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RODRIGO VINÍCIUS DE ALMEIDA ALVES

IMPACTOS DO DERRAMAMENTO DE PETRÓLEO DE 2019 NA COSTA PERNAMBUCANA: a macrofauna do fital como indicadora

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Dissertação apresentada ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Pernambuco, como requisito parcial para a obtenção do título de Mestre em Oceanografia.

Área de concentração: Oceanografia Biológica.

Orientador: Prof. Dr. José Souto Rosa Filho.

Coorientadora: Profa. Dra. Flávia Lucena Frédou.

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BANCA EXAMINADORA

Prof. Dr. José Souto Rosa Filho (Orientador)
Universidade Federal de Pernambuco

Prof. Dra. Flávia Lucena Frédou (Coorientadora)
Universidade Federal Rural de Pernambuco

Prof. Dr. Giuliano Buzá Jacobucci (Examinador Externo)
Universidade Federal de Uberlândia

Prof. Dr. Ralf Schwamborn (Examinador Interno)
Universidade Federal de Pernambuco

Prof. Dr. Paulo Jorge Parreira dos Santos (Examinador Externo)
Universidade Federal de Pernambuco

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When the ebbing tide retreats along the rocky shoreline
It leaves a trail of tide pools in a short-lived galaxy
Each microcosmic planet, a complete society
A simple kind of mirror to reflect upon our own
All the busy little creatures chasing out their destinies
Living in their pools, they soon forget about the sea (LEE; LIFESON; PEART, 1980).

RESUMO

Os recifes coralíneo-algálicos da Praia do Paiva (PE) possuem importante cobertura fitobentônica que abriga diversas comunidades de macrofauna associadas. Esses ambientes foram um dos mais atingidos pelo derramamento de petróleo na Costa Brasileira iniciado em 2019. O presente trabalho teve como objetivo utilizar a macrofauna do fital como indicador dos impactos desse desastre nas comunidades biológicas da Costa Pernambucana. De julho de 2019 a outubro de 2020 foram coletadas mensalmente nos recifes da Praia do Paiva (exceto em março de 2020) dez frondes das algas *Penicillus capitatu*s e *Jania capillacea*, e em mais duas coletas em 2021 (abril e outubro) e em julho de 2022. A abundância dos tanaidáceos *Chondrochelia dubia* coletados entre julho de 2019 e julho de 2020 em frondes de *J. capillacea* correlacionou-se negativamente com a precipitação mensal, com maiores abundâncias nos meses mais secos. Houve inesperada queda significativa na abundância em setembro, possivelmente causada pelo contato com o petróleo bruto, mas a população se recuperou totalmente em dois meses, demonstrando ser uma espécie resiliente e de caráter oportunista, com parâmetros de crescimento e maturação baixos (L_{inf}=5.26 mm; k=3.36/ano; t_{0}=0; L_{50}=2.3 mm) se comparados aos de outras espécies de Tanaidacea. Em nível de comunidades a epifauna das algas como um todo não sofreu quedas expressivas de abundância logo após o contato direto com o óleo, porém alguns grupos como Syllidae (Annelida) e *Janaira gracilis* (Isopoda) provavelmente sofreram com o impacto, enquanto a abundância de poliquetas da família Sabellidae (em especial *Branchiomma luctuosum*) tendeu a crescer após o derramamento. As comunidades epifaunais de ambas as algas apresentaram respostas distintas em relação ao desastre, com perda imediata de táxons (principalmente espécies raras) no fital de *J. capillacea* e aumento de riqueza no fital de *P. capitatus* pouco depois do evento, voltando aos níveis normais em alguns meses. As abundâncias de alguns táxons também se correlacionaram significativamente à abundância de Amphipoda, que pode ter sofrido um impacto de mais longo prazo devido à combinação sinérgica do derramamento de óleo com o período chuvoso. Além de fatores abióticos, destacam-se a heterogeneidade de hábitat, a conectividade e a manutenção de “espécies-chave” engenheiras de ecossistema (em especial anfípodes) como fatores fundamentais para a resiliência e estabilidade das comunidades epifaunais após impactos ambientais como derramamento de óleo.

Palavras-chave: impacto ambiental; epifauna; fital; diversidade; bioindicação.

ABSTRACT

The coral-algal reefs of Paiva Beach (PE) have an important phytobenthic cover that shelter several communities of associated macrofauna. These environments were one of the most affected by the oil spill on the Brazilian Coast that started in 2019. The present work aimed to use the phytal macrofauna as an indicator of the impacts of this disaster on the biological communities of the Pernambuco Coast. From July 2019 to October 2020, ten fronds of the algae *Penicillus capitatus* and *Jania capillacea* were collected monthly on the reefs of Paiva Beach (except in March 2020), and in two more occasions in 2021 (April and October) and in July 2022. The abundance of the *Chondrochelia dubia* tanaids collected between July 2019 and July 2020 in fronds of *J. capillacea* correlated negatively with monthly precipitation, with greater abundances in the driest months. There was a significant drop in abundance in September, possibly caused by contact with crude oil, but the population fully recovered in two months, proving to be a resilient species with an opportunistic character, with low growth and maturation parameters (L_{inf}=5.26 mm; k=3.36 year^{-1}; $t0$=0; L_{50}=2.3 mm) compared to other species of Tanaidacea. At the community level, the algae's epifauna as a whole did not suffer significant declines in abundance soon after direct contact with the oil, but some groups such as Syllidae (Annelida) and *Janaira gracilis* (Isopoda) probably suffered with the impact, while the abundance of polychaetes of the Sabellidae family (in special *Branchiomma luctuosum*) tended to increase after the spill. The epifaunal communities of both algae showed different responses to the disaster, with an immediate loss of taxa (mainly rare species) in the *J. capillacea*'s phytal and an increase in richness in the *P. capitatus*' phytal shortly after the event, returning to normal levels in a few months. The abundances of some taxa also significantly correlated with the abundance of Amphipoda, which may have suffered a longer-term impact due to the synergistic combination of the oil spill with the rainy season. In addition to abiotic factors, habitat heterogeneity, connectivity and maintenance of ecosystem engineer "keystone species" (especially amphipods) stand out as fundamental factors for the resilience and stability of epifaunal communities after environmental impacts such as oil spills.

Keywords: environmental impact; epifauna; phytal; diversity; bioindication.

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1 INTRODUÇÃO

Um dos compartimentos mais importantes dos ecossistemas aquáticos é o bentos, formado por organismos que possuem relação obrigatória com o fundo (sobre ou dentro dele) durante toda a vida ou parte dela (GRAY; ELLIOT, 2009). Em zonas tropicais costeiras, um dos principais ambientes bentônicos são os recifes, estruturas de origem biogênica ou geogênica que formam o substrato consolidado em regiões sublitorais e litorais (LABOREL-DEGUEN et al., 2019). Na costa do Nordeste brasileiro, é notável a presença de arenitos de praia ou *beachrocks,* estruturas sólidas alongadas e dispostas em faixas paralelas à costa, formadas majoritariamente pela concreção de areia quartzosa e carbonato de cálcio (LABOREL-DEGUEN et al., 2019; LEÃO et al., 2016). Esses substratos são caracterizados pela baixa cobertura e alto endemismo de espécies de corais, sendo colonizados principalmente por *turf* e macroalgas frondosas (AUED et al., 2018). Em Pernambuco, destacam-se algas calcárias e os corais *Millepora alcicornis* (Linneaus, 1758)*, Mussismilia hartii* (Verril, 1868)*, Siderastrea* Blainville, 1830, *Montastrea cavernosa* (Linneaus, 1767) e *Porites astreoides* Lamarck, 1816 como principais construtores, e artículos de algas calcárias do gênero *Halimeda* J.V. Lamouruoux, 1812 como principal fonte de sedimento (FERREIRA; MAIDA, 2006). As macroalgas dos gêneros *Palisada* K.W. Nam, 2007, *Gelidiella* Feldmann & G.Hamel, 1934 e *Caulerpa* Lamouruoux, 1809 dominam a cobertura dos recifes pernambucanos, podendo variar em abundância relativa de acordo com o grau de urbanização (VASCONCELOS et al., 2018).

Fundos vegetados como bancos de macroalgas e prados de angiospermas abrigam grande diversidade de espécies marinhas de interesse econômico e ecológico (CHRISTIE; NORDERHAUG; FREDRIKSEN, 2009; FULTON et al., 2019; TANO et al., 2016). Ao ecossistema formado por macrófitas (macroalgas ou angiospermas aquáticas) e demais organismos associados Remane (1933) deu o nome “fital”. A epifauna do fital é dominada por pequenos invertebrados (0,5 – 10 mm) como anfípodes, gastrópodes, isópodes e poliquetas (CHEN; EDGAR; FOX, 2021; EDGAR, 1983; VEIGA; RUBAL; SOUSA-PINTO, 2014). Devido à sua abundância, a epifauna atua como intermediária em importantes processos ecossistêmicos. Isso inclui a ciclagem biogeoquímica de carbono e nitrogênio da coluna d’água para o ambiente bentônico e a transferência de energia via produção secundária dos produtores primários aos níveis tróficos de maior ordem (CHEN; EDGAR; FOX, 2021).

