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Programa de Pós-Graduação em Ecologia, Conservação e Biodiversidade

**Biología populacional e ecología trófica de decápodes dulcícolas do rio
Araguari, Minas Gerais**

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Uberlândia – Minas Gerais

Setembro, 2024

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**Biologia populacional e ecologia trófica de decápodes dulcícolas do rio
Araguari, Minas Gerais**

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Orientador: Prof. Dr. Giuliano Buzá Jacobucci

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Introdução geral

Os ecossistemas aquáticos continentais de regiões tropicais abrigam elevada diversidade, particularmente entre os invertebrados bentônicos, como insetos, anelídeos, moluscos e crustáceos (Esteves, 1988; Crowl et al., 2001; Bobeldyk & Ramírez, 2007). Dentre os crustáceos, representados principalmente por decápodes, que incluem caranguejos braquiúros, camarões carídeos, lagostins e anomuros, os dois primeiros grupos destacam-se como os mais diversificados, com altas densidades e que apresentam grande importância ecológica (Collins et al., 2007; Mancinelli et al., 2013; Magalhães et al., 2016; Emery-Butcher et al., 2020; Bauer, 2023), apesar de ainda serem relativamente pouco estudados, em comparação com suas contrapartes marinhas e estuarinas (Hamid & Wardiatno, 2018). Muitas espécies, particularmente de camarões, são anfídromas, ou seja, dependem de ambientes marinhos ou estuarinos para completarem seus ciclos de vida (Bauer, 2004). No entanto, outras espécies, denominadas hololimnéticas, que incluem braquiúros e carídeos, se desenvolvem exclusivamente em ambientes de águas continentais (Chace & Hobbs, 1969; Benstead et al., 2000).

Em ambientes de águas continentais, os caranguejos braquiúros abrangem, aproximadamente, 1.400 espécies, distribuídas em cinco famílias principais (Potamonautidae, Potamidae, Gecarcinucidae, Pseudothelphusidae e Trichodactylidae) (Yeo et al., 2008; Cumberlidge, 2016). Nas regiões neotropicais, as famílias Pseudothelphusidae e Trichodactylidae são predominantes, com destaque para Trichodactylidae, a mais abundante em rios de planície da América do Sul (Alves et al., 2024) e com 47 espécies (Cumberlidge, 2014; Magalhães et al., 2016). *Dilocarcinus pagei* Stimpson, 1861 é a espécie mais amplamente distribuída, ocorrendo no Peru, Bolívia, Paraguai, Argentina e Brasil. No Brasil, esta espécie é encontrada principalmente nas bacias dos rios Amazonas, Paraguai e Paraná (Magalhães, 2003; Herrera et al., 2013). Neste contexto, cabe ressaltar que no alto da bacia do rio Paraná *D. pagei* pode ter sido introduzido

em áreas não nativas (Magalhães et al., 2005; Azevedo-Santos & Lima-Stripari, 2010; Latini et al., 2016; Garcia et al., 2021), onde demonstrou uma adaptação eficiente, resultando em um aumento considerável em sua população (Pinheiro & Taddei, 2005; Azevedo-Santos & Lima-Stripari, 2010; Davanso et al., 2013; Herrera et al., 2013; Taddei et al., 2015).

Dilocarcinus pagei possui desenvolvimento embrionário direto, no qual os juvenis eclodem dos ovos com morfologia semelhante aos adultos, o que favorece uma rápida colonização e crescimento populacional (Vogt, 2013). Além disso, esses animais são crípticos e noturnos, o que pode ajudar a evitar predadores e a sobreviver em novos habitats (Sant'Anna et al., 2014). A espécie também é capaz de construir tocas em encostas ou viver associado às raízes de macrófitas aquáticas flutuantes, como *Eichhornia crassipes* (Mart.) Solms (aguapé) (Magalhães, 2003; Sant'Anna et al., 2014; Viana et al., 2023) e *Salvinia* sp. (Barboza et al., 2023).

Em ecossistemas aquáticos, especialmente nos artificiais, as macrófitas aquáticas frequentemente ocorrem em grande abundância, criando micro-habitats que servem de abrigo e fonte de alimento para *D. pagei*, o que facilita sua sobrevivência e reprodução (Magalhães et al., 2005; Herrera et al., 2013). Nesse sentido, variações ambientais, como nos níveis de precipitação e água podem mudar a disponibilidade desses recursos alimentares e os micro-habitats (Hawkins et al., 2003; Qin et al., 2024) (Hipótese da Disponibilidade de Recursos), influenciando assim a estrutura populacional da espécie, incluindo a sazonalidade reprodutiva e a razão sexual (Davanso et al., 2013; Taddei et al., 2015; Hudson et al., 2021). Esses efeitos, semelhantes aos observados em outros crustáceos (Gomes et al., 2012; Ozga et al., 2018; da Cruz et al., 2021, 2023) são essenciais para a compreensão de sua dinâmica populacional.

As respostas de *D. pagei* às variações ambientais não apenas moldam sua distribuição, mas também influenciam seu papel nas interações tróficas dos ecossistemas aquáticos. Com características generalistas e oportunistas, *D. pagei* utiliza os recursos

disponíveis, atuando como processador de matéria orgânica, predador (Williner & Collins, 2002; Sichieri et al., 2021) e presa de diversas espécies, incluindo peixes (Peixer & Petrere Jr, 2007), marsupiais (Aragon & Marinho-Filho, 2009) e aves (Olmos et al., 2006), sendo fundamental na transferência de energia entre os ambientes aquático e terrestre por ocupar diferentes níveis tróficos.

Além do seu importante papel ecológico, *D. pagei* tem demonstrado significativa relevância econômica, especialmente no cultivo aquático. Estudos experimentais, baseados na análise de diferentes densidades de cultivo, indicam que é possível otimizar tanto o crescimento quanto a viabilidade econômica de *D. pagei* (Sant'Anna et al., 2015). A finalidade principal é fornecer dados que possam auxiliar no desenvolvimento de técnicas de aquicultura dessa espécie, que é utilizada como isca na pesca esportiva, reduzindo a pressão sobre as populações naturais e oferecendo uma alternativa sustentável para pescador.

Em um outro experimento focado na preferência alimentar e no efeito de abrigos naturais no crescimento e na sobrevivência do *D. pagei*, Viana (2019) explora o potencial dessa espécie para ser cultivada como um recurso pesqueiro (como isca viva para a pesca esportiva, reabastecimento de populações naturais ou, potencialmente, para consumo humano) na região amazônica. O estudo destaca tanto o consumo de material de origem animal quanto de macrófitas, como *E. crassipes* e *Salvinia auriculata* Aubl., evidenciando uma dieta diversificada da espécie e suas implicações para o cultivo.

A espécie também é valorizada como fonte natural de astaxantina, um pigmento importante para a aquicultura de salmonídeos, devido à sua coloração marrom-avermelhada e à sua relativa estabilidade em diversas condições de processamento (Calvo et al., 2020; Pok et al., 2023). *Dilocarcinus pagei* também tem sido reportado como isca na pesca esportiva em algumas regiões do Brasil (Taddei & Herrera, 2010; Garcia et al., 2021), especialmente na captura de *Pseudoplatystoma* spp. (surubim ou pintado) e *Megaleporinus*

obtusidens Valenciennes, 1837 (piapara) na região do Pantanal (Magalhães, 2000; Mussato et al., 2019) e *Megaleporinus macrocephalus* Garavello & Britsky, 1988 (piavuçu) no rio Araguari, Minas Gerais (observação pessoal do autor).

Os camarões carídeos, com cerca de 800 espécies dulcícolas descritas, apesar de possuírem uma diversidade de espécies menor em comparação aos caranguejos braquiúros, estão amplamente distribuídos em ecossistemas continentais ao redor do mundo, com maior prevalência em regiões tropicais (Magalhães et al., 2016). Na América do Sul, a fauna de camarões de água doce é dominada por duas famílias principais: Atyidae, com 10 espécies, e Palaemonidae, com 53 espécie (Magalhães et al., 2016). A família Palaemonidae se destaca por sua ampla distribuição em diferentes ambientes, permitindo uma variedade maior de comportamentos e interações ecológicas, como predação e competição (De Grave et al., 2008). Dentro da família Palaemonidae, o gênero *Macrobrachium* C.S. Bate, 1868 é um dos táxons mais diversos e numerosos de camarões de água doce, com cerca de 40 espécies nas águas doces tropicais e subtropicais da América do Sul (Bauer, 2023), incluindo *Macrobrachium pantanalense* Dos Santos, Hayd & Anger, 2013, uma espécie endêmica do Pantanal (Soares et al., 2017; Freitas et al., 2021).

Muitas espécies do gênero *Macrobrachium* possuem relevância econômica. Entre elas, *Macrobrachium rosenbergii* De Man, 1879, *Macrobrachium amazonicum* Heller, 1862, *Macrobrachium acanthurus* Wiegmann, 1836 e *Macrobrachium carcinus* são amplamente utilizadas tanto na pesca (comercial e recreativa) quanto no cultivo em ambientes controlados, incluindo para consumo humano (Gomes et al., 2012; David et al., 2021; Hooper et al., 2023). Enquanto isso, *Macrobrachium pantanalense* tem ganhado atenção no aquarismo como espécie ornamental e é reconhecido como um importante bioindicador ambiental, dada sua sensibilidade a mudanças antrópicas e seu papel nas teias tróficas de águas continentais (Freitas et al., 2021).

Em geral, a influência dos decápodes nos ecossistemas aquáticos está fortemente relacionada aos seus hábitos alimentares e à variabilidade na composição de suas dietas em diferentes locais (Collins et al., 2012). Embora sejam onívoros, exibem alta variabilidade intra e interespecífica na composição e frequência relativa dos diferentes itens em sua dieta (Albertoni et al., 2003; M. S. de Melo & Nakagaki, 2013; Sethi et al., 2013). Essa variabilidade pode ser influenciada por pressão competitiva, tanto inter quanto intraespecífica, diferenças de sexo, ciclos ontogenéticos, ciclo de ecdise, características demográficas, além de variações diárias, sazonais e anuais. (Collins et al., 2007; Viozzi et al., 2021; Gonçalves-Silva et al., 2022). Em adição, o tipo de ambiente e a disponibilidade de recursos alimentares são fatores que influenciam a adaptabilidade desses crustáceos às condições ecológicas específicas (Lavajoo et al., 2019).

No rio Araguari, localizado na bacia do alto Paraná, Sudeste do Brasil, tanto *D. pagei* quanto *M. pantanalense* coexistem em um ambiente influenciado pela construção de barragens e reservatórios. A construção de barragens, especialmente as UHE (Usina Hidrelétrica de Energia), altera intensamente o ambiente, criando um ecossistema com estrutura e biota diferentes do curso d'água original (Stanford & Ward, 2001). Essas alterações impactam a disponibilidade de recursos alimentares para os decápodes, afetando diretamente sua abundância e interações ecológicas (Baxter, 2003). Além disso, há mudanças na dinâmica hidrológica, como a transformação de ambientes lóticos em lênticos (Nilsson et al., 2005), nos processos de produção de matéria e energia, ciclagem de nutrientes, retenção de sedimentos (Rodrigues & Silva, 2012) e na distribuição da biodiversidade, tanto no espaço quanto no tempo (Havel et al., 2005; Alho, 2020), incluindo a dispersão e estabelecimento de novas espécies (Linares et al., 2017, 2020; Alho, 2020; Wang et al., 2021).

Esses impactos se manifestam claramente no rio Araguari, onde o sistema hidrográfico é caracterizado pela presença de hidrelétricas em cascata, que incluem as usinas

de Nova Ponte, Miranda, Amador Aguiar I (AAI) e Amador Aguiar II (AAII), dispostas sequencialmente de montante para jusante (Loures & Pompeu, 2019). As modificações causadas por essas barragens incluíram desde o alagamento de áreas, a supressão da vegetação ripária e aquática, mudanças na dinâmica dos fluxos de água até o aumento da disponibilidade de nutrientes (Rodrigues & Silva, 2012; Santiago do Vale et al., 2021). Atualmente, nota-se também a presença de algumas espécies de moluscos invasores no rio Araguari (Maroneze et al., 2011; Linares et al., 2017; Anacléto et al., 2018).

Entre as espécies não nativas no rio Araguari estão o gastrópode *Melanoides tuberculata* Müller, 1774 e os bivalves *Corbicula fluminea* Müller, 1774 (amêijoa asiática) e *Limnoperna fortunei* Dunker, 1856 (mexilhão dourado), todos originários, principalmente, do sudeste asiático (Linares et al., 2020). O mexilhão dourado tem alto poder de incrustação em tubulações de usinas hidrelétricas, gerando impactos socioeconômicos consideráveis (Mansur et al., 2004; Darrigan et al., 2020), além dos ecológicos, como alterações na composição do substrato, na disponibilidade de nutrientes e na qualidade da água, o que, por sua vez, impacta as comunidades biológicas que dependem desses habitats (Linares et al., 2019).

Além dos impactos diretos no ambiente físico, esses moluscos invasores também podem competir por recursos, predar ou introduzir doenças as espécies nativas (Sala et al., 2000; Strayer & Dudgeon, 2010; Thomaz et al., 2014; Milardi et al., 2019). Um aspecto importante é que larvas e jovens mexilhões têm sido incorporados nas dietas de vários predadores, incluindo os decápodes (Dudgeon & Catherine, 1990; Quinn, 2020). Isso sugere que esses invasores não apenas representam uma ameaça, mas também podem criar interações ecológicas e servir como um novo recurso alimentar para os decápodes do rio Araguari.

Estudos experimentais laboratoriais têm demonstrado a importância de *L. fortunei* como recurso alimentar para diferentes espécies de caranguejos de água doce da bacia do

rio Paraná. Torres et al. (2012) revelaram que tamanhos variados do mexilhão dourado foram selecionados e incorporados na dieta pelo caranguejo *Zilchiopsis collastinensis* Pretzmann, 1968. Complementando esses achados, Carvalho et al. (2013) confirmaram o mesmo para *Trichodactylus borellianus* Nobili, 1896. Em um experimento piloto conduzido por nós, utilizando aquários experimentais, foram oferecidos simultaneamente três organismos aquáticos: o molusco bivalve *Corbicula fluminea*, o mexilhão dourado *Limnoperna fortunei* e o camarão *Macrobrachium pantanalense* como parte das interações alimentares com o caranguejo *D. pagei*. Através da observação visual direta e da captura de imagens em vídeo, foi possível registrar a manipulação e ingestão de partes do mexilhão dourado e do camarão pelo caranguejo. Esses resultados, embora preliminares e não publicados, fornecem indícios sobre o comportamento alimentar do caranguejo em condições controladas (dados não publicados – observação pessoal do autor).

Apesar disso, os poucos estudos da dieta natural realizados sobre o caranguejo *D. pagei* na Argentina (Williner & Collins, 2002) e no pantanal (Viana et al., 2023), indicam uma dieta predominantemente composta por material vegetal. Em contraste, a dieta natural de *M. pantanalense* ainda não foi documentada, evidenciando uma lacuna significativa no conhecimento sobre suas interações ecológicas.

Nesse cenário, a presente pesquisa tem como objetivo explorar a biologia populacional e a ecologia trófica de *D. pagei*, bem como comparar a dieta desse braquiúro com a do carídeo *M. pantanalense* no rio Araguari, Minas Gerais, Brasil, proporcionando uma visão abrangente de suas interações e adaptabilidades em um ambiente sujeito a múltiplas pressões antropogênicas. Para isso, foram realizadas uma caracterização populacional e uma avaliação da dieta do caranguejo, considerando suas variações demográficas e sazonais, bem como a avaliação da sobreposição de nicho e das posições tróficas de ambas as espécies por meio da análise de isótopos estáveis. Esses elementos são essenciais para uma compreensão mais aprofundada de como essas espécies interagem com

seu ambiente e para o desenvolvimento de estratégias de gestão sustentável em ecossistemas aquáticos impactados.

Assim, este trabalho foi dividido em três capítulos brevemente apresentados a seguir:

Capítulo 1 - Biologia populacional do caranguejo de água doce *Dilocarcinus pagei* Stimpson, 1861 (Decapoda: Trichodactylidae) no rio Araguari, sudeste do Brasil

No primeiro capítulo, nós investigamos a biologia reprodutiva de *D. pagei* em uma área do rio Araguari, bioma Cerrado. Apesar da representatividade da família Trichodactylidae, ainda existem lacunas na literatura acerca de dados básicos da espécie. Assim, nós caracterizamos a estrutura populacional, incluindo (i) a distribuição geral e mensal dos indivíduos por classe de tamanho, (ii) a razão sexual, (iii) recrutamento, (iv) aspectos reprodutivos, (v) a relação entre a frequência dos grupos demográficos (juvenis e adultos) e fatores ambientais (pluviosidade e nível d'água) e (vi) e determinamos a existência de sazonalidade em relação ao aparecimento de fêmeas ovígeras.

