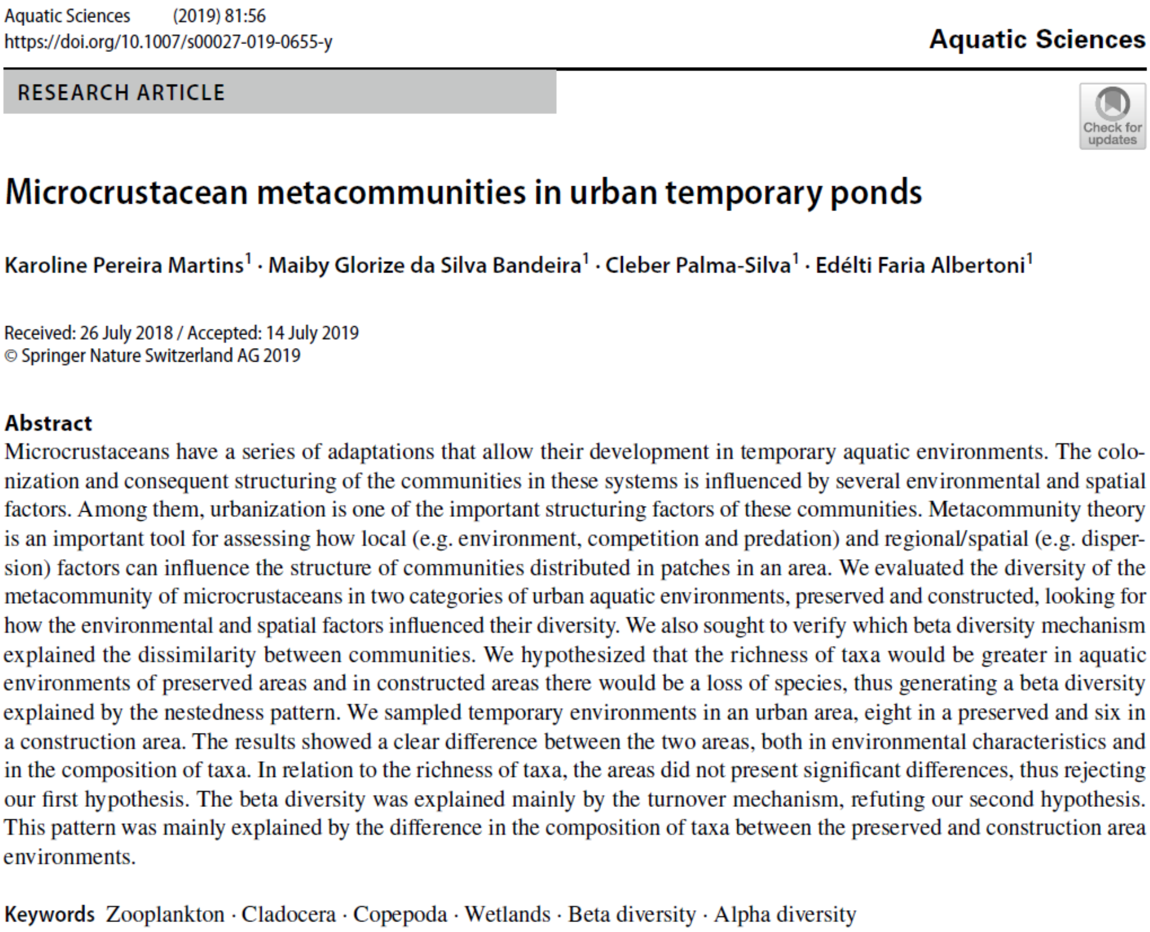
Abstract

The coastal plain of Rio Grande do Sul state, southern Brazil, presents as characteristic large expanses of wetlands. Some of these environments are of a temporary nature, and thus have a community adapted to periods with water and periods of drought. Among these communities we can highlight the Cladocera, which have the capacity to form structures of dormancy, and due to this adaptation are effective at colonizing these environments. This study aims to identify the Cladocera species present in the temporary aquatic environments of the southern coastal region of Brazil. Samples were collected in 14 temporary aquatic environments using a classical filtering methodology. As results we obtained 64 Cladocera taxa, representing 54% of the total number of species described in Brazil. The number of taxa was high, the species accumulation curve showed a tendency to stabilization, demonstrating that this region possesses a greater richness.