Em fundos consolidados, a cobertura de macroalgas pode mudar radicalmente as condições locais para a epibiota através do aumento da oferta de substrato e alimento, e amelioramento das condições ambientais (STACHOWICZ, 2001). As macroalgas disponibilizam microhábitats, amenizam estresses bióticos (predação, competição) e abióticos (dessecação, radiação UV, batimento de ondas), acumulam perifíton e detritos, e servem de locais de reprodução e forrageamento para várias espécies (BATES, 2009; BORST et al., 2019; STACHOWICZ, 2001; VEIGA; RUBAL; SOUSA-PINTO, 2014). Essa facilitação resulta no aumento da diversidade e da produtividade primária e secundária nesses ambientes, com impacto direto na estruturação das comunidades marinhas costeiras (NAVARRO-BARRANCO et al., 2018; TANO et al., 2016). Ambientes bentônicos dominados por macroalgas vêm ganhando atenção nas últimas décadas devido à sua diversidade subestimada e à tendência de declínio e substituição de corais por algas como espécies formadoras de hábitats no mundo todo (FULTON et al., 2019).

Além de estresses naturais causados pelas altas temperaturas e aporte de sedimento terrígeno, os recifes da Costa Nordestina estão tipicamente próximos a grandes centros urbanos, sujeitos então a uma série de pressões antrópicas constantes, tais como pisoteio, sobrepesca e despejo de nutrientes e contaminantes orgânicos (LEÃO et al., 2016; VASCONCELOS et al., 2018). A partir de agosto de 2019, manchas de petróleo de origem desconhecida começaram a aparecer na costa do Nordeste do Brasil (ARAÚJO; RAMALHO; MELO, 2020). Em alguns meses, o óleo já havia se espalhado por mais de 3 mil quilômetros ao longo da Costa Brasileira, do Maranhão ao Rio de Janeiro (LOURENÇO et al., 2020). Em mais ou menos seis meses (agosto de 2019 a janeiro de 2020), foram removidas mais de cinco mil toneladas de óleo (BRUM; CAMPOS-SILVA; OLIVEIRA, 2020), cuja origem na bacia venezuelana foi confirmada após análises geoquímicas (OLIVEIRA et al., 2020). O óleo atingiu, no total, cerca de mil localidades e 55 áreas de proteção marinha, impactando ecossistemas importantes como mangues, praias arenosas, recifes de corais e prados de fanerógamas (LOURENÇO et al., 2020; MAGRIS; GIARRIZZO, 2020). O desastre ambiental também teve graves consequências para as populações humanas mais atingidas e com alta vulnerabilidade socioeconômica, tendo impactos na pesca, turismo e segurança alimentar (SILVA et al., 2022). Este não foi apenas o mais grave acidente de derramamento de petróleo na história do Brasil e do Sudoeste do Atlântico, mas também de todas as regiões oceânicas tropicais até então (SOARES et al., 2022).

Derramamentos de óleo são dos impactos ambientais mais destrutivos em ecossistemas marinhos, especialmente em zonas costeiras, afetando populações humanas, o ambiente físico e a biota em todos os níveis tróficos (SUCHANECK, 1993; YU et al., 2013). A poluição por petróleo e seus derivados pode causar uma série de impactos físicos (sufocamento, bloqueio de luz solar), químicos (alteração no pH, diminuição do oxigênio dissolvido) e ecotoxicológicos sobre a biota marinha, afetando a reprodução, desenvolvimento e alimentação de inúmeras espécies, com efeitos letais e subletais (DE SOUZA et al., 2022; MACIEL et al., 2015; MÜLLER et al., 2021; WEIS, 2014). Os efeitos negativos do óleo em macrolagas podem causar simplificação das comunidades fitais, além de bioacumulação e efeitos-cascata no ambiente (O'BRIEN; DIXON, 1976).

Várias características das comunidades bentônicas as tornam potenciais indicadores de perturbações ambientais: 1) são encontrados em todos os sistemas aquáticos, favorecendo estudos comparativos; 2) a natureza sedentária e os ciclos de vida variados permitem a análise espacial e temporal dos efeitos das perturbações; 3) o elevado número de espécies resulta em amplo espectro de respostas ao stress; 4) facilidade para coleta e análise de amostras quantitativas, uma vez que estas podem ser realizadas com equipamentos simples e baratos; e 5) existem numerosos métodos para a análise dos dados (GRAY; ELLIOT, 2009; PEARSON; ROSENBERG, 1978). A epifauna do fital é formada por grupos com diferentes graus de tolerância aos componentes do petróleo bruto (DAUVIN et al., 2016; ROBERTS; JOHNSTON; POORE, 2008; SUCHANECK, 1993). A proporção grupo sensível/grupo tolerante é a base de diversos índices que visam quantificar os impactos da poluição sobre as comunidades bentônicas (DAUVIN et al., 2016). Mesmo em baixas concentrações, a presença de hidrocarbonetos pode ser facilmente detectada em anfípodes e macroalgas, o que faz desses organismos bons indicadores (LOURENÇO et al., 2019).

1.1 OBJETIVOS

O presente trabalho teve como objetivos:

1.1.1 Objetivo Geral

Utilizar a macrofauna do fital como indicadora dos impactos do derramamento de petróleo de 2019 nas comunidades bentônicas da Costa Perambucana.

1.1.2 Objetivos Específicos

a) Descrever a dinâmica populacional do tanaidáceo *Chondrochelia dubia* (Krøyer, 1842) (crescimento populacional, razão sexual, estrutura etária e mortalidade) associada à alga *Jania capillacea* e apontar possíveis alterações causadas pelo derramamento de óleo;
b) Caracterizar as comunidades macroepifaunais (abundância, composição taxonômica, riqueza, diversidade e equitabilidade) associadas às macroalgas *Penicillus capitatu*s e *Jania capillacea*;
c) Comparar a estrutura das comunidades do fital de *P. capitatu*s e *J. capillacea* antes e depois da chegada do óleo na Praia do Paiva (PE).

1.2 ESTRUTURA DA DISSERTAÇÃO

A presente dissertação é constituída por dois capítulos em formato de artigos. O artigo 1, intitulado "*Life history and population dynamics of the enigmatic tanaid Chondrochelia dubia (Tanaidacea: Leptocheliidae) in a tropical seaweed bed*", aborda aspectos da história de vida e dinâmica populacional do crustáceo tanaidáceo *Chondrochelia dubia* em bancos de macroalgas antigidos pelo derramamento de petróleo em 2019 na Praia do Paiva (PE), aceito para publicação no periódico *Scientia Marina*. O artigo 2, intitulado "*The role of habitat heterogeneity and timescales on the recovery of reef epifaunal communities affected by a massive oil spill in the Tropics*", aborda os impactos causados pelo derramamento de petróleo na estrutura, composição e perfis de diversidade sobre as comunidades epifaunais das algas *Jania capillacea* e *Penicillus capitatus* na Praia do Paiva (PE), a ser submetido ao periódico *Science of the Total Envionrment.*

1.3 ÁREA DE ESTUDO

A zona costeira de Pernambuco (07º32'52''S, 034º50'27''O - 08°54'57''S, 035º09'76''O), localizada na província biogeográfica do Sudoeste do Atlântico Tropical, possui 187 km de extensão, o que representa cerca de 4% do território do estado (IBGE, 2022). O clima é tropical quente/úmido, com média anual acima de 25°C durante todo o ano (DOMINGUES et al., 2017). A precipitação pluviométrica anual varia de 1.800 a 2.500 mm, com balanço hídrico positivo (MANSO, V.A.V.; COUTINHO, P.N.; PEDROSA et al., 2018). Distinguem-se duas estações climáticas: seca, de setembro a fevereiro, e chuvosa, de março a agosto (BONTEMPO FILHO et al., 2022). O regime de maré é do tipo mesotidal semidiurno, com amplitude média entre 0,7 m e 2,5 m (DOMINGUES et al., 2017). Paralelamente à costa, existem várias linhas descontínuas de *beach rocks* alongados, conectados à costa ou a profundidades de cinco a dez metros (LABOREL-DEGUEN et al., 2019) e colonizados por densos bancos de macroalgas características da região ficogeográfica tropical (HORTA et al., 2001).

A praia do Paiva (8°16’46.4’’S, 34°56’47.1’’O) possui aproximadamente 7,8 km de extensão, localizada no litoral sul de Pernambuco, no município de Cabo de Santo Agostinho (HOLANDA et al., 2020). A região é banhada por águas marinhas com temperatura média de 27°C, bem oxigenadas e com salinidade próxima de 36 ‰ (DOMINGUES et al., 2017). O ambiente recifal do Paiva situa-se a cerca de 50 metros da linha de costa e possui 355 metros de largura, 0,85 metro de altura e pouco mais de 2 km de extensão, com rugosidade relativamente alta (VASCONCELOS, 2016). Na região entremarés, é comum a presença das macroalgas perenes *Jania capillacea* (Rhodophyta, Corallinales) e *Penicillus capitatus* (Chlorophyta, Bryopsidales), com distribuição naturalmente fragmentada sobre o recife. Com urbanização ainda não consolidada, a área possui recifes coralíneo-algálicos relativamente bem preservados (VASCONCELOS et al., 2018).