Capítulo 2 - Alimentação natural do caranguejo de água doce *Dilocarcinus pagei* Stimpson, 1861 (Decapoda: Trichodactylidae) na planície de inundação do rio Araguari, sudeste do Brasil

Neste capítulo, avaliamos a dieta natural do caranguejo de água doce *Dilocarcinus pagei* no Rio Araguari, Minas Gerais, Brasil. Diferentes grupos demográficos (fêmeas e machos adultos, fêmeas e machos juvenis) e sazonalidade foram considerados para prever variações na plenitude estomacal, no volume e na frequência dos alimentos consumidos.

Capítulo 3 - Diferenciação de nicho entre duas espécies de decápodes: insights a partir de isótopos estáveis de carbono e nitrogênio

Neste capítulo nós analisamos as assinaturas isotópicas estáveis (de carbono e nitrogênio) de duas espécies de decápodes (*Dilocarcinus pagei* e *Macrobrachium pantanalense*) para entender como as diferenças em suas dietas se refletem em suas composições isotópicas e o que isso revela sobre sua diferenciação de nicho e posição trófica, no rio Araguari, Minas Gerais, Brasil.

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Capítulo 1

Population biology of the freshwater crab *Dilocarcinus pagei* Stimpson, 1861 (Decapoda: Trichodactylidae) in the Araguari River, south-eastern Brazil

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Abstract

Dilocarcinus pagei is a freshwater crab that has a wide distribution in South America, occurring in the main river basins of Brazil. Our study analysed some aspects of the population biology of *D. pagei* in a population that occurs in the Araguari River, in south-eastern Brazil. Crabs were sampled monthly between September 2020 and November 2021. The population structure was analysed according to the organisms' size, sex and life stage. The frequency of demographic groups (adults and juveniles) over months was assessed using an environmental gradient analysis and a canonical correspondence analysis (CCA). A total of 392 crabs were collected, 282 males and 110 females. Male crabs were more abundant during most of the sampling period. Thus, the sex ratio in general and for most months was biased towards males. Gradient and CCA analyses showed seasonality in the occurrence of ovigerous females. This demographic group was more frequently sampled when the local rainfall increased. Our study provides relevant information about the population and reproductive biology of *D. pagei*, which may contribute to the understanding of the reproductive traits of freshwater crabs and the ecological role of this species in the environments it inhabits.

Keywords: Brachyura; Minas Gerais; population dynamics; reproductive biology; seasonality.

Resumo

Dilocarcinus pagei é um caranguejo de água doce que possui ampla distribuição na América do Sul, ocorrendo nas principais bacias hidrográficas do Brasil. Nosso estudo analisou alguns aspectos da biologia populacional de *D. pagei* em uma população que ocorre no rio Araguari, no sudeste do Brasil. Os caranguejos foram amostrados mensalmente entre setembro de 2020 e novembro de 2021. A estrutura populacional foi analisada de acordo com o tamanho, sexo e estágio de vida dos organismos. A frequência dos grupos demográficos (adultos e juvenis) ao longo dos meses foi avaliada utilizando uma análise de gradiente ambiental e uma análise de correspondência canônica (CCA). Foram coletados 392 caranguejos, sendo 282 machos e 110 fêmeas. Os caranguejos machos foram mais abundantes durante a maior parte do período de amostragem. Assim, a proporção entre os sexos em geral e durante a maioria dos meses foi tendenciosa em favor dos machos. As análises de gradiente e CCA mostraram sazonalidade na ocorrência de fêmeas ovígeras. Este grupo demográfico foi amostrado com mais frequência quando a precipitação local aumentou. Nosso estudo fornece informações relevantes sobre a população e a biologia reprodutiva de *D. pagei*, que podem contribuir para a compreensão das características reprodutivas dos caranguejos de água doce e do papel ecológico desta espécie nos ambientes que habita.

Palavras chaves: Brachyura; Minas Gerais; dinâmica populacional; biologia reprodutiva e sazonalidade.

Capítulo 2

Natural feeding of the freshwater crab *Dilocarcinus pagei* Stimpson, 1861 (Decapoda: Trichodactylidae) in the floodplain of the Araguari River, southeastern Brazil

Abstract

Freshwater decapods, such as the crabs in the family Trichodactylidae, are key components of benthic food webs, but research on their trophic ecology is limited. This study aimed to investigate variations in the natural diet of the freshwater crab *Dilocarcinus pagei* in the Araguari River, Brazil. We analyzed demographic groups and seasonal differences in stomach fullness, volume, and frequency of occurrence of various dietary items. Our results revealed that stomach fullness varied among demographic groups, with adult females showing lower levels and juvenile females showing higher levels. Analysis of stomach contents identified 12 types of items, including unidentified animals, detritus, sand, plastic filaments, and mollusks. Juvenile females showed a higher consumption of plant tissue, while only adult males and juveniles showed a consumption of mollusks. Plant tissue and detritus (digested material) were the most frequent items. These findings reveal the feeding habits of *D. pagei* in the sampling area, highlighting the influence of demographic groups and seasonal variations on their diet, including the consumption of plant tissue, predation on mollusks, and ingestion of microplastics.

Keywords: Brachyura; Feeding ecology; Trophic ecology; Aquatic invasions; Cerrado

Resumo

Os decápodes de água doce, como os caranguejos da família Trichodactylidae, são componentes-chave das cadeias alimentares bentônicas, mas a pesquisa sobre sua ecologia trófica é limitada. Este estudo teve como objetivo investigar variações na dieta natural do caranguejo de água doce *Dilocarcinus pagei* no Rio Araguari, Brasil. Analisamos grupos demográficos e diferenças sazonais na plenitude estomacal, volume e frequência de ocorrência de vários itens dietéticos. Nossos resultados revelaram que a plenitude estomacal variou entre os grupos demográficos, com as fêmeas adultas apresentando níveis mais baixos e as fêmeas juvenis apresentando níveis mais elevados. A análise do conteúdo estomacal identificou 12 tipos de itens, incluindo animais não identificados, detritos, areia, filamentos de plástico e moluscos. As fêmeas juvenis apresentaram maior consumo de tecido vegetal, enquanto apenas machos adultos e juvenis apresentaram consumo de moluscos. Tecido vegetal e detritos (material digerido) foram os itens mais frequentes. Estas descobertas revelam os hábitos alimentares de *D. pagei* na área de amostragem, destacando a influência de grupos demográficos e variações sazonais na sua dieta, incluindo o consumo de tecidos vegetais, predação de moluscos e ingestão de microplásticos.

Palavras chaves: Brachyura; Ecologia alimentar; Ecologia trófica; Invasões aquáticas;

Cerrado

Introduction

Freshwater decapods are a diverse group of aquatic animals found in various freshwater environments, such as rivers, streams, lakes, and ponds (Cumberlidge 2014; Magalhães et al. 2016). These animals are adaptable and can change their habitat and nutritional requirements, with the microbiota potentially playing an important role in digestion and nutrient absorption, as observed in various decapod crustaceans (Foysal, 2023), depending on several factors, such as life phases (e.g., juvenile and adult), and seasonal cycles (Collins et al. 2007; Carvalho et al. 2013). Feeding is a significant aspect of the lives of decapods, as they occupy different trophic levels ranging from herbivores to top predators, making them key players in food webs. However, their position in the food web varies depending on the environment and the species present (Cumberlidge et al. 2009).

Studies of freshwater crustacean decapods in the context of trophic ecology are an important approach to understanding their food requirements, trophic relationships with other species, and interactions with the environment (Collins et al. 2007; Toh et al. 2022). Moreover, as the trophic interactions between producers, primary consumers, secondary consumers, and higher-order consumers are the main drivers of energy and nutrient cycling through ecosystems, this approach can provide valuable insights into the functioning of aquatic ecosystems (van der Putten et al. 2004).

Trichodactylidae crabs are fully adapted to freshwater environments, and some species of this freshwater crab group can also be found in semi-terrestrial environments (Yeo et al. 2008). These true freshwater crabs are endemic to the Neotropical region (Bond-Buckup et al. 2008; Magalhães and Turkay 2008; Fernandes et al. 2020) and are important components of the littoral fauna as consumers in benthic food webs, exhibiting an omnivorous and opportunistic diet that includes plant detritus and benthic invertebrates (Williner and Collins 2002; Collins et al. 2007, 2012), and occasionally feeding on vertebrates such as frogs (Affonso and Signorelli 2011). Additionally, they play a crucial

role as shredders in freshwater habitats and are subject to predation by a diverse range of organisms, including fishes, amphibians, reptiles, birds, and mammals (Pardin 1998; Magalhães 2005), serving as an important link between aquatic and terrestrial food chains.

Among the trichodactylid crabs, *Dilocarcinus pagei* Stimpson, 1861, is one of the most widespread species, occurring in various South American countries, primarily distributed in the Amazon, lower Paraná, and Paraguay river basins (Magalhães 2005; Davanso et al. 2013; Herrera et al. 2013). It occurs mainly in lowlands above 100 m above sea level, although there are some records at altitudes above 900 m (Cumberlidge et al. 2009; Cumberlidge 2016). *Dilocarcinus pagei* is a medium-sized crab (up to 60 mm in carapace width) that lives associated with aquatic vegetation (Pinheiro & Taddei 2005a; Davanso et al. 2013; Herrera et al. 2013; Davanso et al. 2016). These crabs are cryptic and nocturnal, with direct embryonic development, where juveniles hatch from eggs with morphology similar to that of adults (Magalhães and Turkay 2008; Williner et al. 2014).

In the context of the expanding distribution of *D. pagei* in the reservoirs of southeastern Brazil (Upper Paraná basin) and its potential link to accidental or deliberate introductions—possibly related to its use as bait in sport fishing (Magalhães et al. 2005)—it becomes crucial to explore the trophic ecology of this species. This crab is becoming increasingly common in the basins of the Grande and Paranaíba Rivers (Taddei and Herrera 2010; Garcia et al. 2021), as well as in some of their principal tributaries, including the Araguari River (Barboza et al. 2023). Moreover, the presence of many large hydroelectric dams in this region is altering aquatic ecosystems (Rodrigues and Silva 2012), potentially facilitating the invasion of alien species (Havel et al. 2005; Rodrigues and Silva 2012; Daga et al. 2014; Coelho et al. 2018; Linares et al. 2019; Alho 2020; Elton 2020).

The Araguari River harbors invasive mollusk species such as *Limnoperna fortunei* Dunker, 1857 (Bivalvia: Mytilidae), *Corbicula fluminea* Müller, 1774 (Bivalvia: Corbiculidae), and *Melanoides tuberculata* Müller, 1774 (Gastropoda: Thiaridae) (Linares

et al. 2017). Although there is no definitive confirmation that these molluscs make new connections within the Araguari River food web, it is possible that they do so, as has been observed in other environments (Boltovskoy & Cataldo, 2009; Sylvester et al., 2007). Studies suggest that invasive mollusk species may create new trophic links that potentially alter energy and nutrient transfer in native ecosystems (Jackson et al. 2017; Boltovskoy et al., 2022). One notable species among them is the golden mussel *L. fortunei*, which has become a substantial part of the diet of fishes, including crabs, as already documented in the Upper Paraná basin (Cantanhêde et al. 2008) and other regions (Williner and Collins 2002; Sylvester et al. 2007; Torres et al. 2012). Additionally, the golden mussel has been responsible for significant economic losses in various sectors related to water, such as public water supply, power generation, industry, and navigation (Boltovskoy and Cataldo 1999; Darrigan 2002; Oliveira et al. 2006; Sylvester et al. 2007; Darrigan and Damborenea 2011; Barbosa et al. 2018; Boltovskoy et al. 2022; Fortunato et al. 2022).

Studies on *D. pagei* have mainly focused on its population biology, including growth, reproduction, and population structure (Taddei and Herrera 2010; Davanso et al. 2013; Herrera et al. 2013; Davanso et al. 2016; Barboza et al. 2023). Furthermore, investigations into the cultivation of the species have been conducted due to its economic potential in aquaculture (Sant'Anna et al., 2015; Viana, 2019) and as live bait in sport fishing (Taddei & Herrera, 2010; Mussato et al., 2019; Garcia et al., 2021). Despite these efforts, little attention has been paid to its trophic ecology, with only two studies conducted on its natural diet, one in the Lower Paraná basin in Argentina (Williner and Collins 2002) and another in the Paraguay basin in Brazil (Viana et al. 2023). Therefore, further research is crucial to gain a more comprehensive understanding of the trophic ecology of the species and its role in the ecosystem.

Addressing this knowledge gap, the present study aims to evaluate the natural diet of the freshwater crab *D. pagei* in the Araguari River, Minas Gerais, Brazil. Different

demographic groups (adult females and males, juvenile females and males) were considered to predict variations in stomach fullness, volume, and frequency of food items consumed. These demographic groups may have distinct dietary requirements influenced by seasonal changes in food resource availability. Moreover, we expect *D. pagei* to have a diverse diet comprising both plant and animal material, including invasive mollusk species, similar to other freshwater crabs.

Materials and methods

Study Area

The study was conducted in a section of the Araguari River, 30 km upstream of its confluence with the Paranaíba River and 50 km downstream of the Amador Aguiar II (AA II) dam in Minas Gerais, Brazil (Figure 1A). The Araguari River is an important tributary of the Paraná River, which ranks as the second largest river in South America (Bonetto et al. 1986). Additionally, the Araguari River flows through the Cerrado biome, recognized as one of the world's most important biodiversity hotspots (Myers et al. 2000).

The Araguari River basin covers approximately 22.000 km² (Salla et al. 2014) and spans 20 municipalities in western Minas Gerais, southeastern Brazil. This river features a system of cascading reservoirs, including several hydroelectric power plants such as Nova Ponte, Miranda, Amador Aguiar I (AAI), and Amador Aguiar II (AAII), arranged in sequence from upstream to downstream (Loures and Pompeu 2019). The presence of these reservoirs has led to changes in water levels and flow velocity, resulting in flooding during the rainy season. These alterations have had a significant impact on both the hydrological regime of the river and the biogeochemical cycles, sediment retention, and biota of the riparian zones (Rodrigues and Silva 2012).

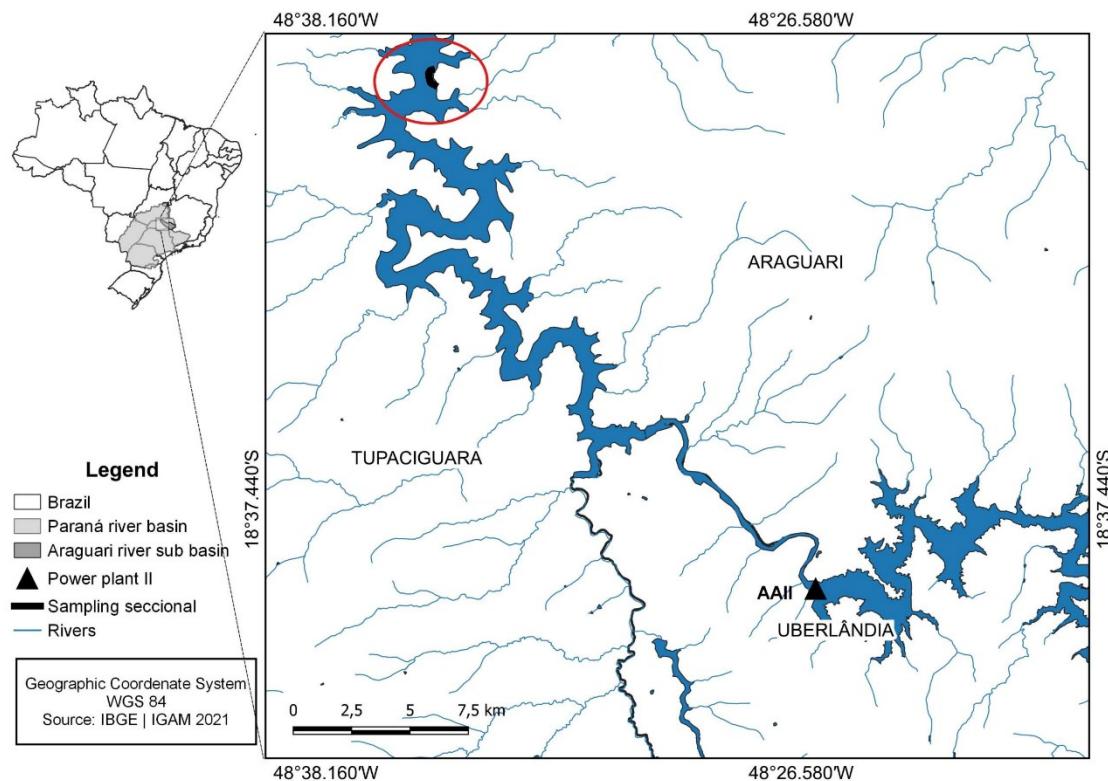


Figure 1. Location of the study area in the Araguari River, Minas Gerais, Brazil (between coordinates -18.4544°S, -48.5925°W and -18.4497°S, -48.5916°W). The sampled section is indicated by the red circle.