Key words: Wetlands, microcrustaceans, neotropical, intermittent

Anexo 3: Artigo publicado como coautora durante o Doutorado em 2019.



Aquatic Sciences (2019) 81:56
https://doi.org/10.1007/s00027-019-0655-y

Aquatic Sciences

RESEARCH ARTICLE

Microcrustacean metacommunities in urban temporary ponds

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Received: 26 July 2018 / Accepted: 14 July 2019

Abstract

Microcrustaceans have a series of adaptations that allow their development in temporary aquatic environments. The colonization and consequent structuring of the communities in these systems is influenced by several environmental and spatial factors. Among them, urbanization is one of the important structuring factors of these communities. Metacommunity theory is an important tool for assessing how local (e.g. environment, competition and predation) and regional/spatial (e.g. dispersion) factors can influence the structure of communities distributed in patches in an area. We evaluated the diversity of the metacommunity of microcrustaceans in two categories of urban aquatic environments, preserved and constructed, looking for how the environmental and spatial factors influenced their diversity. We also sought to verify which beta diversity mechanism explained the dissimilarity between communities. We hypothesized that the richness of taxa would be greater in aquatic environments of preserved areas and in constructed areas there would be a loss of species, thus generating a beta diversity explained by the nestedness pattern. We sampled temporary environments in an urban area, eight in a preserved and six in a construction area. The results showed a clear difference between the two areas, both in environmental characteristics and in the composition of taxa. In relation to the richness of taxa, the areas did not present significant differences, thus rejecting our first hypothesis. The beta diversity was explained mainly by the turnover mechanism, refuting our second hypothesis. This pattern was mainly explained by the difference in the composition of taxa between the preserved and construction area environments.

Keywords Zooplankton · Cladocera · Copepoda · Wetlands · Beta diversity · Alpha diversity

Anexo 4: Artigo publicado como coautora durante o Doutorado em 2020.

Environ Biol Fish
https://doi.org/10.1007/s10641-020-00978-5

Scientific knowledge on threatened species of the Brazilian Red List: freshwater fish as a case study

Manuela P. Tourinho · **Ana Paula T. Costa** ·
Karoline P. Martins · **Maiby Glorize S. Bandeira** ·
Fabiana G. Barbosa

Received: 2 February 2020 / Revised: 1 April 2020 / Accepted: 27 April 2020

Abstract We conducted a bibliometric analysis in order to quantify and characterize the scientific knowledge about threatened freshwater fish species in Brazil based in studies published in peer-reviewed journals from Web of Science database from Clarivate Analytics. We verified an increase in the number of papers for threatened freshwater fish species in Brazil, especially in the last eleven years of studied period. The journals with the most papers were Neotropical Ichthyology, Environmental Biology of Fishes, and Journal of Fish Biology. The number of publications among the Brazilian regions and states is not homogeneous. The most studied threatened fish was piracanjuba *Brycon orbignyanus*. Some important gaps in scientific knowledge need to be addressed, such as the relatively small number and/or lack of studies conducted Brazilian states and with threatened freshwater fish species in Brazil.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10641-020-00978-5) contains supplementary material, which is available to authorized users.