2 ARTIGO 1 - LIFE HISTORY AND POPULATION DYNAMICS OF THE ENIGMATIC TANAID *CHONDROCHELIA DUBIA* (TANAIDACEA: LEPTOCHELIIDAE) IN A TROPICAL SEAWEED BED

Aceito para publicação no periódico *Scientia Marina* (ISSN 0214-8358)

Summary: The present study describes the population dynamics and life history parameters of the enigmatic tanaid *Chondrochelia dubia* collected in Paiva Beach, tropical coast of Brazil. The region was impacted by a large, unexpected oil spill from August to October 2019. Samples were taken monthly between July 2019 and July 2020 in beds of the red seaweed *Jania capillacea*. The abundance of individuals was negatively correlated with monthly rainfall, with higher abundances in drier months. There was an unexpected significant drop in abundance in September, possibly caused by contact with the crude oil, but the population recovered fully within two months. The parameters of the von Bertallanfy growth equation, calculated for the first time for the species, were L_{inf}=5.26 mm; *k*=3.36 year^{-1}; t_0=0.0. Compared with other studies, the specimens are very small (2.04 ± 0.95 mm in length), females reach sexual maturity very early (L_{50}=2.3 mm), and natural mortality is high (Z=M=5.77 year^{-1}), indicating an opportunistic life strategy. This study reinforces the bioindication potential of *C. dubia* and the use of bootstrapped length-based methods to estimate key population parameters in small marine invertebrates.

Running title: Population dynamics of *Chondrochelia dubia*

Keywords: epifauna; Peracarida; Brazilian oil spill; reef; macroalgae; leptocheliids.

Historia de vida y dinámica poblacional de la enigmática tanaide *Chondrochelia dubia* (Tanaidacea: Leptocheliidae) en un lecho de algas tropicales

Resumen: El presente estudio describió la dinámica poblacional y los parámetros de historia de vida de la enigmática tanaide *Chondrochelia dubia* recolectada en la playa de Paiva, costa tropical de Brasil. La región se vio afectada por un gran derrame de petróleo inesperado de agosto a octubre de 2019. Se tomaron muestras mensualmente entre julio de 2019 y julio de 2020 en lechos de algas rojas *Jania capillacea*. La abundancia de individuos se correlacionó negativamente con la precipitación mensual, con mayor abundancia en los meses más secos. Hubo una inesperada caída significativa de la abundancia en septiembre, posiblemente causada por el contacto con el petróleo crudo, sin embargo, la población se recuperó por completo en dos meses. Los parámetros de la ecuación de crecimiento de von Bertallanfy, calculados por primera vez para la especie, fueron: L_{inf}=5.26 mm; k=3.36 año^{-1}; t_{0}=0,0. En comparación con otros estudios, los ejemplares son muy pequeños (2.04 ± 0.95 mm de longitud), las hembras alcanzan la madurez sexual muy temprano (L_{50}=2.3 mm), y la mortalidad natural es relativamente alta (Z=M=5.77 año^{-1}), lo que indica una estrategia de vida oportunista. Este estudio refuerza el potencial de bioindicación de *C. dubia* y el uso de métodos *bootstrap* basados en la longitud para estimar parámetros de población clave en pequeños invertebrados marinos.

Palabras clave: epifauna; Peracarida; derrame de petróleo brasileño; arrecife; Macroalgae; Leptocheliids.

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INTRODUCTION

Marine vegetated habitats such as seaweed and seagrass beds harbour diverse and abundant epifaunal communities as they act as shelter, feeding and reproduction grounds for many species (Carvalho et al. 2018, Martínez-Laiz et al. 2018, Tano et al. 2016). Epifauna is usually dominated by crustaceans of the superorder Peracarida, such as amphipods, isopods and tanaids (Carvalho et al. 2018, Tano et al. 2016). These organisms contribute to the elevated secondary production in macrophyte habitats and act as an important link between primary producers and consumers from higher trophic levels (Tano et al. 2016). Tanaidacea is a diverse order of small peracarid crustaceans with more than 1500 described species worldwide, which occur from intertidal to abyssal zones, inhabiting soft, interstitial and biogenic substrates in a wide variety of ecosystems (e.g. estuaries, mangroves, seagrass meadows, coral reefs and deep sea) (Blazewicz-Paszkowycz et al. 2012, Kakui et al. 2021).

Several complex reproductive and parental behaviours have been observed in Tanaidacea, such as ritualistic fights between males, courtship and the maintenance of a brood nursery for “newborn” larvae (Buckle Ramirez 1965, Highsmith 1983, Johnson and Attramadal 1982). In tube-dwelling species such as *Chondrochelia dubia* and *Tanais dulongii*, successful males enter the female tube, where copulation takes place (Highsmith 1983, Johnson and Attramadal 1982). Fertilized eggs develop within the female marsupium until the first postmarsupial stage (manca II) is achieved (Masunari 1983). In *Tanais dulongii,* released manca II larvae keep contact with the mother until manca III stage, when they leave the mother’s brood nursery to build their own tubes (Johnson and Attramadal 1982). Tanaid postmarsupial development is usually divided into two or three larval (manca) stages, neutrum, and preparatory and copulatory males and females, with slight variations (Holdich and Jones 1983, Leite et al. 2003, Toniollo and Masunari 2007).

Leptocheliids such as *Chondrochelia dubia* (Krøyer, 1842) are frequently found in high abundance in many shallow-water habitats such as seaweeds, corals and soft sediment worldwide (Guțu 2016, Mendoza 1982, Stoner 1986). These organisms are typically tube-dwellers that build their tubes from sediment particles and faecal pellets held together by secreted mucus with the help of the pereopods (Krasnow and Taghon 1997, Mendoza 1982). Most tanaids are raptorial feeders that consume detritus and its associated organisms (e.g. diatoms, bacteria and nematodes) by seizing and breaking up food particles with their mouthparts (Holdich and Jones 1983). As in other species of Leptocheliidae, *C. dubia* show strong sexual dimorphism, with males having much larger antennules (first antenna), chelae, eyes and walking legs (pereopods) (Bamber 2010, Mendoza 1982, Stoner 1986). The female has short antennules with only three longer articles and also short gnathopods with small chelae, whereas the male has large gnathopods with a prominent propodus and each antennule has a long flagellum. Males also have reduced mouthparts (Gardiner 1975).

The taxonomic history of *Chondrochelia dubia* goes back to over 180 years ago when Krøyer (1842) described *Tanais dubia* (now *C. dubia*) from specimens collected in Salvador, northeastern Brazil, and *Tanais savignyi* (now *C. savignyi*) from Madeira, Portugal. These species were later transferred to the genus *Leptochelia*, and then *Chondrochelia* by Guțu (2016). In the last century, many new species of the genus were described, while the Brazilian taxon *Chondrochelia dubia* was “found” in very distinct places worldwide (Bamber 2010). Most of these species were synonymized under the wide “*Leptochelia dubia* group”, which may include several cryptic species in many continents (Bamber 2010). All members of the “*Leptochelia dubia* group” were then synonymized under the cosmopolitan *L. dubia* by Sieg (1983), which started a debate over whether the senior synonym should be *L. dubia* or *L. savignyi* (Bamber 2010). Two major efforts were recently made to solve the problematic “*Leptochelia dubia* group”: Bamber (2010) made a redescription of *C. savignyi* and synonymized some North Atlantic and Mediterranean species under *C. savignyi*, and a robust revision made by Guțu (2016) added a new subfamily, seven genera and 21 species to the

Leptocheliidae family. Consequently, the “*Leptochelia dubia* group” was to a large extent dissolved into several different taxa, including the “Brazilian species” discovered by Krøyer (1842) that is now named *Chondrochelia dubia*. It is now evident that *C. savignyi* and *C. dubia* should no longer be considered synonymous (Bamber 2010, Jarquín-González and Carrera-Parra 2022) and that *C. dubia* is not a cosmopolitan species, since Jarquín-González and Carrera-Parra (2022) recently rejected its hypothetical occurrence in the Mexican Caribbean and Gulf Coast with molecular data.

Though it is very common in several shallow-water environments, only a few studies have focused on the population dynamics of Leptocheliidae (Buckle Ramirez 1965, Masunari 1983, Modlin and Harris 1989, Stoner 1986). Population dynamics studies combined with life histories and morphometric data are powerful tools for understanding ecosystem function at different spatial and temporal scales, managing harvested and threatened species, and quantifying biotic responses to environmental change (Pennafirme and Soares-Gomes 2009, Rumbold et al. 2015). In late 2019, the Brazilian coast was heavily impacted by the largest oil spill in tropical oceans so far (Soares et al. 2020), enabling us to study the potential impacts of this disaster in coastal marine biota. Herein, we aim to describe the population dynamics and life history parameters of *Chondrochelia dubia* on the northeast coast of Brazil (Paiva Beach). Additionally, we make inferences about the effects of the 2019 oil spill on the populations of *C. dubia*. This is also the first study to estimate the natural mortality rate, longevity, maturation and parameters of von Bertalanffy’s growth equation (L_∞, k and t_0) for the tanaid *C. dubia*. Unlike previous studies on Tanaidacea, we used robust bootstrapped versions of the classical length-based methods to quantify key population parameters.