In the analyzed section of the river, small fragments of dry forests are present in the elevated regions of the floodplain (Vale et al. 2021). However, the riparian vegetation in the lower areas was likely displaced due to bank flooding caused by the construction of the Itumbiara/Furnas hydroelectric plant on the Paranaíba River in the 1980s, as well as the impact of the four upstream cascading dams on the Araguari River. Currently, the land-water interface is dominated by angiosperms such as grasses (Poaceae) and pteridophytes (*Salvinia* sp.), along with macrophytes such as *Eichhornia crassipes* (Mart.) Solms (“aguapé”) and others, which exhibit rapid changes as water level fluctuates. Additionally, we have observed the presence of invasive bivalve species in this area, including *L. fortunei*, *C. fluminea*, and *M. tuberculata*.

The climate classification of the study area, based on the Köppen system, is Aw, indicating a tropical climate with two distinct seasons: dry (April–September) and rainy (October–March) (Alvares et al. 2013; Beck et al. 2018). The average annual temperature in the area ranges between 18°C and 21.5°C (Novais et al. 2018). Rainfall data were obtained from the digital platform ‘HidroWeb’ of the Sistema Nacional de Recursos Hídricos (SNIRH), collected from a weather station near the sampling site. Rainfall affects water levels, so access to this data is crucial for monitoring changes in water resources.

Sampling and Measurements

Over a one-year period from September 2020 to August 2021, approximately 30 crabs were collected each month. Collections were made at night, by actively searching a 900-meter section of the riverbank for one hour. Sampling was done randomly, without controlling for sex or age class, with the aim of obtaining a representative sample of the total population. Two sampling methods were employed: manual collection of crabs found along the land-water interface, and the use of a sieve (mesh size of 3 mm), which was handled within the aquatic vegetation present in the area. The entire sampling process lasted one hour. Subsequently, crustaceans were individually placed in labeled plastic bags, anesthetized by cooling, and frozen to avoid the negative effects of digestion after death.

We identified the specimens following taxonomic literature (Melo 2003). Sex was determined by assessing the morphology of the abdomen, including its shape and size (Pinheiro and Taddei 2005a). All specimens had their carapace width (CW) measured, and in males, the right propodus length was also measured using a digital caliper with 0.01 mm accuracy. The measurements of carapace width and right propodus length in males were used to define demographic groups (adults and juveniles), while for females, the smallest ovigerous female was used as the reference to determine adult females, following the methodology employed by Barboza et al. (2023).

Stomach Content Analysis

Each animal was thawed and dissected to remove the stomach. Subsequently, we promptly determined the relative degree of stomach fullness (in percentage terms) by assigning a score according to six classes (Table 1), as proposed by Hyslop (1980) and Williams (1981). This visual assessment was feasible due to the translucent, thin-walled nature of the stomach in *D. pagei* (Collins et al. 2007). Individuals with empty stomachs were excluded from all subsequent calculations and statistical analyses.

Table 1. Relative degree of fullness scaled.

Fullness	Classes (Degree of Fullness – score)
0% (empty)	0
0% < stomach's fullness ≤ 5%	0.02
5% < stomach's fullness ≤ 35%	0.25
35% < stomach's fullness ≤ 65%	0.5
65% < stomach's fullness ≤ 95%	0.75
stomach's fullness > 95% (full)	1

Following this analysis, the entire stomach contents were mounted in a Petri dish covered with millimeter paper containing 1 x 1 mm squares for quantification under a stereomicroscope. We identified all dietary components to the lowest feasible taxonomic level, utilizing partially digested remnants as the basis for identification. Dietary items consisting of macroinvertebrates were identified using taxonomic keys obtained from specialized literature (Mugnai et al. 2010; Hamada et al. 2014), or expert support was sought when necessary. The presence of small leaf fragments indicated macrophyte remains or plant tissue.

Food items were categorized into 12 groups in total: Ant, Coleoptera, Ephemeroptera, Hemiptera, Mollusca (mantle tissues or shell), shrimp (pieces of mouth appendages, chelae, rostrum, cephalothorax, telson, uropods, exuviae from recent molts, and setae), plant tissue (stems, branches, leaves, seeds, flowers, fruits, and roots) or macrophyte, detritus (fragmented or partially digested organic material), sponge spicules, plastic filaments, sand, and unidentified animal. Animal remains that could not be clearly identified (e.g., egg-like structures and exoskeletons) were grouped into an unidentified category.

Additionally, we determined the volume of each item in the stomach, utilizing either the absolute point frequency or the method of points (MP) in a scale form. To achieve this, we quantified the area of each dietary item using 1 mm² squares and calculated the individual dietary proportion for each item by dividing its area by the total area covered by all items. Subsequently, a score was assigned to each item based on five ranking categories (Table 2), following the approach proposed by Williams (1981).

Table 2. Scales that were considered for the application of the Method of Points (MP). These scales vary according to the area occupied by each food item.

Volume by item	Category (Methods of Points – score)
≤ 5%	2.5
5 < volume ≤ 35%	25
35 < volume ≤ 65%	50
65 < volume ≤ 95%	75
> 95%	100

The number of points for each item is determined by multiplying the number of points by the value dependent on the degree of stomach fullness, as defined by the equation $MP_i = (\sum_{j=1}^n a_{ij} / A) \cdot 100$, where a_{ij} is the number of points of item i found in stomach j , A

is the total number of points for all items, and n is the total number of stomachs (Williams 1981). Subsequently, we evaluate the frequency of occurrence (FO) of each food item using the equation: $FO = \left(\frac{bi}{n}\right) \cdot 100$, where bi is the number of stomachs that have item i.

Data Analysis

To compare the fullness degree (FD), absolute frequency of points (MP), and frequency of occurrence (FO) among different seasons (Dry vs. Rainy), demographic groups including adult females (AF), juvenile females (JF), adult males (AM), and juvenile males (JM), as well as different types of food items, we employed a Generalized Linear Model (GLM). Additionally, when necessary, we performed Tukey's Test to compare all possible pairs of means between the groups. FD was modeled using a Gaussian distribution with an "identity" link, while MP was modeled using a Gamma distribution with a "log" link. Furthermore, for FO, we used a binomial distribution with a "logit" link. The analysis was conducted using the GLM package (Brooks et al. 2017), and the significance of variance was assessed using the Wald chi-squared test from the car package (Fox and Weisberg 2011). All statistical analyses were performed in RStudio 3.5.1 software (R Core Team 2018) at a significant level of 5%. To ensure the validity of our results, we tested for the assumptions of normality, heteroscedasticity, and overdispersion of the data.

Results

Throughout the analyzed period, there was notable variation in precipitation, ranging from a complete absence of rainfall, represented by an accumulation of 0 mm in the driest month (July), to a total of 174 mm in the雨iest month (November). A total of 333 crabs were examined, comprising 96 (29%) females and 237 (71%) males. Among the females, 61 (18.32%) were adults, and 35 (10.51%) were juveniles. Among the males, 71 (21.32%)

were adults, and 166 (49.85%) were juveniles. The carapace width (CW) exhibited average values of 39.37 ± 9.57 mm for females and 40.28 ± 7.63 mm for males (Table 3).

Table 3. Carapace width (mm) of *Dilocarcinus pagei* Stimpson, 1861 across different demographic groups, including adult females (AF), juvenile females (JF), adult males (AM), and juvenile males (JM), during both the dry and rainy seasons in Araguari River, Minas Gerais, Brazil.

Season	Demographic groups	N	Mean \pm SD	Minimum	Maximum
Dry	AF	20	43.74 ± 3.63	38.21	50.22
	JF	19	28.18 ± 4.68	20	37.12
	AM	66	47.67 ± 2.01	44.74	53.24
	JM	97	37.72 ± 7.12	12.7	44.54
Rainy	AF	41	46.63 ± 4.72	37.44	53.84
	JF	16	28.62 ± 5.17	18.82	36.12
	AM	5	46.84 ± 1.98	44.99	50.20
	JM	69	36.34 ± 6.71	19.62	44.36

Stomach Content Analysis: Seasons and Demographic Groups

Regarding stomach contents, a total of 191 (57.36%) had some food in their stomachs, while 142 (42.64%) were completely empty. Among the crabs with food in their stomachs, the distribution across demographic groups was as follows: 17 (8.90%) adult females, 33 (17.28%) juvenile females, 45 (23.56%) adult males, and 96 (50.26%) juvenile

males (Table 4). These percentages are based on the subset of individuals with food in their stomachs, not the total sample, which is why the values do not add up to 100%.

Table 4. Absolute and relative frequency (%) of *Dilocarcinus pagei* (Stimpson, 1861) across different demographic groups, including adult females (AF), juvenile females (JF), adult males (AM), and juvenile males (JM), during both the dry and rainy seasons in Araguari River, Minas Gerais, Brazil.

Season	Demographic groups	Empty stomach		Stomach with contents	
		N	%	N	%
Dry	AF	14	9.86	6	3.14
	JF	0	0.00	19	9.95
	AM	23	16.20	43	22.51
	JM	38	26.76	59	30.89
Rainy	AF	30	21.13	11	5.76
	JF	2	1.41	14	7.33
	AM	3	2.11	2	1.05
	JM	32	22.54	37	19.37
Total		142	100	191	100

The degree of stomach fullness exhibited a significant difference among demographic groups (GLM, $\chi^2 = 39.748$, $df = 3$, $p < 0.001$), but no difference was observed between seasons (GLM, $\chi^2 = 0.111$, $df = 1$, $p = 0.739$). Moreover, the interaction between

the factors was not significant, indicating that the variation in stomach fullness among demographic groups was not affected by the season (GLM, $\chi^2 = 3.734$, df = 3, p = 0.291). Thus, based on the comparison between pairs of demographic groups, we can infer those adult females exhibited the lowest level of stomach fullness, while juvenile females consistently showed significantly higher levels of stomach fullness compared to the other groups, approximately 4.5 times higher than adult females (Tukey's Test, p < 0.05; Table S1; see supplementary material). On the other hand, adult and juvenile males did not differ significantly in terms of stomach fullness, regardless of the season (Tukey's Test, p > 0.05, Table S1; see supplementary material) (Figure 2).

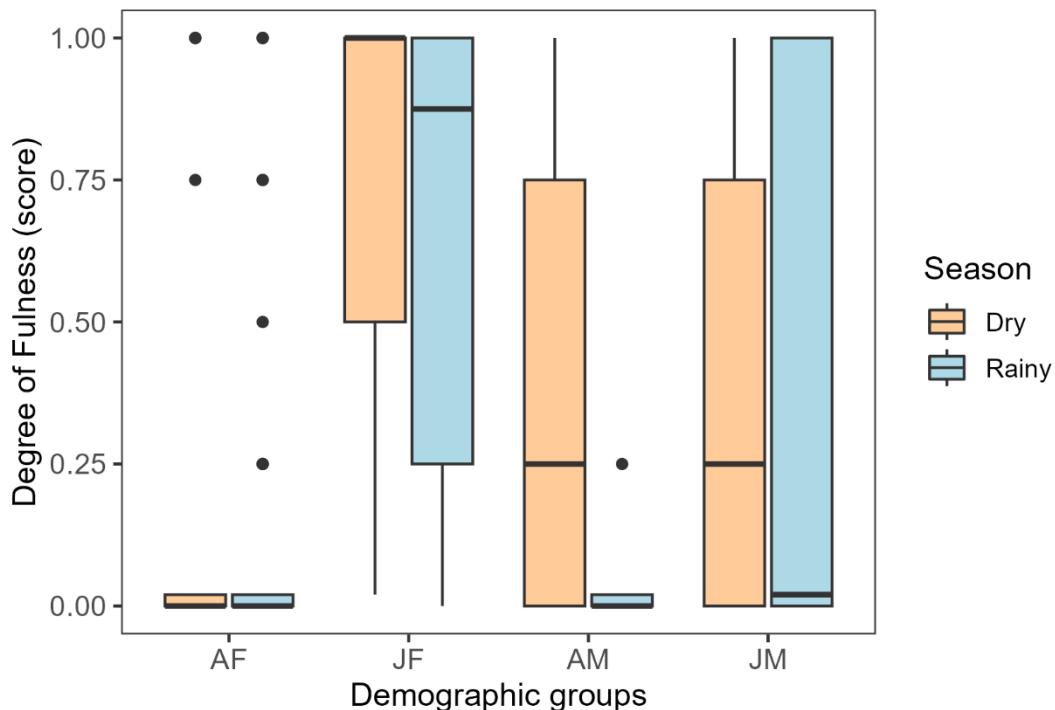


Figure 2. Boxplot with median (trace), minimum and maximum values, representing the degree of fullness observed in the stomachs of *Dilocarcinus pagei* Stimpson, 1861 among different demographic groups, including adult females (AF), juvenile females (JF), adult males (AM), and juvenile males (JM), during both the dry and rainy seasons in Araguari River, Minas Gerais, Brazil. The black circles indicate outliers, which fall outside the interquartile range (IQR).

Based on the absolute and relative frequency of points (%), the proportion of food consumed during the dry season was approximately 63%, while the rainy season accounted for 37%. Notably, during the dry season, the most consumed items were plant tissue (58.08%), followed by detritus (29.35%), unidentified animal matter (4.31%), mollusks (4.04%), and sand (3.23%) (Table 5). During the rainy season, the dominant items were plant tissue (66.78%), detritus (23.25%), unidentified animal matter (3.94%), and mollusks (2.81%) (Table 5).

Table 5. Absolute frequency of points (MP) and relative frequency (%) of the items found in the stomachs of *Dilocarcinus pagei* (Stimpson, 1861) among different demographic groups, including adult females (AF), juvenile females (JF), adult males (AM), and juvenile males (JM), during both the dry and rainy seasons in Araguari River, Minas Gerais, Brazil. The items include Coleoptera (Col), Detritus (Det), Ephemeroptera (Eph), Mollusca (Mol), Plant tissue (Plan), Plastic filaments (Plas), Sand, Shrimp (Shr), Sponge spicules (Spi), and Unidentified animal (Ua).

Season	Item	AF	%	JF	%	AM	%	JM	%
Dry	Ant	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Col	0.00	0.00	0.00	0.00	1.88	0.09	0.00	0.00
	Det	189.00	53.23	369.75	28.16	600.25	28.92	813.13	27.31
	Eph	0.00	0.00	0.00	0.00	25.00	1.20	0.63	0.02
	Hem	0.00	0.00	1.50	0.11	0.00	0.00	0.00	0.00
	Mol	0.00	0.00	0.00	0.00	256.25	12.35	15.00	0.50
	Plant	147.30	41.49	916.80	69.82	1033.13	49.78	1805.65	60.66

Plas	0.00	0.00	0.00	0.00	0.00	0.00	0.63	0.02	
Sand	0.00	0.00	25.00	1.90	41.88	2.02	150.50	5.06	
Shr	0.00	0.00	0.00	0.00	0.00	0.00	18.75	0.63	
Spi	0.00	0.00	0.00	0.00	0.00	0.00	18.75	0.63	
Ua	18.75	5.28	0.00	0.00	116.88	5.63	153.88	5.17	
Subtotal	355.05	100.00	1313.05	100.00	2075.25	100.00	2976.90	100.00	
Ant	0.50	0.09	0.00	0.00	0.00	0.00	0.00	0.00	
Col	1.25	0.24	0.00	0.00	0.00	0.00	50.00	2.02	
Det	111.25	21.03	307.50	31.16	6.25	43.10	506.13	20.46	
Eph	0.00	0.00	0.00	0.00	0.00	0.00	28.50	1.15	
Hem	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
Mol	0.00	0.00	0.00	0.00	0.00	0.00	112.50	4.55	
Rainy	Plant	364.13	68.82	677.00	68.59	8.25	56.90	1624.85	65.67
Plas	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
Sand	18.75	3.54	2.50	0.25	0.00	0.00	27.50	1.11	
Shr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
Spi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
Ua	33.25	6.28	0.00	0.00	0.00	0.00	124.63	5.04	
Subtotal	529.13	100.00	987.00	100.00	14.50	100.00	2474.10	100.00	

Our findings indicate that while there may be apparent differences in consumption percentages between seasons, these visual distinctions do not lead to significant variations in the overall volume consumed (GLM, $\chi^2 = 0.699$, df = 1, p = 0.403). However, we observed variation among demographic groups (GLM, $\chi^2 = 11.256$, df = 3, p = 0.010), as well as among different food item types (GLM, $\chi^2 = 83.054$, df = 11, p < 0.001). Furthermore, significant differences were observed between seasons and demographic groups when examining their interaction (GLM, $\chi^2 = 9.399$, df = 3, p = 0.024), indicating that the impact of the season on food consumption varied among different demographic groups. For example, during the rainy season, adult females, juvenile females, and juvenile males exhibited higher levels of resource consumption compared to adult males (Tukey's Test, p < 0.05, Table S2; see supplementary material). Particularly, juvenile females demonstrated a food consumption volume that was 2.26 times greater than that of adult males, representing an approximate difference of 127%. Conversely, during the dry season, no variations in consumption were detected among the groups (Tukey's Test, p > 0.05, Table S2; see supplementary material). When comparing consumption between seasons and the corresponding demographic groups (e.g., AF vs AF, JF vs JF), no significant variations were observed (Tukey's Test, p > 0.05, Table S2; see supplemental material).