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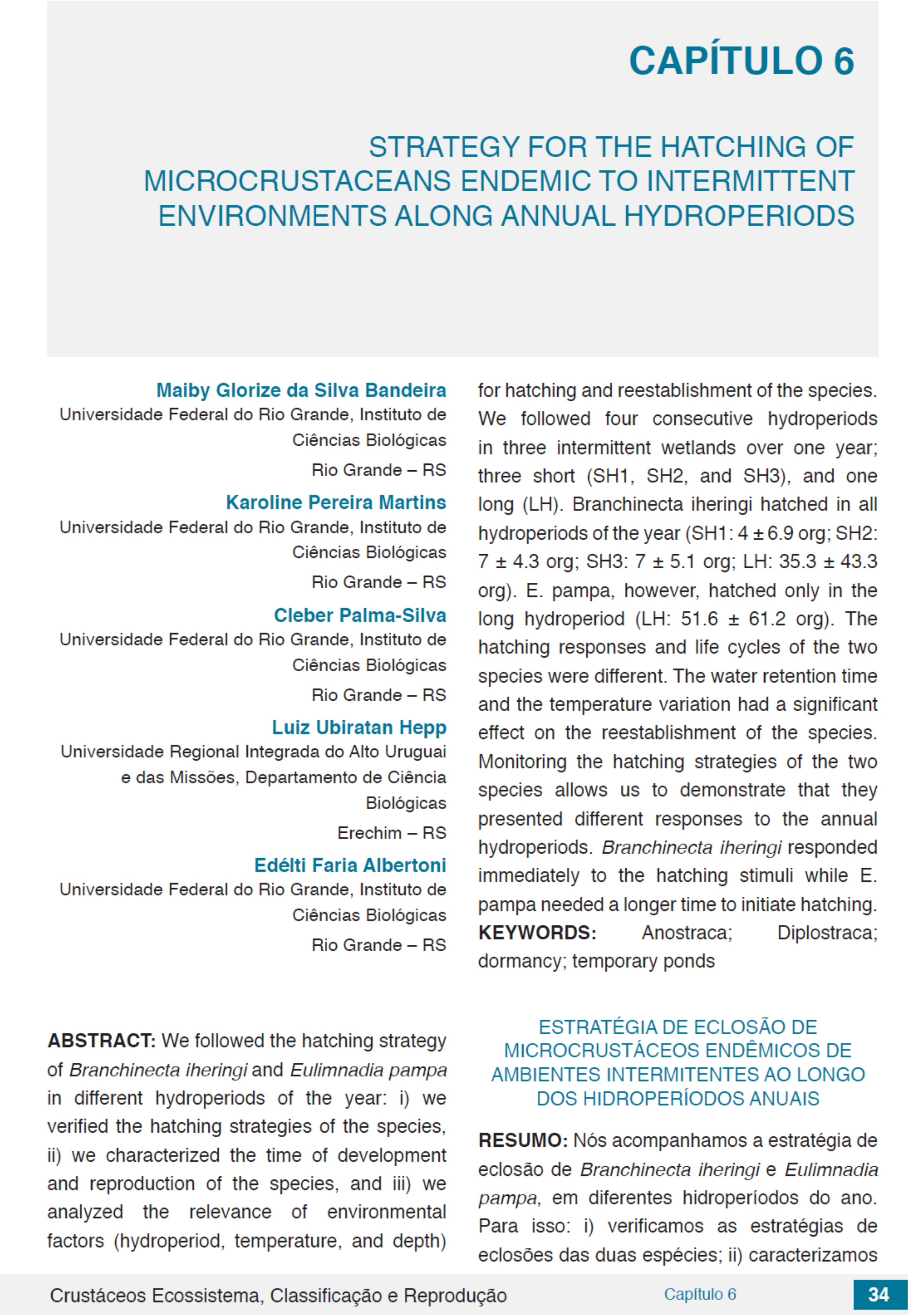
Keywords Bibliometric analysis · Conservation · Knowledge gaps · Ichthyofauna · Research bias

Introduction

Climate change (Thomas et al. 2004), habitat change (May et al. 2019), invasive species (Clavero and Garcia-Berthou 2005), pollution, and overexploitation (Dudgeon et al. 2006) are regarded as major drivers of global biodiversity loss and are associated with species declines and extinctions. Thus, there are several categorization systems for selecting species at risk (Andelman et al. 2004; de Grammont and Cuaron 2006). Globally, the most widely used is the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (hereafter IUCN Red List) which plays an important role in classifying species according to their risk of extinction (Mace et al. 2008). Additionally, many countries have developed national red lists of threatened species (Rodríguez 2008; see http://www.nationalredlist.org/ for countries with national red lists). These Red Lists provide a basis for biodiversity conservation, management, monitoring, and decision making (Rodrigues et al. 2006; Farrier et al. 2007).

The development and update of red lists has been accompanied by increasing interest to quantify and assess scientific knowledge (measured by number of publications in peer-reviewed journals) about threatened species to address knowledge gaps (e.g., Brodie 2009; Ducatez and Lefebvre 2014; Donaldson et al. 2016; Jarić et al. 2017; Shabani et al. 2017). According to

Anexo 5: Artigo da tese publicado como capítulo do livro *Crustáceos: ecossistemas, classificação e reprodução*.