MATERIALS AND METHODS

Study area

Paiva Beach (8°16’S; 34°56’W) is an open ocean tropical sandy beach approximately 7.8 km long located in the Cabo de Santo Agostinho municipality (Pernambuco State, northeast Brazil) (Holanda 2020). The sandstone reefs of Paiva Beach are elongated and occur parallel to the shore (Laborel 1970). The reef line closest to the beach is 2.5 km long and 1 km wide and densely colonized by macroalgal assemblages that are typically found in the tropical phycogeographic region (Horta et al. 2001). The climate is tropical hot/humid, with average annual temperatures above 25°C throughout the year (Domingues et al. 2017). The tidal regime can be classified as a mesotidal semi-diurnal type, with tide height averaging 0.7 m (neap tide) to 2.5 m (spring tide) (Domingues et al. 2017). The reefs and their diverse intertidal communities were severely impacted by the 2019 Brazilian Oil Spill. In only one week (19-28 October 2019), more than 1000 t of crude oil were collected from the Cabo de Santo Agostinho municipality alone (Craveiro et al. 2021). Although less perceptible, oil strains started appearing in Pernambuco’s beaches in August 2019 (Soares et al. 2020), months before the main sheet of crude oil arrived at Paiva Beach.

Sampling design and laboratory procedures

Sampling was performed monthly from July 2019 to July 2020. In March 2020, samples were not taken because of COVID-19 lockdown restrictions. On each sampling occasion, ten fronds of the red seaweed *Jania capillacea* were collected in intertidal tide pools. The fronds were wrapped with plastic bags to prevent motile animals from escaping and then removed from the substrate. Samples were fixed with 4% saline formalin. In the laboratory, the samples were sieved (0.3 mm mesh size) and the retained epifaunal organisms were sorted under the stereomicroscope. Specimens of *C. dubia* were separated, counted and preserved in 70% ethanol. For each month, approximately 120 to 170 individuals were randomly chosen (in some months fewer than 120 individuals were found) to be measured from the tip of the carapace to the end of the telson with a stereo microscope with an eyepiece reticle (body length, mm). For males, the length and width of chelae were measured. The individuals were classified into five categories, as proposed by Masunari (1983): juveniles/mancas – larval MII and MIII stages; pre-ovigerous (preparatory) females – those with oostegites; ovigerous females – those with marsupia; non-reproductive females – those with adult appearance but no sign of reproductive activity; and males – those with characteristic male features (Fig. 1).

Statistical analysis

Monthly densities and lengths of *C. dubia* were log-transformed and compared by one-way ANOVA followed by pairwise Tukey tests. Chi-square tests ($\chi2$) were performed to compare sex ratio between months and size classes. The parameters of the von Bertalanffy growth function (VBGF) were estimated through the ELEFAN_GA_Boot method, which is based on a bootstrapped genetic algorithm that provides a range of likely best fits for the VBGF parameters (Schwamborn et al. 2019). This approach is highly applicable for rapid assessment in data-poor situations such as data collected from short time periods (e.g. one year) (Mildenberger et al. 2017). Intervals of L_∞, k and t_0 (pooled data) were chosen based on published studies about similar species from the southwestern Atlantic Ocean (Almeida 1994, Fonseca and D’Incao 2003, Leite et al. 2003, Pennafirme and Soares-Gomes 2017, Rumbold et al. 2015). Analyses were made in the *TropFishR* (Mildenberger et al. 2017) and *fishboot* (Schwamborn et al. 2019) packages.

The growth performance index (Φ’) was calculated from von Bertalanffy’s equation parameters as Pauly and Munro (1984):

$$\Phi' = log\,k + 2 \cdot log\,Linf$$

The length at which 50% of females are sexually mature (L_{50}) was estimated through a logistic function using two sets of variables: length-frequency (LFQ) data and categorical "gonadal maturation stages" (Torrejon-Magallanes 2020). Since the mean length of the individuals at MIII stage (1.75 mm) is lower than the smallest reproductive female (2.1 mm), all specimens in this category were treated as "immature". L_{50} was calculated as

$$Pi = A \cdot (1 + e^{(-r(Lt - L50))})^{-1}$$

where Pi is the proportion of reproductive females for each (0.2 mm) size class; A is the curve asymptote; r is a rate parameter related to the speed of size change from non-reproductive to reproductive status; Lt is the total length (mm); and L_{50} is the size at first maturity (mm) (Fontoura et al. 2009).

Morphometric maturity in males was estimated using a regression analysis where X (body length) is considered the explanatory variable and the classification of maturity (juveniles, 0; adults, 1) is considered the response variable (binomial) through the form (Torrejon-Magallanes 2020):

$$Pcs = 1 / (1 + e^{-(\beta 0 + \beta 1 \cdot X)})$$

where Pcs is the probability of an individual being mature at a determinate X length. β0 (intercept) and β1 (slope) are estimated parameters. Both gonadal (females) and morphometric (males) maturities were calculated using the "sizeMat" package (Torrejon-Magallanes 2020).

The instantaneous mortality rate (Z) was calculated through a linear capture curve based on length composition data (Sparre and Venema 1998). Estimates for maximum individual age within the population were based on Taylor (1958). The maximum longevity (t_{max}) was calculated from 95% of the asymptotic length, where

$$tmax = (2.996/k) + t0$$

All data analyses were performed using R software (R Core Team 2022). For all tests a significance level of 5% was considered.

RESULTS

A total of 1513 individuals (583 females, 34 males and 896 mancas) were included in the analysis. The abundance of *C. dubia* varied significantly between months (F=10.55; p<0.01) and was negatively correlated with monthly rainfall (S=458, Rho=-0.601; p=0.04). Months with the highest abundances were August, November and December 2019 (Fig. 2A).

Body lengths varied significantly between months (F=19.9; p<0.01). In general, the smallest individuals were found in August 2019 (1.58 ± 0.99 mm), whereas the largest ones were found in February (2.63 ± 0.93 mm) and April 2020 (2.61 ± 0.9 mm) (Fig. 2B). Specimens were categorized into six developmental stages (Fig. 3): MII (0.99 ± 0.2 mm), MIII (1.75 ± 0.3 mm), neutrum (3.05 ± 0.48 mm), males (2.82 ± 0.4 mm), pre-ovigerous females (2.87 ± 0.35 mm) and ovigerous females (3.16 ± 0.39 mm).

The population was dominated by non-reproductive individuals. Those with clear sexual characteristics (males and ovigerous and pre-ovigerous females) accounted for less than 10% of the total. *Chondrochelia dubia* had multiple cohorts throughout the year. Reproductive individuals had discrete abundance peaks throughout the year, especially in December (Fig. 4). Except for February and April, juveniles (MII and MIII stages) accounted for more than 50% of all individuals in all months. The sex ratio was significantly female-biased in all months and size classes. The general sex ratio was approximately 17:1 and maximum female dominance occurred in November 2019 (no males) and July 2020 (56 females: 1 male) (Table 1).

Female size at first maturity was 2.3 mm (Fig. 5A). For males, the inflection point, which indicates the size of morphometric maturity, was 3.0 mm (Fig. 5B). Longevity (t_{max}) was 0.89 years (10-11 months) and natural mortality (M=Z), 5.77 years^{-1}. There was a positive and significant correlation between body size and chela length ($R^{2=}0.64$; $p<0.01$) and body size and chela width ($R^{2=}0.57$; $p<0.01$) in males. The parameters of the von Bertalanffy growth formula were L_∞=5.26 mm; k=3.36 year^{-1}; t_0=0.0 (Fig. 6).

DISCUSSION

Populational fluctuations and morphometry

The maximum abundance of *C. dubia* in Paiva Beach (tropical Brazilian coast) occurred in drier months, particularly in August, November and December 2019. Despite the stable conditions of tropical environments, even slight variations in temperature, photoperiod, salinity and nutrient concentration might cause perceptible oscillations in population size and structure (Pandian 2016). Estuarine tanaid species have generally shown abundance peaks in rainy periods and under mesohaline conditions (Modlin and Harris 1989, Pennafirme and Soares-Gomes 2009). Marine species, in contrast, are generally more abundant during the dry season, when salinity is higher (de Souza et al. 2013, Tuya et al. 2001). Warmer temperatures in the dry season may also enhance microbial growth (Longo et al. 2019), which might contribute to the detritus chain, which is useful for both feeding and tube-building in Tanaidacea (Krasnow and Taghon 1997). In the rainy season, wave action, river discharge and sediment resuspension are considerably higher (Medeiros et al. 2001), which may cause higher mortality owing to physical and chemical stressors and reduction of available algal biomass.