We observed a significant interaction between season and food types (GLM, $\chi^2 = 11.871$, df = 5, p = 0.036), indicating that the volume of food consumed varied between different food types in both seasons. Plastic filaments, sponge spicules, and shrimp were only observed in the stomachs of animals sampled during the dry season, while ants (although appearing only once throughout the sampling) were found during the rainy season (Tukey's Test, p < 0.05, Table S3; see supplementary material).

The significant interaction observed between demographic groups and food types (GLM, $\chi^2 = 25.074$, df = 11, p = 0.008) indicates that the volume of food consumed varied among different demographic groups, particularly in relation to different food types. For

example, all groups had higher proportions of plant tissues in their diet, but juvenile females consumed at a rate 1.23 times higher than adult males (Tukey's Test, $p < 0.05$, Table S4; see supplementary material).

However, no significant interaction was found between season, demographic groups, and food types regarding the volume of food consumed (GLM, $\chi^2 = 6.134$, $df = 5$, $p = 0.293$). Although the season had varying effects on food consumption among demographic groups, the impact of food type on the combined interaction between season and demographic groups was not evident.

The frequency of occurrence of the most representative items reveals that during the dry season, plant tissue accounted for 46.64%, detritus for 36.19%, sand for 6.72%, and unidentified animals for 4.85% (Table 6). In the rainy season, plant tissue represented 46.56%, detritus accounted for 37.40%, unidentified animals were observed at 6.87%, and sand at 3.05% (Table 6) (Figure 3).

Table 6. Frequency of occurrence (FO) of the items found in the stomachs of *Dilocarcinus pagei* (Stimpson, 1861) among different demographic groups, adult females (AF), juvenile females (JF), adult males (AM), and juvenile males (JM), during both the dry and rainy seasons in Araguari River, Minas Gerais, Brazil. The items include Ant, Coleoptera (Col), Detritus (Det), Ephemeroptera (Eph), Hemiptera (Hem), Mollusca (Mol), Plant tissue (Plan), Plastic filaments (Plas), Sand, Shrimp (Shr), Sponge spicules (Spi), and Unidentified animal (Ua).

Season	Item	AF	%	JF	%	AM	%	JM	%
Dry	Col	0.00	0.00	0.00	0.00	1.00	1.08	0.00	0.00
	Det	5.00	41.67	15.00	41.67	32.00	34.41	45.00	35.43

	Eph	0.00	0.00	0.00	0.00	1.00	1.08	1.00	0.79
	Hem	0.00	0.00	1.00	2.78	0.00	0.00	0.00	0.00
	Mol	0.00	0.00	0.00	0.00	5.00	5.38	2.00	1.57
	Plan	6.00	50.00	19.00	52.78	43.00	46.24	57.00	44.88
	Plas	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.79
	Sand	0.00	0.00	1.00	2.78	6.00	6.45	11.00	8.66
	Shr	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.79
	Spi	0.00	0.00	0.00	0.00	0.00	0.00	2.00	1.57
	Ua	1.00	8.33	0.00	0.00	5.00	5.38	7.00	5.51
	Subtotal	12.00	100.00	36.00	100.00	93.00	100.00	127.00	100.00
	Ant	1.00	4.17	0.00	0.00	0.00	0.00	0.00	0.00
	Col	1.00	4.17	0.00	0.00	0.00	0.00	1.00	1.32
	Det	8.00	33.33	13.00	46.43	1.00	33.33	27.00	35.53
	Eph	0.00	0.00	0.00	0.00	0.00	0.00	3.00	3.95
Rainy	Mol	0.00	0.00	0.00	0.00	0.00	0.00	2.00	2.63
	Plan	10.00	41.67	14.00	50.00	2.00	66.67	35.00	46.05
	Sand	1.00	4.17	1.00	3.57	0.00	0.00	2.00	2.63
	Ua	3.00	12.50	0.00	0.00	0.00	0.00	6.00	7.89
	Subtotal	24.00	100.00	28.00	100.00	3.00	100.00	76.00	100.00
	Total	36.00	9.02	64.00	16.04	96.00	24.06	203.00	50.88

Our results showed significant variations in the frequency of occurrence among the different items studied (GLM, $\chi^2 = 1133.33$, df = 11, p < 0.001) (Figure 4). Plant tissue, followed by detritus, was found to occur most frequently, while shrimp and plastic filaments were the least frequent (Tukey's Test, p < 0.05; Table S5; see supplementary material). However, we did not observe significant differences in the frequency of occurrence of items based on season (GLM, $\chi^2 = 12.56$, df = 11, p = 0.323). On the other hand, significant differences were found in the frequency of occurrence of items between demographic groups (GLM, $\chi^2 = 60.56$, df = 33, p = 0.002).

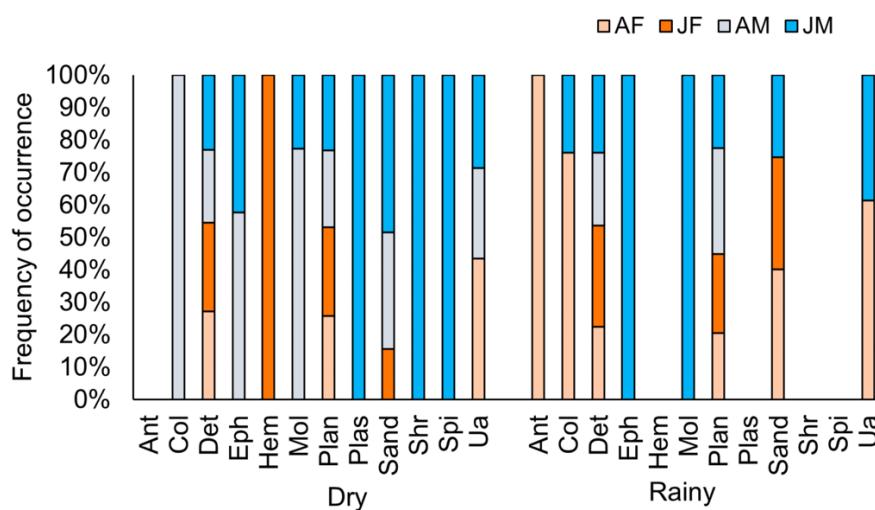


Figure 3. Plot representing the frequency of occurrence of the items found in the stomachs of *Dilocarcinus pagei* Stimpson, 1861 among different demographic groups, including adult females (AF), juvenile females (JF), adult males (AM), and juvenile males (JM), during both the dry and rainy seasons in Araguari River, Minas Gerais, Brazil. The items include Ant, Coleoptera (Col), Detritus (Det), Ephemeroptera (Eph), Hemiptera (Hem), Mollusca (Mol), Plant tissue (Plan), Plastic filaments (Plas), Sand, Shrimp (Shr), Sponge spicules (Spi), and Unidentified animal (Ua).

Although plant tissues and detritus were present in all demographic groups, plants were more frequent in juvenile females, adult males, and juvenile males, while detritus was more frequent in adult females. Certain items, such as mollusks, were found exclusively in

adult and juvenile males (Tukey's Test, $p < 0.05$; Table S6; see supplementary material).

When exploring interactions between factors such as items, seasons, and demographic groups, no significant differences were observed (GLM, $\chi^2 = 7.39$, $df = 33$, $p = 0.999$).

These results indicate that the combined effects do not lead to noticeable variations in the observed patterns.

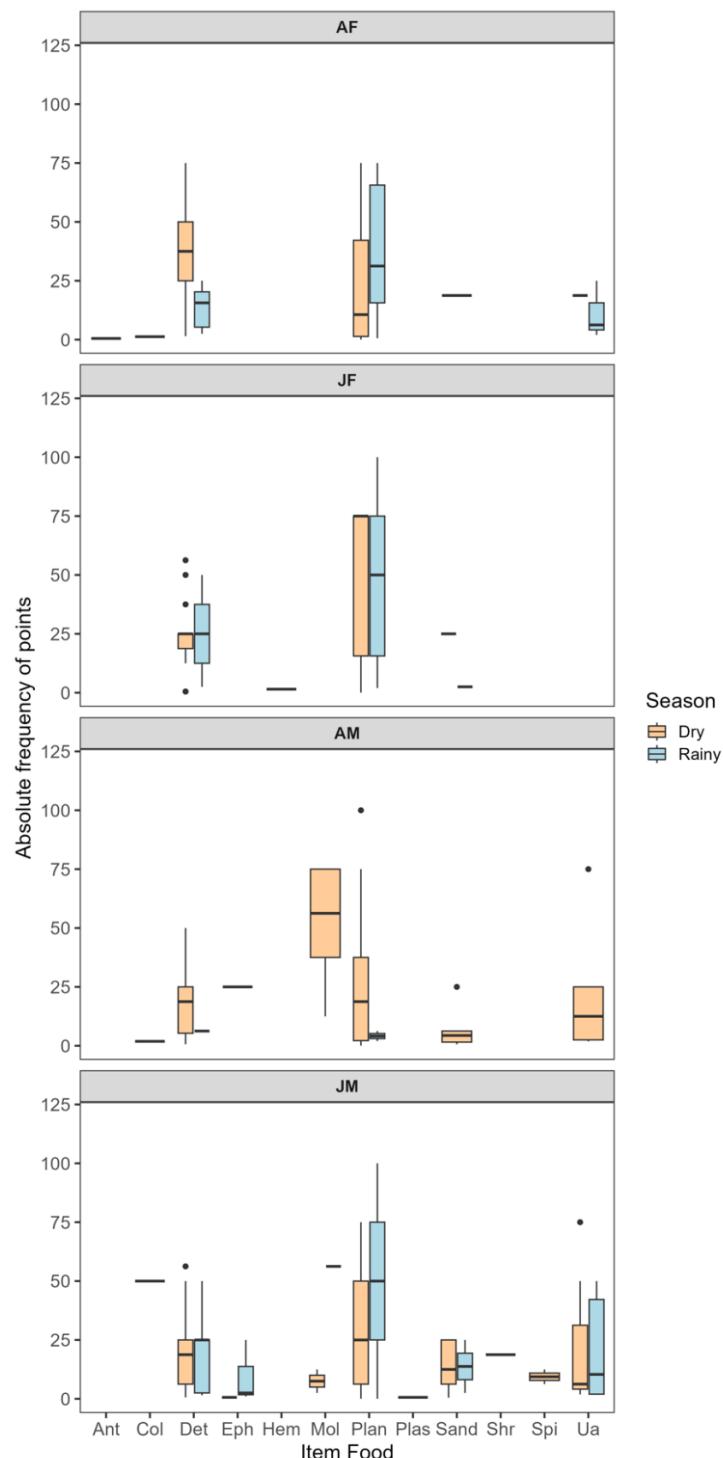


Figure 4. Boxplot with median (trace), minimum and maximum values, representing the absolute frequency of points of the items found in the stomachs of *Dilocarcinus pagei* Stimpson, 1861 among different demographic groups, including adult females (AF), juvenile females (JF), adult males (AM), and juvenile males (JM), during both the dry and rainy seasons in Araguari River, Minas Gerais, Brazil. The items include Ant, Coleoptera (Col), Detritus (Det), Ephemeroptera (Eph), Hemiptera (Hem), Mollusca (Mol), Plant tissue (Plan), Plastic filaments (Plas), Sand, Shrimp (Shr), Sponge spicules (Spi), and Unidentified animal (Ua).

Discussion

The analysis of the stomach contents in *Dilocarcinus pagei* crabs unveiled nuanced feeding patterns influenced by demographic groups and seasonal dynamics. Additionally, our findings indicate that the dietary habits of *D. pagei* align with those of conspecific populations and other trichodactylid crabs, showing a predilection for plant tissue consumption. However, we also noted occasional consumption of animal-derived items, such as mollusks, albeit in lesser proportions. These results provide support for the hypotheses posited in this study. The ability of *D. pagei* to efficiently digest plant tissue may be related to the microbiota in its digestive tract, which facilitates the breakdown of complex polysaccharides such as cellulose. Although there are few specific studies on *D. pagei*, research on other crustaceans, including marine species, suggests that the presence of microbial symbionts in the digestive tract plays an important role in the digestion of plant material (Harris, 1993; Zhang et al., 2020).

Regarding the degree of stomach fullness, encompassing both empty and filled stomachs, we observed a relatively constant level throughout the year, regardless of whether it was the dry or rainy season. In contrast, a study by Williner et al. (2013) on *Trichodactylus borellianus* Nobili, 1896 (Trichodactylidae) in the La Plata basin, Argentina, characterized

by a temperate climate, reported a lower stomach fullness index in winter and a higher index in spring. These findings suggest that feeding patterns and stomach fullness may be influenced by distinct climatic and seasonal factors compared to other regions, such as the tropical Cerrado biome in Brazil. Alternatively, when considering all stomachs combined in our analysis of fullness, the seasonal difference may not be readily apparent. This discrepancy could arise from the presence of empty stomachs during the rainy season, albeit in a lower proportion, potentially equalizing the overall average and masking the seasonal variation.

In terms of stomach fullness across groups, juvenile females exhibited a higher degree compared to adult females, even surpassing adult and juvenile males. This suggests that the increased food consumption by juvenile females may be directly related to accelerated body growth during this life phase to attain morphological maturity and gonadal development. This observation is further supported by the fact that females reach morphological sexual maturity at a carapace width (CW) of 37.44 mm, while males attain sexual maturity at a larger size, 44.74 mm CW (Barboza et al., 2023). The higher stomach fullness in juvenile females likely reflects the increased energy requirements necessary for reaching reproductive maturity, a process that occurs earlier in females compared to males, potentially driving this differential feeding behavior.

Previous studies on *D. pagei* have shown that females have faster growth rates than males, a phenomenon associated with their reproductive strategy (Pinheiro & Taddei, 2005b; Taddei & Herrera, 2010). However, adult females of this species may reduce their activity patterns during certain reproductive processes, thereby decreasing the frequency at which this group ingests food (Herrera et al. 2013; Marciano et al. 2020). The observation of ovigerous females of *D. pagei* in natural environments is rare, as noted in previous studies (Mansur and Hebling 2002; Davanso et al. 2013; Taddei et al. 2015; Barboza et al. 2023). It is believed that reproductively active or ovigerous females of *D. pagei* exhibit highly

cryptic behaviors (Davanso et al. 2013), remaining sheltered after mating as a strategy to avoid predators and ensure the development of embryos and early juvenile stages (which remain attached inside the females' abdomen). Consequently, due to this behavior, these organisms may refrain from feeding, thus justifying the differences found in the present study.

In the method of points, only stomachs with contents were considered, revealing a more pronounced difference in the volume consumed among items, with variations depending on the specific demographic group. This observation likely arises from the direct correlation between food availability and crab consumption, reflecting the crabs' response to seasonal fluctuations in food resources. Higher consumption rates were observed during the rainy season, particularly among juvenile females. The increased consumption by juvenile females suggests a heightened demand to support body growth and the development of reproductive structures, as evidenced by stomach fullness. These findings highlight distinct patterns of food consumption across different life stages during both the dry and rainy seasons. The rainy season, characterized by increased prey availability and nutrient content in the water, may stimulate heightened food intake by juvenile females (Kennish, 1997).