CAPÍTULO 6

STRATEGY FOR THE HATCHING OF MICROCRUSTACEANS ENDEMIC TO INTERMITTENT ENVIRONMENTS ALONG ANNUAL HYDROPERIODS

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ABSTRACT: We followed the hatching strategy of *Branchinecta iheringi* and *Eulimnadia pampa* in different hydroperiods of the year: i) we verified the hatching strategies of the species, ii) we characterized the time of development and reproduction of the species, and iii) we analyzed the relevance of environmental factors (hydroperiod, temperature, and depth) for hatching and reestablishment of the species. We followed four consecutive hydroperiods in three intermittent wetlands over one year; three short (SH1, SH2, and SH3), and one long (LH). Branchinecta iheringi hatched in all hydroperiods of the year (SH1: 4 ± 6.9 org; SH2: 7 ± 4.3 org; SH3: 7 ± 5.1 org; LH: 35.3 ± 43.3 org). E. pampa, however, hatched only in the long hydroperiod (LH: 51.6 ± 61.2 org). The hatching responses and life cycles of the two species were different. The water retention time and the temperature variation had a significant effect on the reestablishment of the species. Monitoring the hatching strategies of the two species allows us to demonstrate that they presented different responses to the annual hydroperiods. *Branchinecta iheringi* responded immediately to the hatching stimuli while E. pampa needed a longer time to initiate hatching.

KEYWORDS: Anostraca; Diplostraca; dormancy; temporary ponds

ESTRATÉGIA DE ECLOSÃO DE MICROCRUSTÁCEOS ENDÊMICOS DE AMBIENTES INTERMITENTES AO LONGO DOS HIDROPERÍODOS ANUAIS

RESUMO: Nós acompanhamos a estratégia de eclosão de *Branchinecta iheringi* e *Eulimnadia pampa*, em diferentes hidroperíodos do ano. Para isso: i) verificamos as estratégias de eclosões das duas espécies; ii) caracterizamos

Anexo 6: Artigo da tese publicado na revista *Hydrobiologia*.

Hydrobiologia
https://doi.org/10.1007/s10750-020-04315-w

PRIMARY RESEARCH PAPER

Hydration time influences microcrustacean hatching in intermittent wetlands: in situ and ex situ approaches

Maiby Glorize da Silva Bandeira · Karoline Pereira Martins · Cleber Palma-Silva · Luiz Ubiratan Hepp · Edélti Faria Albertoni

Received: 22 November 2019 / Revised: 14 May 2020 / Accepted: 26 May 2020

Abstract Organisms living in intermittent wetlands present adaptations to cope with the inundation-desiccation process. Microcrustaceans are commonly found in intermittent wetlands because they present reproductive strategies able to synchronize with the hydroperiod. To know the dynamic of the microcrustaceans, that inhabit these wetlands of the subtropical coastal plain, which predominate the Pampas biome in Brazil, we analyzed the influence of hydration time and temperature on the hatching of microcrustaceans, comparing in situ and ex situ approaches. We followed hatching 34 days after in situ flooding and tested three temperatures (10, 15, and 20°C) 30 days after laboratory flooding. In both approaches, we classified the hydration time as the beginning, middle, and end of the hydroperiod. We recorded a total of 41 taxa distributed in Cladocera (26 taxa), Ostracoda (8), Copepoda (3), Anostraca (1), and Conchostraca (1). We observed that in situ hydration time was the most important factor for hatching. Ex situ hydration time was also important, but the increase in temperature positively affected the hatching of organisms. We also found that in both approaches, the beginning of hydration time is the most important period for the hatching of microcrustaceans.

Keywords Dormancy · Hatching stimuli · Hydration time · Resilience · Zooplankton

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Introduction

Intermittent wetlands are shallow aquatic environments that mainly depend on the climatic conditions (e.g., rainfall) to the permanence of water in the inundation-desiccation process, which results in seasonal and interannual periodicity (Maltchik et al., 2004). Intermittent environments are characterized by distinct water periods, alternating the presence (wet phase or hydroperiod) and absence (dry phase) of water (Batzer & Boix, 2016). During the dry phase, local extinctions and/or the migration of organisms occur (Sim et al., 2013; Chaparro et al., 2016). Some