There was a significant reduction in the size of individuals in August and October/November 2019. Despite the arrival of oil in these months, abundances continued to grow, so the lower body lengths might be a consequence of the recruitment of new juveniles into the population instead of a mass mortality event. The months of August (end of the rainy season), October and November (peak of the dry season) coincide with the highest salinities. However, other factors rather than just salinity might help to explain this pattern, such as the decrease in predators and/or competitors, or better conditions for the seaweed that provides refuges. However, a significant reduction in abundance was observed in September, the beginning of the dry season. This unusual decrease might have been caused by the contact with the oil that killed mainly juveniles, who are more vulnerable to harmful effects of pollutants than adults (Keesing et al. 2018). However, the population continued to grow and quickly recovered in the following months, which can be seen as the second peak in November/December. In laboratory experiments, *C. dubia* has shown to be relatively tolerant to changes in water chemistry (Araújo-Silva et al. 2022). Much of its resistance is attributed to the construction of tubes, which protect these animals protected from external agents and may help them colonize a wide variety of habitats within medium and infralittoral zones (Araújo-Silva et al. 2022).

Male size of morphometric maturity was 3.0 mm, and males larger than that were very rare. When males moult into their mature phase, they lose their functional mouthparts and cannot feed anymore, so they must die soon after reproduction (Highsmith 1983, Gardiner 1975), which explains the almost complete absence of males larger than 3 mm. Also, a positive correlation was observed between body length and chela length in males. The differential growth rate of chelae has an important role in crustacean reproduction (Ewers-Saucedo 2019). In Tanaidomorpha, chelipeds are used to access the female tube, hold females during mating and fight with other males (Buckle Ramirez 1965, Highsmith 1983, Johnson and Attramadal 1982). The copulatory male is considered the only free walking instar, so developed chelipeds are essential to climb and hold onto algae in turbulent environments (Johnson and Attramadal 1982). These features might give a reproductive advantage to larger males (Highsmith 1983). Another possible function of male aggression in leptocheliids is the exclusion of other males of sympatric species that might cohabit the algal frond (Stoner 1986).

A large size overlap between the sexes, mainly among more advanced developmental stages, was recorded. This is mainly because of the progressive decrease in growth rate with age (Sparre and Venema 1998). Pre-ovigerous females have a very small growth from the preparatory to marsupial stages because they allocate more resources to reproduction than to somatic growth (Masunari 1983). The largest individuals in our samples were female. This is probably because of the low survival rate and premature deaths of males (Mendoza 1982). More specifically, the largest individuals found were in fact non-reproductive adult females. It is very likely that they were multiparous females with interspaced "pregnancies" (Masunari 1983). The wide overlap between non-reproductive individuals with adult appearance (neuters) and reproductive ones suggests the existence of at least one intermediary instar between successive marsupial stages in *C. dubia* (Fig. 3). However, we did not find external marks (as in Johnson and Attramadal 1982) or any direct sign of previous "pregnancies" in large non-reproductive females.

Reproduction and sex ratios

The scarcity of reproductive individuals was notable. A few observations might explain this annual pattern, such as high natural mortality (5.77 year^{-1}) and possible competition among individuals to mate; the aggressiveness of males and possible formation of "harems" or highly condensed mating aggregations (Stoner 1986); interspaced "pregnancies" with intermediary instars (multiparity); and pre-ovigerous females with microscopic oostegites in early development, only visible through histological analysis (Masunari 1983). The last two factors might have produced a bias in the counting of reproductive/non-reproductive individuals.

The maintenance of a skewed sex ratio towards females during the entire year has also been observed in many previous studies on tanaids (e.g. Leite et al. 2003, Masunari 1983, Modlin and Harris 1989). Biased sex ratios have long been observed in several crustacean species (Ewers-Saucedo 2019). Some evolutionary and ecological mechanisms might explain the highly female-biased sex ratio in *C. dubia* (Ewers-Saucedo 2019):

1. Local mate competition: Because males add little to increase the mother's fitness, this favours the production of the lowest number of males sufficient to fertilize the highest number of females possible. This strategy is common in brooding and low-dispersive taxa, where brothers frequently compete for mating. Stoner (1986) proposed that aggregations with high densities of females might actually benefit males, since it would be easier for them to find partners.
2. Sexual selection: Producing males is a high-cost activity, because they have to grow up and compete to have a chance of mating—because of this, only females in good condition are likely to generate more males, making them less frequent in the population.
3. Environmental sex determination: Warm temperatures can turn the sex ratio towards females (Masunari 1983), and the stable, tropical climate of the study area might help maintain the female-skewed sex ratio year-round despite the seasonal oscillations.
4. Sex specific mortality: In Tanaidacea, the small relative number of males has been mainly attributed to their sexual behaviour: males experience higher mortality than females as a result of competition and aggressive behaviour with other males and are more vulnerable to predators because they have to walk to the female tube to mate (Highsmith 1983). Developed males also lack functional mouthparts, which might significantly decrease their lifespan (Highsmith 1983).
5. Sex reversal: Diverse reproductive strategies are observed in Tanaidomorpha and Apseudomorpha, including gonochoristic development and simultaneous, protandrous and protogynous hermaphroditism (Gardiner 1975).

The last strategy has been widely proposed to occur in many species of Tanaidacea (Gardiner 1975). It has been theorized that protogyny is an effective strategy for maximizing fitness (reproductive success) in all life stages (Highsmith 1983). Basically, males take too long to be able to reproduce (they must grow enough to fight with other males), whereas females mate as soon as they reach maturity. There is therefore a selective pressure for being a female at small (younger) stages and then becoming a male at larger (older) stages, because only the large males will be successful (Highsmith 1983). Alternatively, protogyny may also have evolved as a mechanism for counterbalancing the high mortality of males (Leite et al. 2003).

Although it is observed in many tanaids, there is no clear evidence that *C. dubia* is a sequential hermaphroditic species. If that were true, it would be expected to observe a dominance of one sex in smaller size classes and a gradual shift towards the other sex in larger size classes (Ewers-Saucedo 2019). The opposite occurred in Paiva Beach, where the sex ratio was strongly female-biased in all size classes. However, this might still be true if only a small percentage of females is able to become male. It has been observed in similar species that dominant males can inhibit sex reversal of nearby females (Highsmith 1983), which might keep the number of males in the aggregation low. The presence of two types of males based on their size differences has been treated as more evidence of protogynous hermaphroditism in Tanaidacea. The smallest males were considered gonochoristic (male-born) whereas the largest ones were protogynous (female-born) (Gardiner 1975). Interestingly, individuals identified as "*Leptochelia dubia*" collected from different parts of the West Coast of the USA have been treated either as dioecious (Mendoza 1982) or hermaphroditic (Highsmith 1983) on different occasions. Considering the lack of detailed natural observations, the taxonomic uncertainties and the geographic distances (tanaids are known to have low dispersive capacity; Bamber 2010), the best way to solve questions regarding the reproductive behaviour of *C. dubia* in the tropics would be to cultivate these organisms under controlled and realistic conditions.

Life histories and population growth

The year-long presence of reproductive adults and juveniles indicates continuous reproductive activity, a common pattern observed in many crustacean species, especially in the tropics (Pandian 2016, Pennafirme and Soares-Gomes 2009). Specimens in Paiva Beach are much smaller (2.04±0.95 mm in length) than other tanaid species from the southwestern Atlantic (Table 2), and their natural mortality is relatively high. *C. dubia* also has multiple short cohorts, a relatively high growth rate (*k*) and a short lifespan (<11 months). All of these features indicate that it has a short and opportunistic life strategy (Pennafirme and Soares-Gomes 2009).

Latitudinal trends in life history parameters are commonly observed in Tanaidacea (Pennafirme and Soares-Gomes 2017). Warmer temperatures generally accelerate growth and maturity in ectotherms (Sudo 2003), and tropical marine invertebrates generally have shorter lifespans and smaller individual sizes than their temperate counterparts (Cardoso and Defeo 2004). Furthermore, unlike *Monokalliapseudes schubartii* and *Tanais dulongii* (Table 2), *C. dubia* is a seaweed-dweller, meaning that its size is highly dependent upon the interstitial size and volume of the host algae (Hacker and Steneck 1990). However, in a subtropical area in southern Brazil, Fonseca and D'Incao (2003) found a growth rate (*k*) of 4.54 year^{-1} for *M. schubartii*. It is possible that other factors rather than temperature, such as food quality/availability (Berrigan and Charnov 1994), were responsible for the higher growth rate of this species than of our tropical species. The population studied by Fonseca and D'Incao (2003) inhabits a nutrient-rich protected estuarine bay (Patos Lagoon), which is very different from the open, nutrient-variable waters of tropical Brazilian beaches.