Furthermore, we noted variations in the volume of consumed items across different demographic groups. Plant tissue, particularly macrophytes, comprised a substantial portion of the diet for all demographic groups compared to other food types. Macrophytes are widely acknowledged as the preferred food source for trichodactylid crabs. Studies indicate that both crabs, *Trichodactylus petropolitanus* (Goeldi, 1886), and *D. pagei*, consume a significant proportion of macrophytes, with reported values exceeding 35% (Viana et al., 2023). Adult and juvenile males exhibited a more diverse diet, including the consumption of mollusks, whereas adult and juvenile females did not display this behavior. During our field observations, we documented the presence of *Pomacea* sp. gastropod and invasive

bivalves such as *L. fortunei* (golden mussel), *C. fluminea*, and *M. tuberculata*. Although it was challenging to distinguish them in the crab's stomach contents, we directly observed *D. pagei* primarily feeding on *Pomacea* sp. and *L. fortunei*. This observation suggests that these mollusk species, as documented for other decapods, may represent significant dietary components for *D. pagei* crabs. The presence of these specific prey items may contribute to the observed differences in diet among sexes or life stages, as discussed earlier. These findings highlight the potential existence of distinct food preferences or foraging behaviors among various demographic groups of the studied species.

Variations in diet composition among demographic groups can be influenced by several factors, including food resource availability, prey structure in the sampling area, foraging behavior, and claw morphology, which varies according to life phase. Ontogenetic changes may lead to shifts in crab food preferences (Viozzi et al., 2021). It is plausible that differences in claw morphology and the capacity to manipulate mollusks contribute to more efficient consumption of these items by males, as observed in certain marine brachyuran crabs (Schenk and Wainwright, 2001). In the case of *D. pagei*, previous studies have suggested that both adult males and females possess robust claws, potentially broadening their dietary repertoire (da Silva & Nogueira, 2023). However, sexual dimorphism in claw morphology is primarily evident in males (Davanso et al., 2016; da Silva & Nogueira, 2023), indicating potential disparities in feeding behavior and resource utilization between sexes. This could elucidate the findings of our study, where only male crabs (juveniles and adults) were seen consuming mollusks. However, a study in Argentina found no significant difference in the general composition of the diet between juveniles and adults or between males and females (Williner and Collins, 2002). These outcomes imply that dietary variations may be population-specific or influenced by environmental factors and resource availability in the studied region. Furthermore, another factor potentially influencing the dietary repertoire of this *D. pagei* population in Argentina is the size of individuals. Williner

and Collins (2002) investigated relatively small individuals compared to *D. pagei* populations in Brazil, with crabs ranging from 4.4 to 39.4 mm CW, and the majority falling between 7.5 and 17.5-mm CW (see figure 3 in Williner and Collins, 2002). Consequently, these individuals likely possessed smaller and less dimorphic claws, potentially limiting access to certain food resources.

Additionally, plastic filaments were found in one of the examined stomachs, indicating the ingestion of microplastics. It is well-documented that microplastics are ingested by various benthic invertebrates, including decapods (Browne et al., 2008; Devriese et al., 2015; Windsor et al., 2019; Villagran et al., 2020; Wang et al., 2021; Viana et al., 2023). This ingestion can occur through diverse mechanisms, such as accidental consumption during foraging (e.g., filtering or detritivory), opportunistic feeding, or bioturbation activities. Notably, a study on the crab *Minuca rapax* (Smith, 1870) revealed that bioturbation activity within burrows can influence the distribution of microplastics in sediments (Capparelli et al., 2022). These results underscore the potential impacts of microplastic pollution on decapod crustaceans and emphasize the necessity for further research to comprehend the ecological implications in aquatic environments.

Conclusion

This study offers valuable insights into the feeding habits of *D. pagei* crabs within the Cerrado biome. Our findings highlight the influence of demographic groups and seasonal variations on their dietary preferences. Understanding these variations in diet composition among different groups sheds light on the ecological and behavioral adaptations of these animals across various environmental conditions. Moreover, it provides insight into the potential impacts of invasive species and microplastic pollution on decapod crustaceans. Further research is imperative to deepen our comprehension of the ecological implications of these feeding patterns and the consequences of microplastic ingestion in the freshwater

environment. Such knowledge is essential for formulating effective conservation and management strategies aimed at preserving the health and functionality of aquatic ecosystems.

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Supplementary material

Article title: Natural feeding of the freshwater crab *Dilocarcinus pagei* Stimpson, 1861 (Decapoda: Trichodactylidae) in the floodplain of the Araguari River, southeastern Brazil

Journal name: Animal Biology

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Table captions

cat = demographic groups, AF = adult female, JF = juvenile female, AM = adult male, JM = juvenile male, Col = coleoptera, Det = detritus, Eph = Ephemeroptera, Mol = Mollusca, Plan = plant tissue, Plas = plastic filaments, Shr = shrimp, Spi = sponge spicules, Ua = unidentified animal.

Table S1. Tukey test comparing the degree of stomach fullness among the different demographic categories. Different letters indicate different means among the compared categories.

emmean	SE	df	lower.CL	upper.CL	group	differences
AF	0.157	0.0504	329	0.0578	0.256	a
AM	0.336	0.0468	329	0.2445	0.428	b
JM	0.357	0.0306	329	0.2967	0.417	b
JF	0.688	0.0666	329	0.5570	0.819	c

Table S2. Tukey test comparing the volume of food consumed by each demographic category across different seasons (season*cat). Different letters indicate different means among the compared categories.

emmean	SE	df	lower.CL	upper.CL	group	differences
Rainy_AF	3.09	0.191	391	2.718	3.47	b
Rainy_JF	3.56	0.177	391	3.215	3.91	b
Rainy_AM	1.58	0.540	391	0.513	2.64	a
Rainy_JM	3.48	0.107	391	3.272	3.69	b
Dry_AF	3.39	0.270	391	2.856	3.92	ab
Dry_JF	3.60	0.156	391	3.290	3.90	b
Dry_AM	3.11	0.097	391	2.914	3.30	ab
Dry_JM	3.15	0.083	391	2.991	3.32	ab

Table S3. Tukey test comparing the volume of items consumed across each season (season*item). Different letters indicate different means among the compared categories.

emmean	SE	df	lower.CL	upper.CL	.group	differences
RainyAnt	-0.693	0.8512	380	-2.37	0.98	a
DryPlas	-0.470	0.8512	380	-2.14	1.20	ab
DryHem	0.405	0.8512	380	-1.27	2.08	abc
DryCol	0.629	0.8512	380	-1.04	2.30	abcde
DrySpi	2.238	0.6019	380	1.05	3.42	abcdef
RainyEph	2.251	0.4914	380	1.29	3.22	abcdef
DrySand	2.491	0.2006	380	2.10	2.89	bcd
RainySand	2.500	0.4256	380	1.66	3.34	abcdef
DryEph	2.550	0.6019	380	1.37	3.73	abcdef
RainyUa	2.865	0.2837	380	2.31	3.42	cdef
DryShr	2.931	0.8512	380	1.26	4.60	abcdef
RainyDet	2.945	0.1216	380	2.71	3.18	cde
DryDet	3.012	0.0864	380	2.84	3.18	cd
DryUa	3.103	0.2361	380	2.64	3.57	cdef
RainyCol	3.244	0.6019	380	2.06	4.43	cdef
DryPlan	3.441	0.0761	380	3.29	3.59	ef
DryMol	3.657	0.3217	380	3.02	4.29	def
RainyPlan	3.781	0.1090	380	3.57	3.99	f
RainyMol	4.030	0.6019	380	2.85	5.21	cdef

Table S4. Tukey test comparing the volume of items consumed by different demographic categories (cat*item). Different letters indicate different means among the compared categories.

emmean	SE	df	lower.CL	upper.CL	.group	differences
AF_Ant	-0.693	0.8565	372	-2.38	0.991	a
JM_Plas	-0.470	0.8565	372	-2.15	1.214	ab
AF_Col	0.223	0.8565	372	-1.46	1.907	abc
JF_Hem	0.405	0.8565	372	-1.28	2.090	abc
AM_Col	0.629	0.8565	372	-1.06	2.313	abcde
AM_Sand	1.943	0.3497	372	1.26	2.630	abc
JM_Eph	1.985	0.4282	372	1.14	2.827	abcd
JM_Spi	2.238	0.6056	372	1.05	3.429	abcdef
AF_Ua	2.565	0.4282	372	1.72	3.407	abcdef
JM_Sand	2.617	0.2375	372	2.15	3.084	abcd
JF_Sand	2.621	0.6056	372	1.43	3.812	abcdef
JM_Det	2.908	0.1009	372	2.71	3.107	cd
AM_Det	2.911	0.1491	372	2.62	3.204	cd
JM_Shr	2.931	0.8565	372	1.25	4.615	abcdef
AF_Sand	2.931	0.8565	372	1.25	4.615	abcdef
JM_Ua	3.064	0.2375	372	2.60	3.532	cdef
AF_Det	3.140	0.2375	372	2.67	3.607	cdef
AM_Plan	3.142	0.1277	372	2.89	3.393	cde
AM_Ua	3.152	0.3830	372	2.40	3.905	cdef
JF_Det	3.186	0.1619	372	2.87	3.504	cdef
AM_Eph	3.219	0.8565	372	1.53	4.903	Abcdef

JM_Mol	3.462	0.4282	372	2.62	4.304	Cdef
AF_Plan	3.465	0.2141	372	3.04	3.886	Cdef
JM_Plan	3.619	0.0893	372	3.44	3.794	Ef
JF_Plan	3.877	0.1491	372	3.58	4.171	F
JM_Col	3.912	0.8565	372	2.23	5.596	Bcdef
AM_Mol	3.937	0.3830	372	3.18	4.690	Def

Table S5. Tukey test comparing the frequency of occurrence of different food items.

Different letters indicate different means among the compared categories.

	emmmean	SE	Df	asymp.LCL	asymp.UCL	.group	differences
Ant	-5.805	1.001	Inf	-7.768	-3.842	ab	
Plas	-5.805	1.001	Inf	-7.768	-3.842	ab	
Shr	-5.805	1.001	Inf	-7.768	-3.842	ab	
Hem	-5.805	1.001	Inf	-7.768	-3.842	ab	
Spi	-5.109	0.709	Inf	-6.499	-3.719	a	
Col	-4.700	0.580	Inf	-5.837	-3.564	a	
Eph	-4.184	0.451	Inf	-5.067	-3.300	ab	
Mol	-3.584	0.338	Inf	-4.246	-2.921	ab	
Sand	-2.649	0.221	Inf	-3.081	-2.216	b	
Ua	-2.649	0.221	Inf	-3.081	-2.216	b	
Det	-0.248	0.110	Inf	-0.464	-0.031	c	
Plan	0.235	0.110	Inf	0.019	0.452	c	

Table S6. Tukey test comparing the frequency of occurrence of each food item among different demographic categories (cat*item). Different letters indicate different means among the compared categories.

emmmean	SE	Df	asympt.LCL	asympt.UCL	.group	differences
JF_Ant	-20.566	2.996.979	Inf	-5.894.538	5.853.406	abcdefg
JF_Plus	-20.566	2.996.979	Inf	-5.894.538	5.853.406	abcdefg
JF_Col	-20.566	2.996.979	Inf	-5.894.538	5.853.406	abcdefg
JF_Eph	-20.566	2.996.979	Inf	-5.894.538	5.853.406	abcdefg
AF_Eph	-20.566	2.270.141	Inf	-4.469.961	4.428.829	abcdefg
JM_Hem	-20.566	1.376.144	Inf	-2.717.758	2.676.626	abcdefg
AM_Spi	-20.566	2.104.208	Inf	-4.144.738	4.103.605	abcdefg
AM_Hem	-20.566	2.104.208	Inf	-4.144.738	4.103.605	abcdefg
AF_Shr	-20.566	2.270.141	Inf	-4.469.961	4.428.829	abcdefg
AF_Plus	-20.566	2.270.141	Inf	-4.469.961	4.428.829	abcdefg
AF_Spi	-20.566	2.270.141	Inf	-4.469.961	4.428.829	abcdefg
JM_Ant	-20.566	1.376.144	Inf	-2.717.758	2.676.626	abcdefg
JF_Mol	-20.566	2.996.979	Inf	-5.894.538	5.853.406	abcdefg
JF_Shr	-20.566	2.996.979	Inf	-5.894.538	5.853.406	abcdefg
AM_Shr	-20.566	2.104.208	Inf	-4.144.738	4.103.605	abcdefg
JF_Ua	-20.566	2.996.979	Inf	-5.894.538	5.853.406	abcdefg
AM_Plus	-20.566	2.104.208	Inf	-4.144.738	4.103.605	abcdefg
AF_Hem	-20.566	2.270.141	Inf	-4.469.961	4.428.829	abcdefg
JF_Spi	-20.566	2.996.979	Inf	-5.894.538	5.853.406	abcdefg
AM_Ant	-20.566	2.104.208	Inf	-4.144.738	4.103.605	abcdefg
AF_Mol	-20.566	2.270.141	Inf	-4.469.961	4.428.829	abcdefg

JM_Plas	-5.106	1.003	Inf	-7.072	-3.140	ab
JM_Shr	-5.106	1.003	Inf	-7.072	-3.140	ab
JM_Col	-5.106	1.003	Inf	-7.072	-3.140	ab
JM_Spi	-4.407	0.711	Inf	-5.801	-3.012	a
AM_Eph	-4.248	1.007	Inf	-6.222	-2.275	abc
AM_Col	-4.248	1.007	Inf	-6.222	-2.275	abc
AF_Sand	-4.094	1.008	Inf	-6.071	-2.118	abc
AF_Col	-4.094	1.008	Inf	-6.071	-2.118	abc
AF_Ant	-4.094	1.008	Inf	-6.071	-2.118	abc
JM_Mol	-3.701	0.506	Inf	-4.693	-2.709	a
JM_Eph	-3.701	0.506	Inf	-4.693	-2.709	a
JF_Hem	-3.526	1.015	Inf	-5.515	-1.538	abcde
JF_Sand	-2.803	0.728	Inf	-4.231	-1.376	abc
AF_Ua	-2.657	0.517	Inf	-3.671	-1.643	ab
AM_Ua	-2.580	0.464	Inf	-3.489	-1.671	ab
AM_Mol	-2.580	0.464	Inf	-3.489	-1.671	ab
JM_Ua	-2.465	0.289	Inf	-3.032	-1.899	ab
JM_Sand	-2.465	0.289	Inf	-3.032	-1.899	ab
AM_Sand	-2.383	0.427	Inf	-3.219	-1.546	ab
AF_Det	-1,306	0.313	Inf	-1,919	-0.693	bc
AF_Plan	-1,034	0.291	Inf	-1,605	-0.464	bcd
JM_Det	-0.267	0.157	Inf	-0.574	0.040	cdef
AM_Det	-0.141	0.238	Inf	-0.607	0.325	cdefg
JM_Plan	0.218	0.156	Inf	-0.088	0.524	defg
AM_Plan	0.549	0.246	Inf	0.066	1.031	Efg

JF_Det	1.386	0.423	Inf	0.558	2.215	fg
JF_Plan	2.803	0.728	Inf	1.376	4.231	g

Capítulo 3

Niche differentiation between two sympatric decapod species: insights from carbon and nitrogen stable isotopes

Abstract

Decapods are abundant and diverse, playing significant ecological roles in freshwater ecosystems. Further, additional research on their trophic ecology and interactions is crucial. Stable isotopes, especially carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), offer valuable insights into their food consumption, ecological niches, trophic positions, and interspecific interactions. The aim of this study was to investigate isotopic signatures, niche overlap, and trophic interactions between crab *Dilocarcinus pagei* (Trichodactylidae) and shrimp *Macrobrachium pantanalense* (Palaemonidae), in the Araguari River in the Brazilian Cerrado. Sampling was carried out during the dry season (June 2022) and included potential food sources for decapods. The samples were dried and homogenized, and isotopic ratios were determined using Continuous Flow Isotope Ratio Mass Spectrometry for stable isotope analysis. Carbon and nitrogen isotopic compositions were plotted on a bi-plot graph to evaluate the trophic structure and interactions between the decapod species and their resources. Additionally, the isotopic niche (evaluated through the Standard Ellipse Area - SEA) was calculated to assess niche size and overlap among species, while the trophic position was determined to identify the trophic levels of each species. *Dilocarcinus pagei* exhibited a greater variation in $\delta^{13}\text{C}$ values, resulting in a larger isotopic niche (SEA = 12.91) than *M. pantanalense* (SEA = 3.55). This outcome implies that *D. pagei* exploits a broader range of resources within the ecosystem. In addition, the niche overlap between the two species was relatively low, suggesting that *D. pagei* and *M. pantanalense* feed differently and likely utilize different

habitats or carbon sources. The enriched $\delta^{15}\text{N}$ values observed in *M. pantanalense* compared to *D. pagei* indicate significant differences in trophic hierarchy, indicating that *M. pantanalense* feeds at higher trophic levels and may consume more nitrogen-rich prey. These findings enhance our understanding of the trophic ecology and interactions between these two species, highlighting the importance of niche differentiation for their coexistence.