The absence of other studies that address the population parameters of *C. dubia* makes it difficult to evaluate the influence of environmental variables and regional variability in the growth of this species. However, compared with other Tanaidacea species of the southwestern

Atlantic, *C. dubia* also showed the lowest growth performance index (Φ'). Zamora-Sarabia et al. (2022) found a negative correlation between Φ' and sea surface temperature for a commercially important fish species in the southern Gulf of California. This correlation might explain the low Φ' value compared with other tanaid populations from colder areas at higher latitudes (Table 2). Combined with the high mortality rate and low percentage of reproductive individuals, *C. dubia* apparently faces harsh environmental conditions at Paiva Beach, such as resource limitation, high temperatures, predation and strong hydrodynamics (Domingues et al. 2017). Moreover, the size of the largest individual found (4.6 mm in length) was about 87% of the theoretical maximum length (L_{inf}=5.26 mm). It is possible that these natural stressors are a strong limitation for the growth and survival of these organisms. This may make the studied population of *C. dubia* vulnerable to extreme climatic events caused by anthropogenic warming and/or El Niño oscillations (Zamora-Sarabia et al. 2022), although Araújo-Silva et al. (2022) showed that this species is still more tolerant to warming effects than other tropical peracarids. Growth parameters such as Φ' are often used as an important reference for stock management and choosing appropriate species for aquaculture (Mathews and Samuel 1990, Pauly and Munro 1984, Zamora-Sarabia et al. 2022). Because peracarids have been recently studied as a valuable food resource for aquaculture (Abundez et al. 2021, Guevara et al. 2005), the present study should be taken into consideration for future decisions regarding the commercial use of this species.

In conclusion, *C. dubia* at Paiva Beach (tropical Brazilian coast) has a short-living, opportunistic life history that may be favoured by high-salinity conditions. The sex ratios are heavily female-skewed throughout all months and size classes. The species was apparently little impacted by the 2019 Oil Spill at the populational level, a sign of high tolerance to environmental impacts and great plasticity of lifestyle, which are interesting features of a possible bioindicator species. This study reinforces the need for cultivation techniques in order to solve key questions regarding the reproductive behaviour of the species and the high applicability of robust, bootstrapped length-based methods in population studies of small marine invertebrates.

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Fig. 1. Fixed specimens of *Chondrochelia dubia* (Krøyer, 1842) collected in Paiva Beach, northeastern Brazil: adult male (♂) (left); manca III juvenile (centre) and ovigerous female (♀) (right). L, chela length; W, chela width. Scale bar, 1 mm.

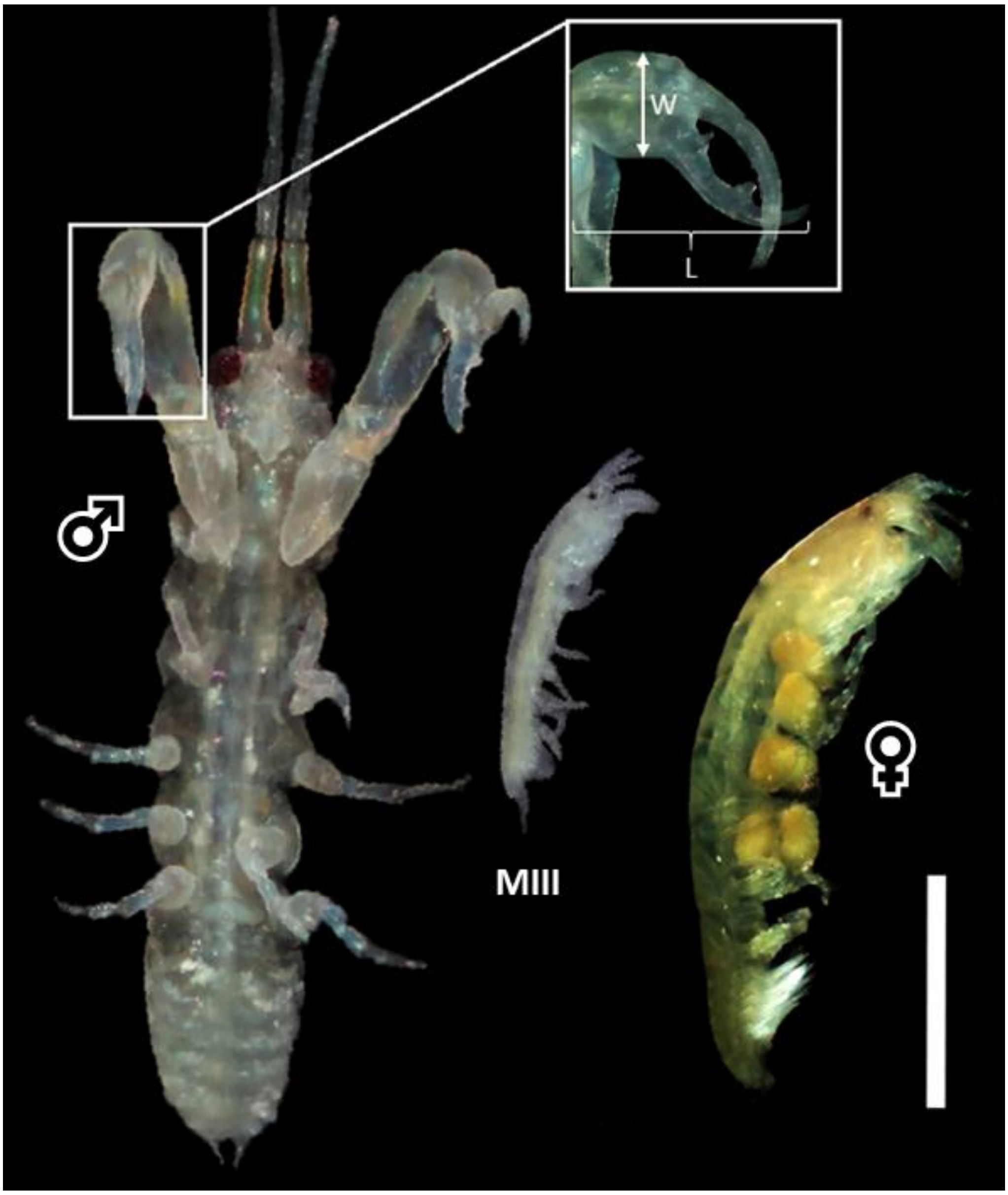


Fig. 2. (A) Abundances of *Chondrochelia dubia* between July 2019 and July 2020 (black line) and cumulative rainfall (grey bars). (B) Body length (mm) of *C. dubia* between July 2019 and July 2020. The light grey rectangle indicates the period of weak oil arrival at the location (August and September 2019) and the dark grey rectangle indicates the period of strong oil arrival (October 2019). Vertical bars represent standard errors and letters indicate the results of Tukey tests (p<0.05).

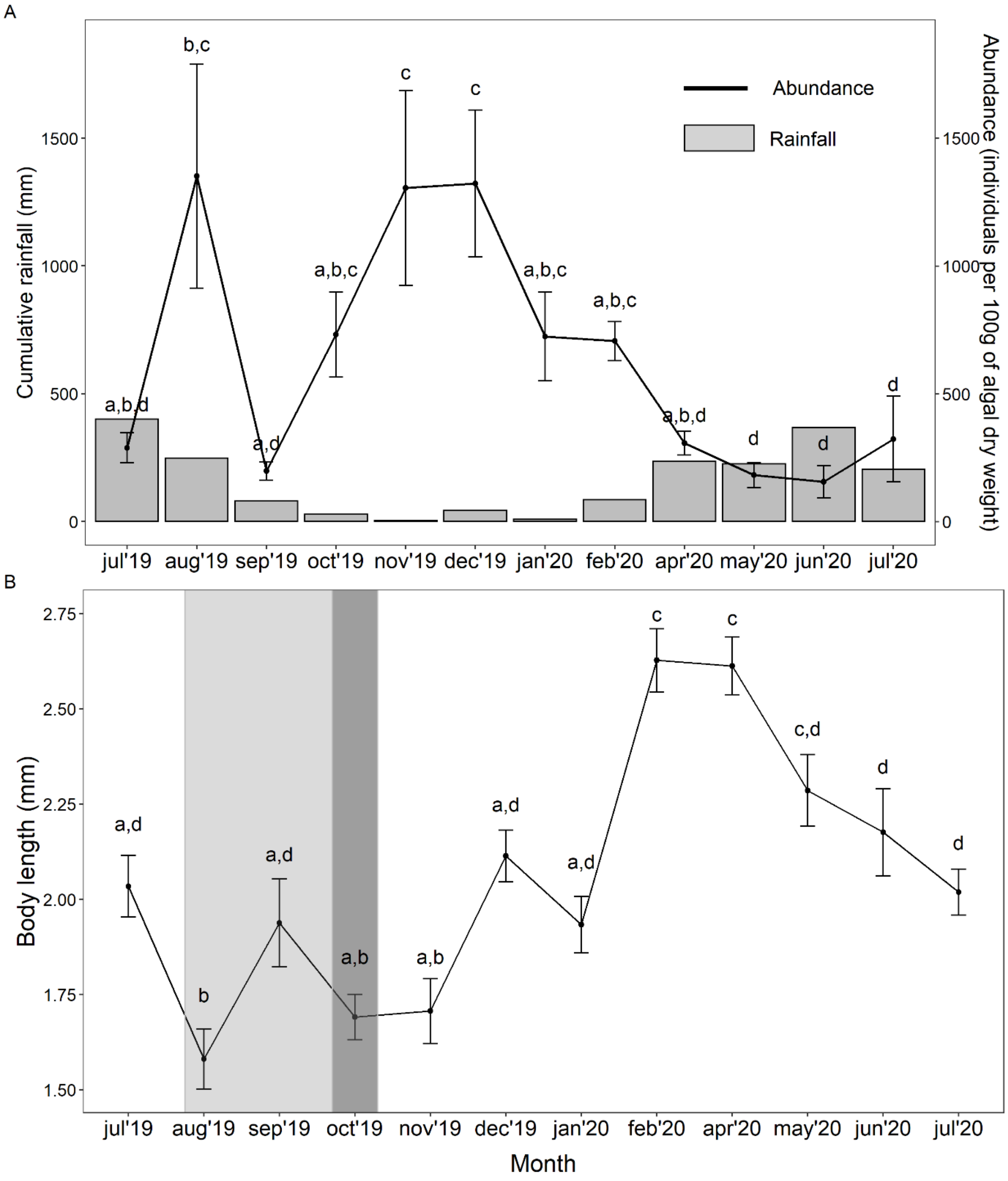


Fig. 3. Violin plot combined with boxplot of length distributions within different developmental stages in *Chondrochelia dubia*. Grey dots are the mean values.

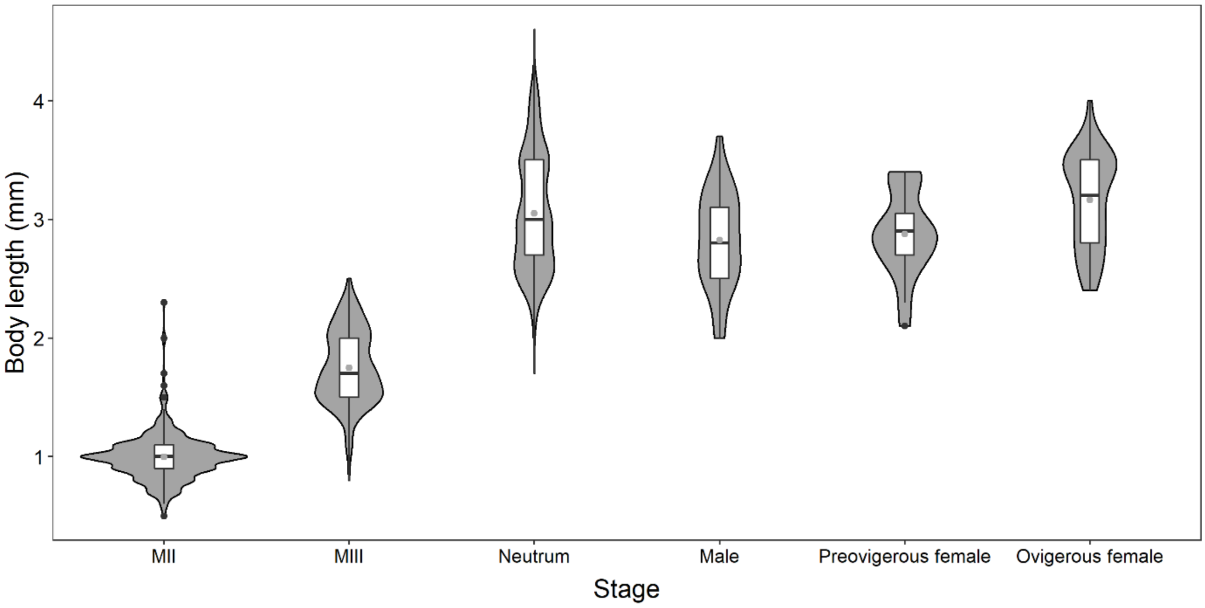


Fig. 4. (A) Number of juvenile, non-reproductive and reproductive individuals (males, pre-ovigerous and ovigerous females) per month. (B) Proportion of different sex categories of *Chondrochelia dubia* between July 2019 and July 2020.

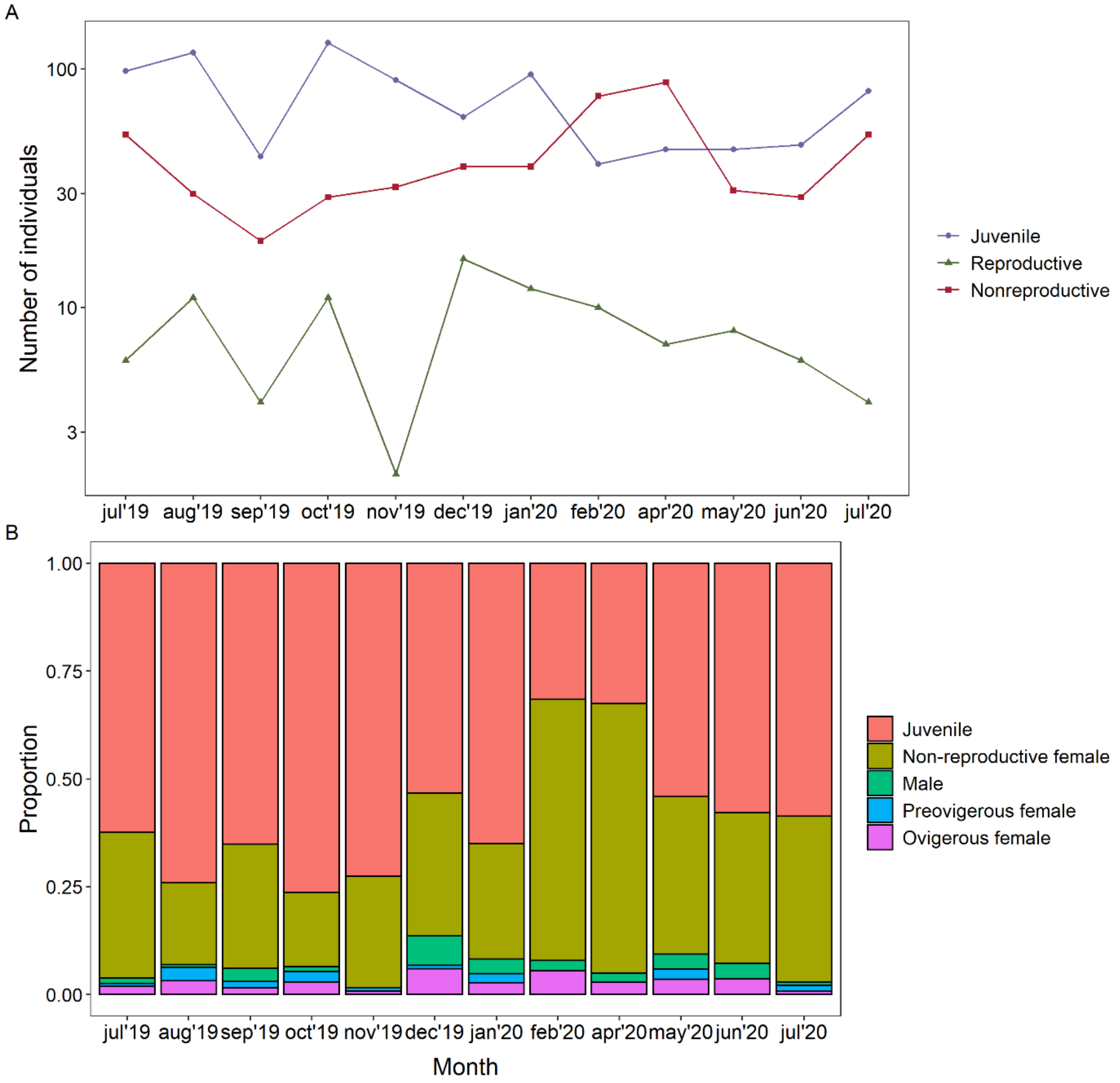


Table 1. Number of males and females, sex ratio of *Condrochelia. dubia* between July 2019 and July 2020, and results of chi-squared tests per month and size class.

Months	Females	Males	F:M ratio	Chi-squared	p-value
2019/07	57	2	33.5:1	59.362	<0.01
2019/08	40	1	40:1	36.214	<0.01
2019/09	21	2	12.5:1	17.926	<0.01
2019/10	38	2	19:1	42.481	<0.01
2019/11	34	-	-	34.028	<0.01
2019/12	47	9	5.2:1	31.641	<0.01
2020/01	46	5	9.2:1	37.123	<0.01
2020/02	84	3	28:1	77.538	<0.01
2020/04	92	3	30.6:1	87.485	<0.01
2020/05	36	3	12:1	35.021	<0.01
2020/06	32	3	10.6:1	27.225	<0.01
2020/07	56	1	56:1	51.158	<0.01
Total	583	34	17.14:1	453.17	<0.01

Size classes (mm)	Females	Males	F:M ratio	Chi-squared	p-value
1.5	2	1	2:1	-	-
2	34	4	8.5:1	20.25	<0.01
2.5	229	16	14.3:1	184.44	<0.01
3	162	12	13.5:1	127.59	<0.01
3.5	129	1	129:1	124.07	<0.01
4	26	-	-	24.038	<0.01
4.5	1	-	-	-	-

Fig. 5. (A) Logistic curve and size at first maturity (L_{50}) for females of *Chondrochelia dubia*. Blue envelope represents the 95% confidence interval. (B) Regression lines indicating morphometric maturity in males of *C. dubia*.