Keywords: Stable isotopes; food web; aquatic environments; crustacean; diets

Resumo

Os decápodes são abundantes e diversos, desempenhando papéis ecológicos significativos nos ecossistemas de água doce. Além disso, pesquisas adicionais sobre sua ecologia trófica e interações são cruciais. Isótopos estáveis, especialmente carbono ($\delta^{13}\text{C}$) e nitrogênio ($\delta^{15}\text{N}$), oferecem informações valiosas sobre seu consumo alimentar, nichos ecológicos, posições tróficas e interações interespecíficas. O objetivo deste estudo foi investigar assinaturas isotópicas, sobreposição de nichos e interações tróficas entre o caranguejo *Dilocarcinus pagei* (Trichodactylidae) e o camarão *Macrobrachium pantanalense* (Palaemonidae), no rio Araguari, no Cerrado brasileiro. A amostragem foi realizada durante a estação seca (junho de 2022) e incluiu potenciais fontes de alimento para decápodes. As amostras foram secas e homogeneizadas, e as razões isotópicas foram determinadas usando espectrometria de massa de razão isotópica de fluxo contínuo para análise de isótopos estáveis. As composições isotópicas de carbono e nitrogênio foram plotadas em um gráfico bi-plot para avaliar a estrutura trófica e as interações entre as espécies de decápodes e seus recursos. Adicionalmente, o nicho isotópico (avaliado através da Standard Ellipse Area - SEA) foi calculado para avaliar o tamanho do nicho e a sobreposição entre as espécies. *Dilocarcinus pagei* exibiu uma maior variação nos valores de $\delta^{13}\text{C}$, resultando em um nicho isotópico (SEA = 12.91) maior do que o de *M. pantanalense* (SEA = 3.55). Esse resultado sugere que *D. pagei* explora uma gama mais ampla de recursos dentro do ecossistema. Além disso, a sobreposição de nicho entre as duas espécies foi relativamente baixa, sugerindo que *D. pagei* e *M. pantanalense* possuem estratégias alimentares distintas e provavelmente utilizam habitats ou fontes de carbono diferentes. Os valores enriquecidos de $\delta^{15}\text{N}$ observados em *M. pantanalense* em comparação com *D. pagei* indicam diferenças significativas em suas hierarquias tróficas, sugerindo que *M. pantanalense* se alimenta em níveis tróficos mais altos e pode consumir

presas mais ricas em nitrogênio. Esses achados ampliam nossa compreensão sobre a ecologia trófica e as interações entre essas duas espécies, destacando a importância da diferenciação de nicho para sua coexistência.

Palavras chaves: Isótopos estáveis; rede alimentar; ambientes aquáticos; crustáceos; dietas

Introduction

In tropical rivers, decapod crustaceans, such as crabs and shrimps, are numerically dominant and play a crucial role in aquatic food webs, contributing to the trophic ecology of these environments (Collins et al., 2007; Wantzen et al., 2016). These organisms are typically found in floodplains rich in aquatic vegetation, which serve as essential refuges and primary food sources (Burns & Walker, 2000). Acting as detritivores, primary and secondary consumers, and occasionally as predators or prey, decapods are vital in transferring energy and nutrients along the food chain (Collins et al., 2007). Through these roles, decapods can regulate the availability of resources across different trophic levels, influencing the structure and function of aquatic ecosystems (Cumberlidge, 2014; Mao et al., 2016; Toh et al., 2022).

In South America, the decapod families Trichodactylidae and Palaemonidae are well represented and are known for their high densities and significant contribution to the trophic structure of local aquatic habitats (Collins et al., 2012). Among the species in these families are the crab *Dilocarcinus pagei* Stimpson, 1861 (Trichodactylidae) and the shrimp *Macrobrachium pantanalense* (Palaemonidae). *Dilocarcinus pagei* is native to the Amazon basin, Paraguay and the lower Paraná (Magalhães, 2003; Herrera et al., 2013), while *M. pantanalense* is originally found in the upper Paraguay basin, particularly in the Pantanal region (Dos Santos et al., 2013; Soares et al., 2017).

Demonstrating considerable ecological adaptability, *D. pagei* has established itself in various Brazilian river basins, including the Upper Paraná Basin (Pinheiro & Taddei, 2005; Darim et al., 2007; Azevedo-Santos & Lima-Stripari, 2010; Taddei & Herrera, 2010; Davanso et al., 2013, 2016; Herrera et al., 2013; Taddei et al., 2015; Garcia et al., 2021; Barboza et al., 2023; da Silva & Nogueira, 2023), where it may have been introduced through sport fishing activities or accidentally transported with the roots of

aquatic macrophytes or by other anthropogenic actions (Magalhães, 2003; Magalhães et al., 2005, 2016; Silva-Junior et al., 2017).

Dilocarcinus pagei and *M. pantanalense* have significant economic value. *Dilocarcinus pagei* has an optimal potential for aquaculture and is used as a fishery resource in the Amazon region (Sant'Anna et al., 2015; Viana, 2019). In the same way, *M. pantanalense* is widely used in commercial fishing, aquaculture, and aquarism (David et al., 2021; Hooper et al., 2023). Additionally, it is recognized as an important environmental indicator because of its sensitivity to anthropogenic changes and its role in the food chain (Freitas et al., 2021).

Recently, *D. pagei* and *M. pantanalense* were reported in the Araguari River, in the upper Paraná basin, by Barboza et al. (2023) and Calixto-Cunha et al. (2021), respectively. The Araguari River has a significant history of cascade dams, which have led to the formation of reservoirs and various environmental impacts, such as flooding of areas, suppression of riparian and aquatic vegetation, changes in hydrodynamics and increased nutrient availability (Santiago do Vale et al., 2021). These changes have created opportunities for invasive species from the Asian continent, such as the golden mussel *Limnoperna fortunei* Dunker, 1856 (Linares et al., 2017), the Asian clam *Corbicula fluminea* Müller, 1774 (Maroneze et al., 2011; Linares et al., 2017) and *Melanoides tuberculata* Müller, 1774 (Maroneze et al., 2011; Martins et al., 2015), which have established populations in the river. Mussels, *L. fortunei*, readily encrust in the pipelines of hydropower plants, leading to significant socio-economic impacts (Mansur et al., 2004; Darrigran et al., 2020). In addition, these organisms, including Asian clam, cause significant ecological impacts, including changes in substrate composition, where they act as ecosystem engineers, and changes in nutrient availability and water quality, which in turn affect the biological communities that depend on these habitats (Robinson &

Wellborn, 1988; Voelz et al., 1998; Ricciardi, 1998; Cataldo & Boltovskoy, 1998; De Oliveira et al., 2006; Pimpão & Martins, 2008; Boltovskoy & Cataldo, 2009; Darrigran & Damborenea, 2011; Lucy et al., 2012; Barbosa et al., 2018; Fortunato et al., 2022; Linares et al., 2019).

These molluscs are known to be part of the diet of various predators, including decapods (Dudgeon & Catherine, 1990; Torres et al., 2012; Carvalho et al., 2013; Quinn, 2020). For instance, *D. pagei* feeds primarily on plant material and organic detritus, but occasionally also on small invertebrates (Williner & Collins, 2002; Viana et al., 2023; author's personal observation - unpublished data), and potentially invasive molluscs (author's personal observation - unpublished data), as has also been observed in other freshwater crabs (Rudnick, 2005; Sylvester et al., 2007). Experimental studies have demonstrated the importance of *L. fortunei* as a food source for various species of freshwater crabs. Torres et al. (2012), showed that *L. fortunei* was selected in different sizes and included in the diet of the crab *Zilchiopsis collastinensis* Pretzmann, 1968. Complementing these results, Carvalho et al. (2013) confirmed the same for *Trichodactylus borellianus* Nobili 1896.

In contrast, the natural diet of *M. pantanalense* was still unknown at the time of this study. It is expected that it does not differ significantly from that of its close relative, *Macrobrachium amazonicum* Heller 1862, due to the close phylogenetic relationship (Calixto-Cunha et al., 2021). This species is known for their varied diet, reflecting an adaptation to the available resources in the aquatic environment. *Macrobrachium amazonicum* consumes a higher proportion of aquatic invertebrates, such as insect larvae, depending on their availability in the habitat (da Cruz et al., 2023).

Omnivorous benthic decapods facilitate the flow of energy between different trophic levels by occupying multiple trophic levels and integrating into the food web

(Simon et al., 2019) and contribute to the regulation of prey populations by avoiding outbreaks that could destabilize the ecosystem (Collins et al., 2012). The coexistence of species such as the decapods in the Araguari River and their dietary adaptations provides an opportunity to study niche overlap and competition for resources in this ecosystem (Lawlor, 1980; Siqueira et al., 2009; Hill et al., 2015; De Castro et al., 2016; Galvez et al., 2022). Niche overlap, including the trophic positions species occupy, within the food web is an important aspect of community structure and can be studied using stable isotope analysis (Lawlor, 1980; Wada et al., 1991; Rudnick & Resh, 2005; Jackson et al., 2011). This method provides information on the isotopic signatures of species, reflecting their diet and habitat use, by examining differences in the isotopic ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) (Wada et al., 1991).

Therefore, the aim of this study was to investigate the trophic ecology of decapod species in the Araguari River, Minas Gerais, Brazil, by analyzing stable isotopes of carbon and nitrogen. Specifically, our study analyzed the stable isotope signatures of two decapod species to understand how differences in their diets are reflected in their isotopic compositions, and what this reveal about their niche differentiation and trophic position. To answer these questions, we tested the following hypotheses: i) *Dilocarcinus pagei* and *M. pantanalense* exhibit differences in $\delta^{13}\text{C}$ signatures that reflect their different food sources. It is expected that the $\delta^{13}\text{C}$ signatures of *D. pagei*, which consumes more plant material, reflect aquatic plant sources, while the $\delta^{13}\text{C}$ signatures of *M. pantanalense*, which eats more invertebrates, are closer to those of aquatic consumers. ii) We expect a low niche overlap between these two decapod species due to their different diets; iii) We hypothesize that if *D. pagei* consumes mainly plant material, exhibiting lower $\delta^{15}\text{N}$ ratios indicating a lower trophic position in the Araguari River ecosystem. In contrast, if *M. pantanalense* relies more on animal resources than *D. pagei*, it will present higher $\delta^{15}\text{N}$

ratios, reflecting its higher trophic level; iv) If *D. pagei* eats invasive mussels and gastropods, its $\delta^{13}\text{C}$ signature will match that of the mussels, indicating a similarity in $\delta^{13}\text{C}$ values.

Materials and methods

Study area

The study area is located along the lower Araguari River, 30 km upstream of its confluence with the Paranaíba River and 50 km downstream of the Amador Aguiar II (AA II) dam in Minas Gerais, Brazil (Figure 1). The Araguari River has its headwaters in the heights of the Serra da Canastra National Park, situated within the Brazilian Cerrado biome and the Paraná basin (Alvares et al., 2013; Beck et al., 2018). The area is characterized by a Köppen Cw climate, which is described as semi-humid tropical with an average temperature of 23°C. There are dry months from April to September, followed by humid months from October to March (Rodrigues & Silva, 2012).

The Araguari River is influenced by four cascade dams (Amador Aguiar I, Amador Aguiar II, Nova Ponte and Miranda) built for hydroelectric power generation, which have altered its hydrological system. These structures regulate water flow, influence the dynamics of floods and droughts, and define the characteristics of the wetland area within the floodplain.

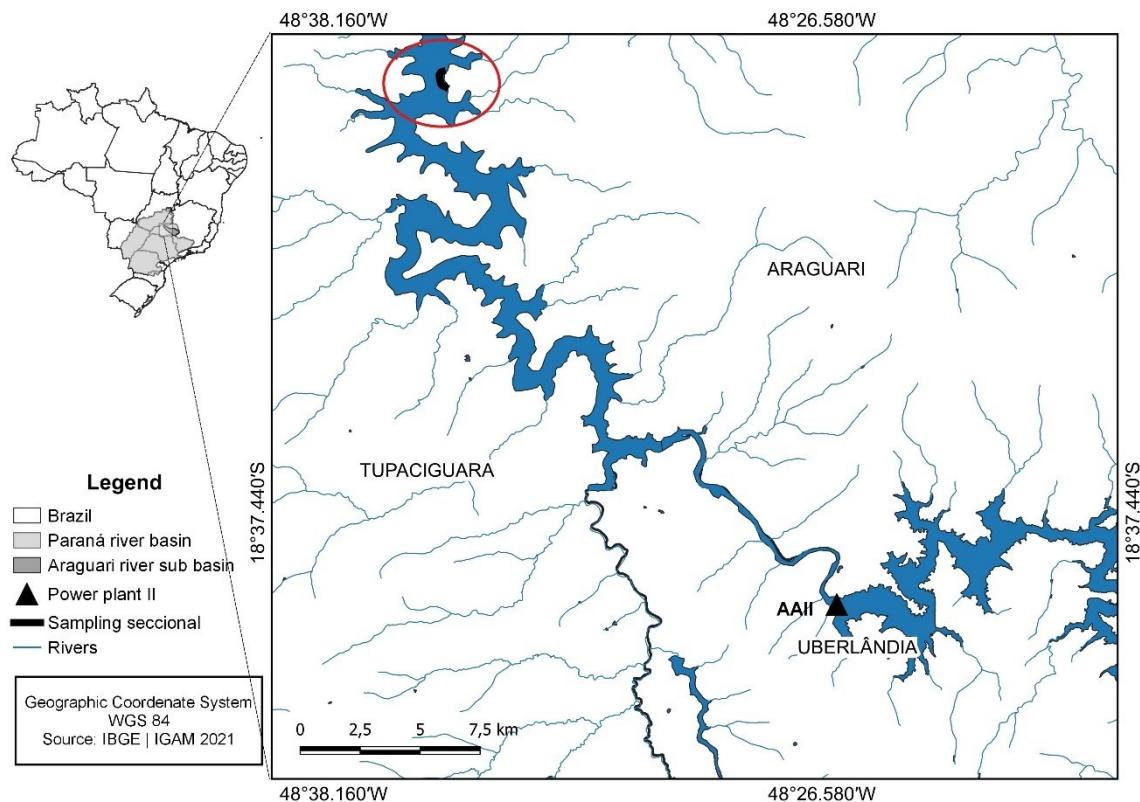


Figure 1. The red circle shows the sampled section in the Araguari River, Minas Gerais, Brazil, which marks the study area between -18.4544°S , -48.5925°W and -18.4497°S , -48.5916°W .

In this area there are remnants of Cerrado biome forests in the upper floodplain, but the riparian vegetation in the lower areas has been displaced by the flooding of the Itumbiara/Furnas hydroelectric plant on the Paranaíba River in the 1980s (Santiago do Vale et al., 2021) and also, by the impact of four cascade dams upstream on the Araguari River. The land is mainly used for grazing and shows signs of degradation such as exposed soils and contraction fissures during river water recession. Various angiosperms dominate the land-water interface (author's personal observation), including grasses (Poaceae family), pteridophytes such as *Salvinia* sp. (Salviniaceae family) and macrophytes such as *Eichhornia crassipes* (Pontederiaceae family), which respond to water level changes. Non-native mollusc species such as *Limnoperna fortunei* (golden

mussel), *Corbicula fluminea* (Asian clam) and *Melanoides tuberculata* were also observed in the area.

Sampling

Sampling was conducted once during the dry season (June) in 2022. Our sampling for isotopic analysis included organisms that could represent potential resources in the decapod crustacean food web, such as benthic insects, molluscs, aquatic plants, and terrestrial plants (see Table 1). This method allowed us to focus on the decapods while considering the broader context of their food chain and sources from aquatic and terrestrial environments. Availability of food resources was sampled simultaneously with the collection of decapods (see supplementary material Table S1).

Table 1. Number of samples collected for isotopic analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) during the dry season (June 2022) in the Araguari River, Minas Gerais, Brazil.

Category	N sample ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$)
Decapoda	
<i>Dilocarcinus pagei</i> Stimpson, 1861	7
<i>Macrobrachium pantanalense</i> Dos Santos, Hayd & Anger, 2013	7
Food Resources	
Benthic insect larvae (Mixing: Aeshnidae+Libellulidae+Hemiptera)	5
<i>Corbicula fluminea</i> Müller, 1774	5
<i>Limnoperna fortunei</i> Dunker, 1857	5
<i>Melanoides tuberculata</i> Müller, 1774	5
Aquatic plant (Mixing: <i>Eichhornia crassipes</i> + <i>Salvinia sp.</i>)	5
Terrestrial plant (Mixing: <i>Alberta edulis</i> + <i>Annona crassifolia</i> + <i>Hirtella gracilipes</i>)	5

For decapods, such as the crab *Dilocarcinus pagei*, we used manual collection methods and a sieve (3 mm mesh size) for both *D. pagei* and *M. pantanalense*, targeting

individuals hidden in aquatic vegetation or under leaf litter in the riverbed. All collected decapods were adults

Benthic insects and molluscs were sampled with a D-frame (30 cm opening, 250 µm mesh) and an area of 0.09 m² (Peck et al., 2006). Sampling occurred from downstream to upstream, following a zigzag route along the substrate and among aquatic plants where these organisms are commonly found (Castro et al., 2017). Both terrestrial and aquatic plants (fresh leaves) were collected by hand, and the species were placed in plastic bags individually. Subsequently, all captured invertebrates were stored in a thermal container with ice and transported together with the plants to the Laboratory of Aquatic Ecosystem Ecology (LEEA/UFU). For the taxonomic identification of organisms, we relied on specific literature, including Melo (2003) for crustaceans and taxonomic keys for benthic invertebrates (Hamada et al., 2014; Mugnai et al., 2010). Molluscs were sent to the Zoological Museum of the USP (MZUSP) for identification, and plants were identified with the help of specialists from the Department of Botany of the Federal University of Uberlândia.

Stable isotope analysis

For isotope analysis, we extract at least 2-5 mg of animal tissue (muscle tissue), and 5-10 mg of aquatic and terrestrial plant samples, which were dried for 48 hours at 50°C (de Carvalho et al., 2019). Subsequently, the samples were stored in Eppendorf tubes and sent to the Stable Isotopes Center (CEI) at Paulista State University (UNESP) in Botucatu, São Paulo. At the CEI, the samples were homogenized using a cryogenic mill (Geno/Grinder 2010 – SPEX SamplePrep, USA), and a 0.800 to 1.200 mg aliquot was weighed into 5.0 x 8.0 mm tin capsules using a balance with a 0.001 mg resolution

(XP6 – Mettler Toledo, Switzerland). The drying and homogenization of the samples were necessary to obtain representative aliquots of dry mass in the capsules.

To determine the stable isotope ratio, encapsulated samples were analyzed using a continuous-flow isotope ratio mass spectrometry system (CF-IRMS) comprising an IRMS (Delta V, Thermo Scientific, Germany) coupled to an elemental analyzer EA (Flash 2000, Thermo Scientific, Germany) through a gas interface (ConFlo IV, Thermo Scientific, Germany). The CF-IRMS determined the isotopic ratios of stable nitrogen R($^{15}\text{N}/^{14}\text{N}$) and carbon R ($^{13}\text{C}/^{12}\text{C}$), which were expressed as relative differences in isotopic ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) based on international standards PeeDeeBelemnite (VPDB) e Air (atmospheric Nitrogen), as per equations 1 and 2, respectively (Coplen, 2011). For each element, CF-IRMS also determined the levels of total nitrogen (TN) and total organic carbon (TOC), expressed in relation to dry mass, as per equations 3 and 4.

$$(1) \delta^{15}\text{N}_{(\%)} = \frac{R\left(\frac{^{15}\text{N}}{^{14}\text{N}}\right)_{\text{sample}}}{R\left(\frac{^{15}\text{N}}{^{14}\text{N}}\right)_{\text{Air}}} - 1 \quad (2) \delta^{13}\text{C}_{(\%)} = \frac{R\left(\frac{^{13}\text{C}}{^{12}\text{C}}\right)_{\text{sample}}}{R\left(\frac{^{13}\text{C}}{^{12}\text{C}}\right)_{\text{VPDB}}} - 1$$

$$(3) TN_{(\%)} = \frac{\text{nitrogen mass}}{\text{dry mass}} \quad (4) TOC_{(\%)} = \frac{\text{organic carbon mass}}{\text{dry mass}}$$

The results were standardized using the NBS-22 and IAEA-N1 standards. The standard uncertainty of the IRMS for $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ is $\pm 0.15\%$, and for TN or TOC, it is $\pm 0.30\%$. Each isotope value represents a specific measurement of a single.

Data analysis

To investigate the trophic structure of *D. pagei* and *M. pantanalense*, we utilized a four-step approach. **Step 1:** We performed a t-test to determine if there were significant differences in the isotopic compositions of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between the decapod species. This test helped us to determine whether the two species utilize different food resources or occupy different positions within the food chain. **Step 2:** Next, the isotopic compositions of carbon (x-axis) and nitrogen (y-axis) were plotted in a bi-plot graph to assess the trophic structure and interactions between the decapod species and their resources. These plots show the decapod samples along with the means and standard deviations of the potential food resources and provide a clear visualization of the isotopic relationships between sources and consumers. This method helps to identify key food resources, determine species' positions in the food web and distinguish between species with similar or different diets, providing information on their trophic interactions and food consumption (Wada et al., 1991; McCutchan et al., 2003; Vander Zanden et al., 2015).

Step 3: We calculated the isotopic niche of *D. pagei* and *M. pantanalense* using the Standard Ellipse Area (SEA - expressed in ‰²) to assess niche size and overlap between species. This analysis was performed using the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson, 2011). The application of SEAc (corrected for differences in sample size) improves the accuracy of comparisons by facilitating the assessment of niche differences between species, even when sample sizes vary. The SEAc metric allows us to calculate the degree of niche overlap (as a percentage, where 100% represents complete overlap) and serves as a quantitative measure of dietary similarity between different species (Hill et al., 2015).

Step 4: Finally, we then calculated the trophic position (T_p) occupied by *D. pagei* and *M. pantanalense*, using the formula described by Vander Zanden et al. (1997): $T_p = [(\delta^{15}\text{N}_{\text{decapod}} - \delta^{15}\text{N}_{\text{resources}}) \div 3.0] + 1$, where $\delta^{15}\text{N}_{\text{decapod}} = \delta^{15}\text{N}$ values of decapod, $\delta^{15}\text{N}_{\text{resources}} = \text{mean values of } \delta^{15}\text{N}$ of basal resources (aquatic plant), 3.0 represents the fractionation per trophic level (McCutchan et al., 2003), and 1 is the position of producers within the food chain. This allows us to compare whether each species feeds at the same trophic levels at the sampling site. To determine if there were significant differences in the trophic levels occupied by the decapods, we performed a t-test.

Results

The isotopic compositions varied between decapods for both carbon ($t = 2.429$, $p = 0.038$) and nitrogen ($t = -2.679$, $p = 0.0218$) (Fig. 2a,b). Stable isotope values of $\delta^{13}\text{C}$ were more enriched for *D. pagei* than for *M. pantanalense*. In contrast, values of $\delta^{15}\text{N}$ were more enriched for *M. pantanalense* than for *D. pagei*.

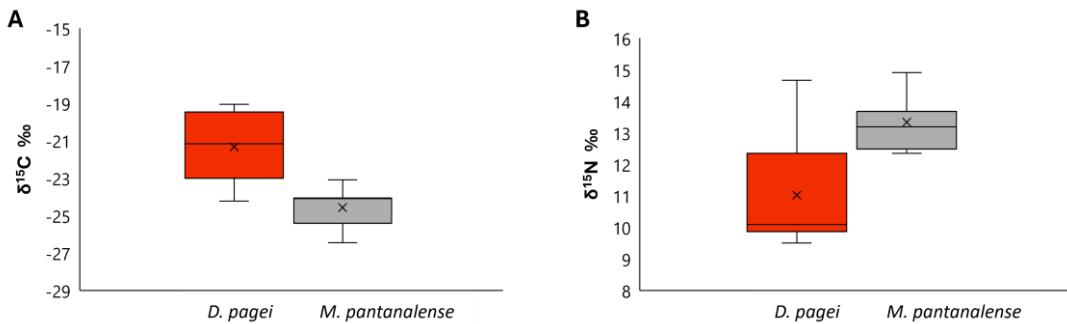


Figure 2. Variation in $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) values of *D. pagei* and *M. pantanalense* in the Araguari River, Minas Gerais, Brazil. The central line represents the median, the box represents the interquartile range (IQR), the whiskers represent the minimum and maximum values, and "X" represents the mean.

Differences between decapod resource utilization were further reflected by their distributions in carbon-nitrogen bi-plot space (Fig. 3), in the amplitude of the isotopic niche (Fig. 4a) and in its trophic position (Fig. 4b).

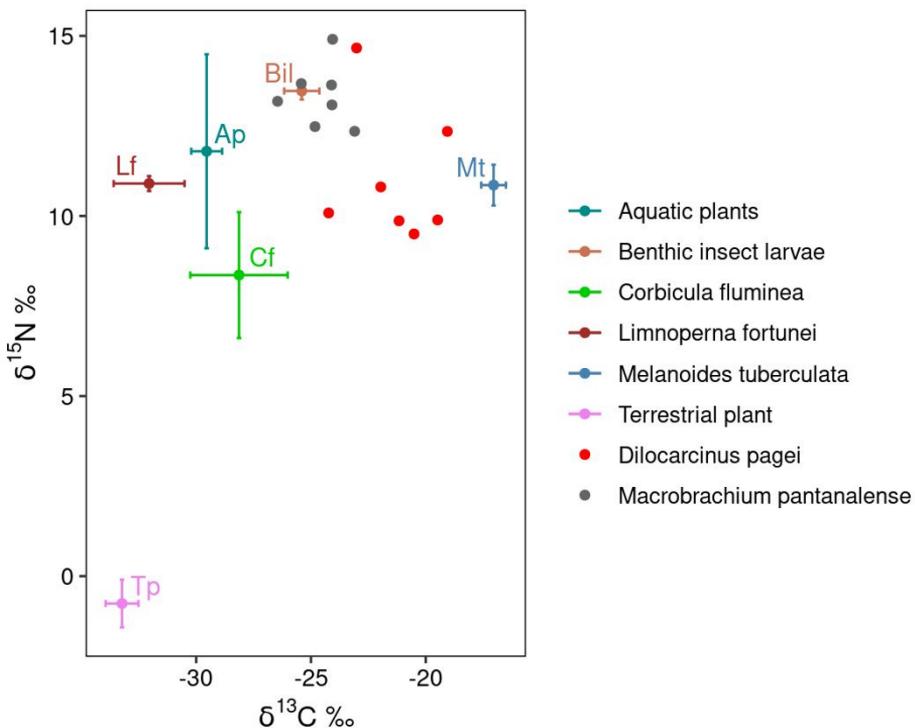


Figure 3. Stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, mean \pm SD) and food web representation (bi-plot space) for decapod species (red and gray symbols) and their potential basal food resources sampled from the Rio Araguari, Minas Gerais, Brazil. (AP = Aquatic plants; Bil = Benthic Insect larvae; Cf = *Corbicula fluminea*; Lf = *Limnoperna fortunei*; Mt = *Melanoides tuberculata*; Tp = Terrestrial plant).

The isotopic niche was wider for *D. pagei* (TA = 17.37; SEA = 10.76; SEAc = 12.91), than for *M. pantanalense* (TA = 4.39; SEA = 2.96; SEAc = 3.56) (Fig. 4a). The niche overlap between the two species was relatively low, with only 20% overlap observed, indicating distinct diets. Regarding trophic hierarchy, *M. pantanalense* displayed higher trophic positions than *D. pagei* ($F = 8.83$, $p = 0.01$) (Fig. 4b).

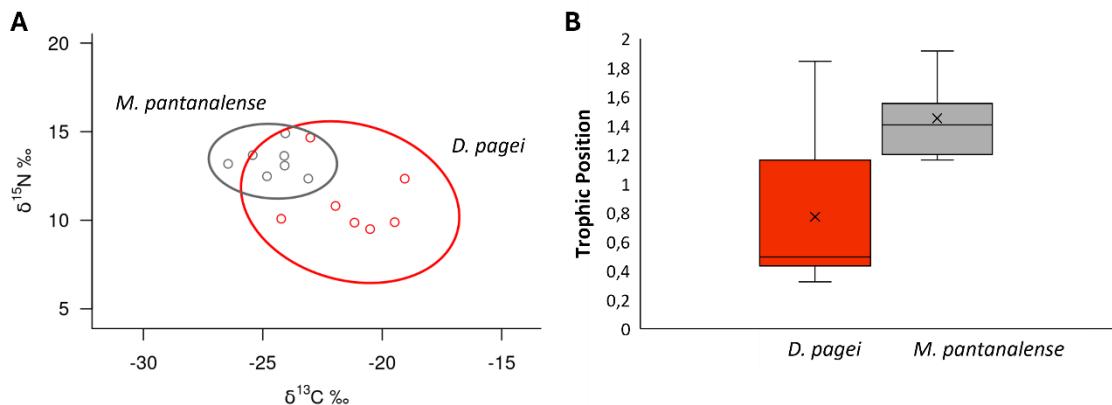


Figure 4. Isotopic niche (**a**) (evaluated by the ellipse area with 95% confidence interval) and trophic position (**b**) of *Dilocarcinus pagei* (red color) and *Macrobrachium pantanalense* (gray color) in the Araguari River, Minas Gerais, Brazil. In (**b**), the central line represents the median, the box represents the interquartile range (IQR), the whiskers represent the minimum and maximum values, and "X" represents the mean.

Discussion

Differences in the $\delta^{13}\text{C}$ isotope signatures

Our first hypothesis that *M. pantanalense* and *D. pagei* would exhibit distinct $\delta^{13}\text{C}$ isotopic signatures reflecting their different food sources was supported. Our results show that *M. pantanalense* has a $\delta^{13}\text{C}$ signature closer to aquatic organisms, with a narrower isotopic range compared to *D. pagei*. Similar to *M. pantanalense*, other species in the genus *Macrobrachium* may have a more specialized diet, with less variation in carbon sources, suggesting a more consistent and specific feeding behavior. Supporting this idea, studies on *M. amazonicum* and *Macrobrachium brasiliense* Heller, 1862 in natural environments highlight the crucial role of aquatic invertebrates in the diet of these species (da Cruz et al., 2021). In particular, *M. brasiliense* shows a notable increase in insect consumption as the shrimp matures suggests an adaptive shift in food sources during

growth. Similarly, an experimental study on *M. amazonicum* found that aquatic invertebrates made a significant contribution to biomass growth, as estimated using stable isotope techniques (Heldt et al., 2019). Other examples, in species like *Macrobrachium hainanense* Parisi, 1919, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic analyses confirm its predatory trophic status, with all life stages exhibiting higher isotopic signatures compared to other sympatric predatory invertebrates (Mantel & Dudgeon, 2004). *Macrobrachium borelli* Nobili, 1896 also displays a varied diet, with a marked tendency towards larger, protein-rich prey, reflecting a distinctly predatory behavior (Collins & Paggi, 1997). *Macrobrachium nipponense* De Haan 1849 in the Anzali Wetland (Iran) has a diet primarily composed of aquatic invertebrates, occupying a high trophic position (TL = 3.38), which reinforces its specialized diet (Mirzajani et al., 2020).

In contrast, *D. pagei* exhibits more enriched $\delta^{13}\text{C}$ isotopic signatures and a broader niche, reflecting a diet composed of a greater diversity of carbon sources. This suggests that *D. pagei* feeds on both aquatic plants and carbon sources derived from lower trophic level aquatic organisms. This interpretation is supported by the significant volume of macrophytes found in the stomachs of *D. pagei* crabs compared to other food items, such as aquatic insects (Chapter 2 of this thesis; Williner & Collins, 2002; Viana et al., 2023). Furthermore, a similar pattern is observed in other members of the Trichodactilidae family, indicating an adaptation to exploit the available plant resources in their environment. Although the isotopic analysis in this study focused on a mixture of two aquatic macrophyte species (*Eichhornia crassipes* and *Salvinia sp.*), whose isotopic signatures do not directly correspond to those observed in *D. pagei*, this discrepancy does not rule out the possibility that *D. pagei* may be utilizing other aquatic plants that were not sampled and analyzed in our study. Alternatively, there may be significant variation within the populations of these macrophytes or in specific parts of the plants that were

not represented in the collected samples. Indeed, the literature indicates that aquatic plants can exhibit considerable isotopic variability, even within a single population, due to differences in microhabitats, access to dissolved inorganic carbon in the water, plant types (C3, C4, CAM), and the influence of environmental factors such as light, temperature, and the presence of organic matter (Osmond et al., 1981; Farquhar et al., 1989). Moreover, isotopic variation observed within the same plant species can exceed 10‰ within a single frond of algae, indicating that plants of the same type and location can contribute to a wide range of $\delta^{13}\text{C}$ values (Osmond et al., 1981; LaZerte & Szalados, 1982).

The broad range of $\delta^{13}\text{C}$ values observed in aquatic plants highlights the complexity of carbon sources available in aquatic environments. In the case of *D. pagei*, this variation suggests that its diet may include a mixture of these plants, each contributing differently to the final isotopic signature observed, resulting in an average signature that does not directly correspond to any specific species. This preference may be related to the abundance or accessibility of these plants in the crab's environment, or perhaps to the ease of processing and digesting these plant sources compared to more complex foods. It is relevant to mention that crustaceans have evolved to host specific endosymbiotic organisms in their digestive tracts, which may facilitate the digestion of plant materials (Štrus et al., 2019; Williner et al., 2013).

In addition to plants, *D. pagei* may include mollusks in its diet, which also contributes to the complexity of its isotopic signature. Filter-feeding mollusks, such as mussels, exhibit a wide range of $\delta^{13}\text{C}$ values that vary significantly depending on the organic particles they filter (Riera et al., 1999). Including these organisms in *D. pagei*'s diet may enrich $\delta^{13}\text{C}$ values, bringing them closer to those of aquatic plants, but with additional variation that could explain the lack of a direct match with the macrophytes

and mussels. Thus, the presence of a diverse range of aquatic plants, each with different isotopic signatures, along with the inclusion of mollusks and aquatic insects in the diet, could explain part of the broad range of $\delta^{13}\text{C}$ values observed in *D. pagei*. These factors emphasize the complexity of its diet and its ability to exploit different ecological niches, characterizing it as an opportunistic omnivorous species.

Isotopic Niche Overlap

The second hypothesis predicted a low isotopic niche overlap between the two decapod species due to expected dietary differences. The results support this, showing a 20% overlap in isotopic space, indicating that the species utilize different trophic niches. *Dilocarcinus pagei* exhibits a broader niche breadth, likely due to its consumption of a diverse range of food resources, including plant material, invertebrates, and detritus, as indicated in Chapter 2. In contrast, *M. pantanalense* shows a more specialized diet, reflected in its narrower isotopic niche breadth. The higher consumption of aquatic plants by *D. pagei* and the greater reliance on insects by *M. pantanalense* (Barboza et al., 2023) further support these dietary distinctions, with *M. pantanalense* demonstrating a stronger dependence on animal-derived resources in the Araguari River.

Trophic level and $\delta^{15}\text{N}$ isotope signatures

The third hypothesis predicted that *M. pantanalense* would exhibit higher $\delta^{15}\text{N}$ isotope ratios than *D. pagei*, reflecting a higher trophic position due to its greater dependence on animal resources. The data confirmed this, with *M. pantanalense* having elevated $\delta^{15}\text{N}$ values, indicating its superior trophic niche. This is consistent with the stomach content analysis, where *D. pagei* had a higher frequency of occurrence (FO) of aquatic plants (46.61%), while *M. pantanalense* was more dependent on insects, similar

to *M. brasiliense*, which had the highest FO of insects (40.42%) compared to other species (Barboza et al., 2023). These results emphasize the dietary differences between the species, with *M. pantanalense* occupying a higher trophic level due to its consumption of animal resources, while *D. pagei* is more dependent on plant material.

Additional studies by da Cruz et al. (2021, 2023) also investigated the diets of *M. brasiliense* and *M. amazonicum*, highlighting the importance of insects in the diet of these species, particularly in habitats where animal resources are abundant. These studies underscore that an omnivorous diet, with a strong inclination toward animal resources, is a critical factor for the elevated trophic position of these species in aquatic ecosystems. Furthermore, stable isotope analysis of *M. amazonicum* revealed that this species occupies a higher trophic position within tropical stream ecosystems (Heldt et al., 2019; Winemiller et al., 2011). These findings corroborate the notion that species within the genus *Macrobrachium*, despite having variations in their diets, including *M. pantanalense*, can play crucial roles as predators and processors of organic matter in their natural habitats, occupying elevated trophic levels.

Consumption of invasive molluscs by D. pagei

Finally, the fourth hypothesis states that if *D. pagei* consumed invasive molluscs, its $\delta^{13}\text{C}$ signatures would reflect these food sources. Although the specific consumption of invasive molluscs was not directly associated with the items (prey) collected, the broad isotopic spectrum of $\delta^{13}\text{C}$ observed in *D. pagei* could indicate the ingestion of various carbon sources, possibly including molluscs. This possibility is supported by evidence of molluscan feeding by other species in the family Trichodactylidae. For example, *Zilchiopsis collastinensis* and *Trichodactylus borellianus* have been documented as a selective predator of the invasive bivalve *Limnoperna fortunei* (Torres et al., 2012;

Carvalho et al., 2013). In addition, *T. borellianus* was found to be an epibiont of this mussel, suggesting a complex interaction between these species (Molina & Williner, 2014).

In our study on the diet of *D. pagei* (Chapter 2 of this thesis), we observed the presence of shell fragments from the golden mussel *Limnoperna fortunei* in the stomach contents of some individuals, particularly during the dry season (early June). Our sampling of organisms for isotope analysis also took place during the dry season. According to Viozzi, et al. (2021) the isotopic incorporation rate of carbon (τ) for $\delta^{13}\text{C}$ in the muscles of shrimps (*Macrobrachium borellii*), is about 75.8 days. This means that the muscles primarily reflect what the organism has metabolized over a long period, especially in ectotherms like crustaceans (Vander Zanden et al., 2015). Although this test was performed in shrimp, given the physiological similarities between decapod crustaceans, this rate of incorporation may be a useful reference for interpreting the results in crabs (Peterson & Fry, 1987; Fry & Sherr, 1989).

Considering this, it is likely that the carbon signature observed in *D. pagei* reflects feeding during the rainy season (March), when more plant material is available for *D. pagei* to consume in higher quantities (Williner & Collins, 2002; unpublished data by the author). The isotopic composition could therefore represent an average value for the crab's diet during this period, reflecting the most abundant and consistent food sources. However, further specific studies on the isotopic incorporation rate in crabs would be necessary to confirm whether this estimate based on shrimp can be directly applied to *D. pagei*.

Conclusion

The results presented confirm many of the hypotheses formulated and illustrate the complexity of trophic interactions for *M. pantanalense* and *D. pagei*. The marked difference in trophic levels and niche breadth suggests that these two species coexist by minimizing direct competition and exploiting different food resources in the Araguari River ecosystem. These results contribute to a better understanding of the trophic ecology of decapod species in tropical aquatic systems and may inform management and conservation strategies, particularly in contexts where invasive species introductions and habitat modification have significant impacts.

Limitations and future directions

This study encountered some limitations that may have affected the ability to establish clear relationships between decapod species and their food resources. One of the main limitations was the scale of sampling, which may not have been comprehensive enough to capture the full range of potential food sources (or proper prey collection) in the ecosystem. In addition, the methods used in this study to infer trophic interactions between species (such as isotope signature analysis) provide valuable information but may not be sufficient to capture the full complexity of feeding relationships within the ecosystem. Future research could consider expanding sampling and applying complementary approaches, such as refining direct stomach content analysis, using molecular techniques to identify specific food sources more accurately, or conducting laboratory and field experiments to better understand the trophic ecology of species in the Araguari River ecosystem.

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Disclosure statement

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Supplementary material

Table S1. Results of isotopic analyses performed by the Stable Isotope Center (CEI). N = sample number; NT (%) = Percentage of Total Nitrogen in relation to the mass of the sample (with an uncertainty of $\pm 0.20\%$); $\delta^{15}\text{N}$ (‰) = Relative difference in the isotopic ratio or δ -value (with an uncertainty of $\pm 0.15\%$); TOC (%) = Percentage of Total Organic Carbon in relation to the mass of the sample (with an uncertainty of $\pm 0.20\%$); $\delta^{13}\text{C}$ (‰) = Relative difference in the isotopic ratio or δ -value (with an uncertainty of $\pm 0.15\%$).

Decapoda	N	NT	$\delta^{15}\text{N}$	COT	$\delta^{13}\text{C}$
<i>Dilocarcinus pagei</i>	1	16.13	9.89	48.52	-19.48
<i>Dilocarcinus pagei</i>	2	16.67	10.08	49.83	-24.23
<i>Dilocarcinus pagei</i>	3	16.44	9.50	51.39	-20.51
<i>Dilocarcinus pagei</i>	4	16.38	10.81	50.96	-21.96
<i>Dilocarcinus pagei</i>	5	16.57	9.87	48.63	-21.16
<i>Dilocarcinus pagei</i>	6	16.18	12.35	47.85	-19.06
<i>Dilocarcinus pagei</i>	7	11.85	14.66	33.17	-23.01
<i>Macrobrachium pantanalense</i>	8	16.04	13.18	51.18	-26.45
<i>Macrobrachium pantanalense</i>	9	16.32	12.35	49.59	-23.10
<i>Macrobrachium pantanalense</i>	10	16.03	13.08	49.70	-24.09
<i>Macrobrachium pantanalense</i>	11	14.39	12.48	44.45	-24.83
<i>Macrobrachium pantanalense</i>	12	15.80	14.91	49.20	-24.06
<i>Macrobrachium pantanalense</i>	13	15.47	13.64	45.53	-24.10
<i>Macrobrachium pantanalense</i>	14	15.26	13.68	48.50	-25.42

Food resources

Benthic insect larvae (Mixing: Aeshnidae+Libellulidae+Hemiptera)	15	13.35	13.39	50.29	-26.73
Benthic insect larvae (Mixing: Aeshnidae+Libellulidae+Hemiptera)	16	10.50	13.36	39.48	-24.80
Benthic insect larvae (Mixing: Aeshnidae+Libellulidae+Hemiptera)	17	11.33	13.30	42.24	-25.18
Benthic insect larvae (Mixing: Aeshnidae+Libellulidae+Hemiptera)	18	14.57	13.89	51.71	-25.03
Benthic insect larvae (Mixing: Aeshnidae+Libellulidae+Hemiptera)	19	13.43	13.43	47.09	-25.26
Aquatic plants (Mixing: <i>Eichhornia crassipes</i> + <i>Salvinia</i> sp.)	20	4.59	16.60	53.56	-30.53
Aquatic plants (Mixing: <i>Eichhornia crassipes</i> + <i>Salvinia</i> sp.)	21	4.39	10.31	47.85	-28.85
Aquatic plants (Mixing: <i>Eichhornia crassipes</i> + <i>Salvinia</i> sp.)	22	4.11	10.84	44.84	-29.06
Aquatic plants (Mixing: <i>Eichhornia crassipes</i> + <i>Salvinia</i> sp.)	23	4.21	10.79	47.75	-29.88
Aquatic plants (Mixing: <i>Eichhornia crassipes</i> + <i>Salvinia</i> sp.)	24	4.42	10.44	53.90	-29.41
Terrestrial plant (Mixing: <i>Alberta edulis</i> + <i>Annona crassifolia</i> + <i>Hirtella gracilipes</i>)	25	1.10	0.21	44.42	-32.26

Terrestrial plant (Mixing: <i>Alberta edulis</i> + <i>Annona crassifolia</i> + <i>Hirtella gracilipes</i>)	26	3.83	-1.30	49.01	-32.73
Terrestrial plant (Mixing: <i>Alberta edulis</i> + <i>Annona crassifolia</i> + <i>Hirtella gracilipes</i>)	27	4.03	-1.23	67.31	-33.46
Terrestrial plant (Mixing: <i>Alberta edulis</i> + <i>Annona crassifolia</i> + <i>Hirtella gracilipes</i>)	28	4.08	-0.35	63.63	-33.73
Terrestrial plant (Mixing: <i>Alberta edulis</i> + <i>Annona crassifolia</i> + <i>Hirtella gracilipes</i>)	29	3.90	-1.14	68.47	-33.97
<i>Melanoides tuberculata</i>	30	15.26	11.64	49.30	-16.60
<i>Melanoides tuberculata</i>	31	8.40	10.58	32.55	-16.82
<i>Melanoides tuberculata</i>	32	10.55	10.31	39.27	-17.50
<i>Melanoides tuberculata</i>	33	10.56	10.50	41.06	-16.56
<i>Melanoides tuberculata</i>	34	10.99	11.26	44.12	-17.73
<i>Limnoperna fortunei</i>	35	11.02	10.82	59.10	-34.77
<i>Limnoperna fortunei</i>	36	13.74	10.98	51.05	-31.03
<i>Limnoperna fortunei</i>	37	13.54	10.61	49.56	-31.22
<i>Limnoperna fortunei</i>	38	14.18	10.92	50.64	-31.71
<i>Limnoperna fortunei</i>	39	13.99	11.17	51.29	-31.54
<i>Corbicula fluminea</i>	40	11.27	11.35	42.59	-31.88
<i>Corbicula fluminea</i>	41	12.08	7.27	51.27	-27.19
<i>Corbicula fluminea</i>	42	13.58	7.41	50.69	-27.18
<i>Corbicula fluminea</i>	43	14.08	8.48	50.88	-27.70

Corbicula flumínea 44 13.02 7.29 53.60 -26.73

Conclusão geral

Os estudos apresentados nesta tese fornecem insights sobre a biologia populacional e os hábitos alimentares do caranguejo de água doce *Dilocarcinus pagei*, além de investigar a dieta e as interações tróficas de *D. pagei* e *Macrobrachium pantanalense* sob a perspectiva da análise de isótopos estáveis, em um trecho de amostragem do rio Araguari.

A estrutura populacional de *D. pagei* varia ao longo do ano e é influenciada por fatores ambientais como precipitação e níveis de água do reservatório. A variação na composição populacional, particularmente a ocorrência sazonal de fêmeas ovígeras, indica que a reprodução nesta espécie é um evento sazonal associado ao aumento das chuvas. Esses achados ampliam a compreensão das características reprodutivas dos caranguejos de água doce e do papel ecológico desta espécie nos ambientes que habita.

Em termos de ecologia trófica, a pesquisa sobre a dieta alimentar de *D. pagei* revelou os hábitos alimentares, evidenciando a influência de diferentes grupos demográficos e variações sazonais em sua dieta. O estudo destacou o consumo de tecidos vegetais, a predação de moluscos e a ingestão de microplásticos.

Por fim, a análise das interações tróficas de *D. pagei* e *M. pantanalense* revelou a complexidade dessas interações em sistemas aquáticos tropicais. As diferenças na amplitude dos nichos e dos níveis tróficos são indicativas de que essas espécies coexistem minimizando a competição direta e utilizando diferentes recursos alimentares, ampliando nossa compreensão sobre a ecologia trófica dessas duas espécies, destacando a importância da diferenciação de nicho para sua coexistência.

Em termos gerais, pesquisas sobre biologia populacional e ecologia trófica das espécies podem ser utilizadas como base para estratégias de manejo e conservação dos

ecossistemas aquáticos dulcícolas, particularmente no contexto de introduções de espécies invasoras e modificação de habitats.

Sugestões para pesquisas futuras

1. **Impactos de poluentes e espécies invasoras:** Considerando os potenciais impactos dos microplásticos e das espécies invasoras, futuros estudos devem se concentrar nos efeitos a longo prazo desses fatores na dieta e ecologia dos crustáceos decápodes. Uma compreensão mais profunda desses impactos poderia informar ações de manejo visando mitigar os efeitos negativos desses poluentes e espécies não nativas nos ecossistemas aquáticos.
2. **Integração de técnicas complementares:** A aplicação de técnicas, como a espectrometria de massa de isótopos, em outras populações e espécies, poderia ajudar a expandir a compreensão das interações tróficas e padrões de coexistência em diferentes ecossistemas. O uso de técnicas moleculares poderia, por exemplo, aumentar a precisão na identificação das fontes alimentares, complementando assim as análises de isótopos e a convencional do conteúdo estomacal.
3. **Modelagem ecológica:** O desenvolvimento de modelos ecológicos que integrem dados sobre reprodução, dieta e interações tróficas pode ser uma ferramenta poderosa para prever como essas espécies responderão às mudanças ambientais. Esses modelos poderiam ajudar a desenvolver políticas de conservação mais eficazes, adaptadas às necessidades específicas das espécies e ecossistemas envolvidos.
4. **Estudos experimentais:** Experimentos focados no consumo de diferentes tipos de presas por *Dilocarcinus pagei*, incluindo moluscos, macroinvertebrados e diversas fontes de material vegetal, como macrófitas. Esses experimentos devem

avaliar a seleção de presas com base em diferentes tamanhos e tipos, observando as preferências alimentares do caranguejo.