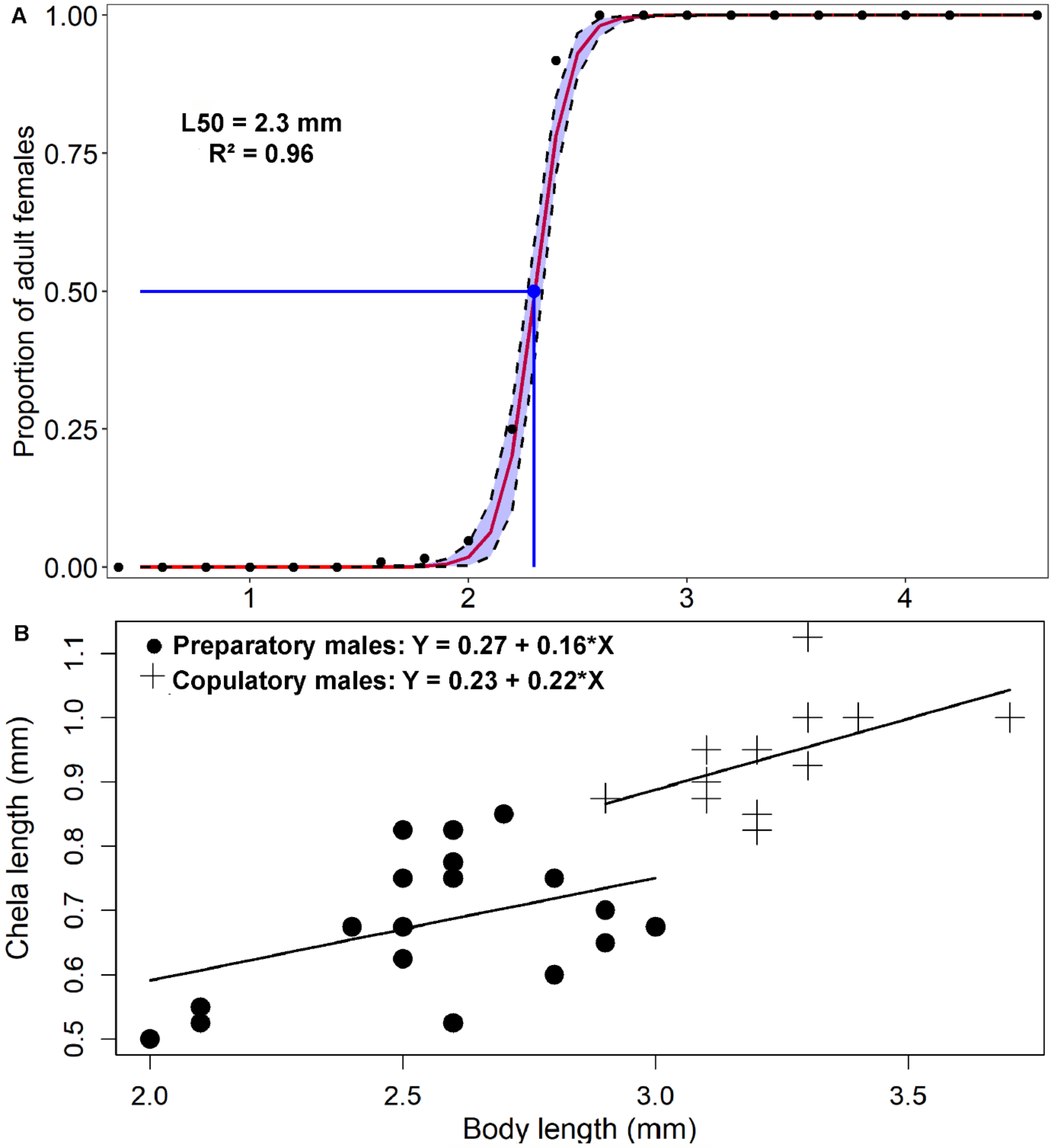


Fig. 6. von Bertalanffy growth curve and parameters for *Chondrochelia dubia* (pooled sexes). CI=95% confidence interval.

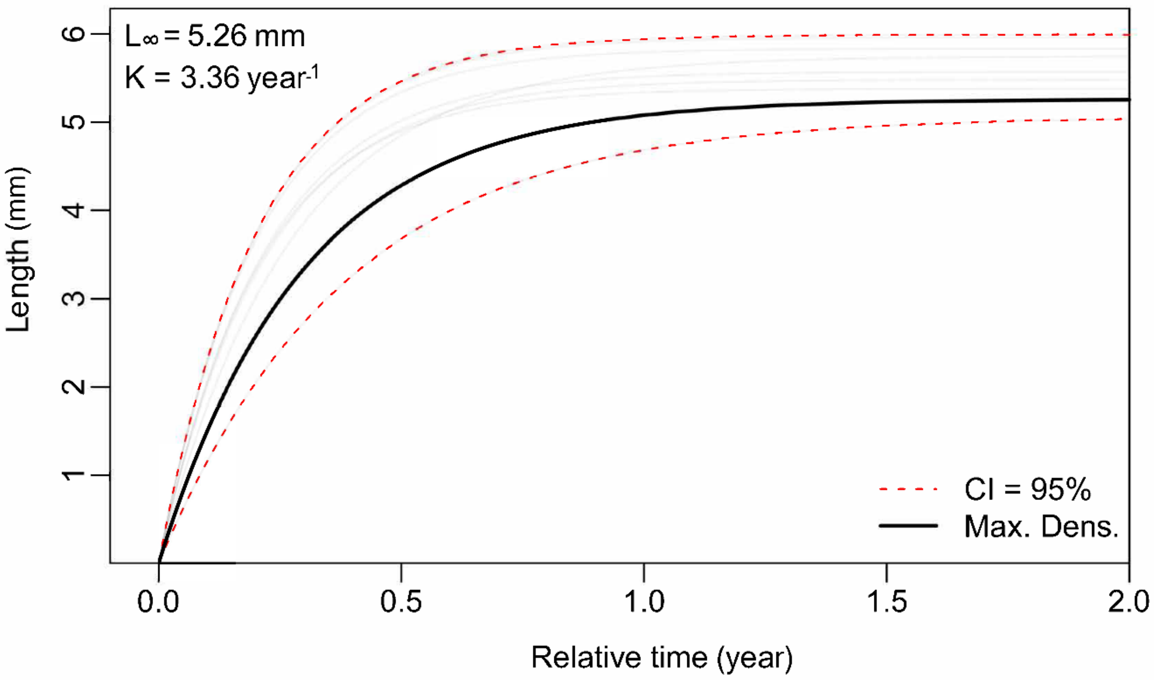


Table 2. Tanaid species and their respective von Bertallanfy population growth parameters estimated in previous studies from the southwestern Atlantic. M, natural mortality; SST, sea surface temperature (mean) (Boyer et al. 2018).

Species	***Chondrochelia dubia***	***Monokalliapseudes schubartii***	***Monokalliapseudes schubartii***	***Monokalliapseudes schubartii***	***Monokalliapseudes schubartii***	***Tanais dulongii***
Location	Paiva Beach, Pernambuco, Brazil	Itaipu Lagoon, Rio de Janeiro, Brazil	Araçá Region, São Paulo, Brazil	Mel Island, Paraná, Brazil	Patos Lagoon, Rio Grande do Sul, Brazil	Mar del Plata, Argentina
Coordinates	8°16′ S; 34°56′W	22°58’ S; 43°02’ W	23°49’ S; 45°24’ W	25°33’ S; 48°19’ W	32°01’ S; 52°07’ W	38°02’ S; 57°32’ W-38°10’ S; 57°38’ W
SST (°C)	27-28	25	23	21	19	14-15
L_∞(mm)	5.26	12.5	10.7	11	13.22	7-8
k (year^{-1})	3.36	2.8	3	3	4.54	0.55-0.63
t_0	0	-0.04	0	0	0	-
L_{50} (mm)	2.3	5.9	-	-	6.6	-
ф’	1.97	2.6	2.5	2.6	2.9	-
Longevity (year)	0.89	0.84	1	0.66 – 1	1	-
M (year^{-1})	5.77	0.99	-	-	-	-
Reference	Present study	Pennafirme and Gomes 2017	Leite et al. 2003	Almeida 1994	Fonseca and DIncao 2003	Rumbold et al. 2015

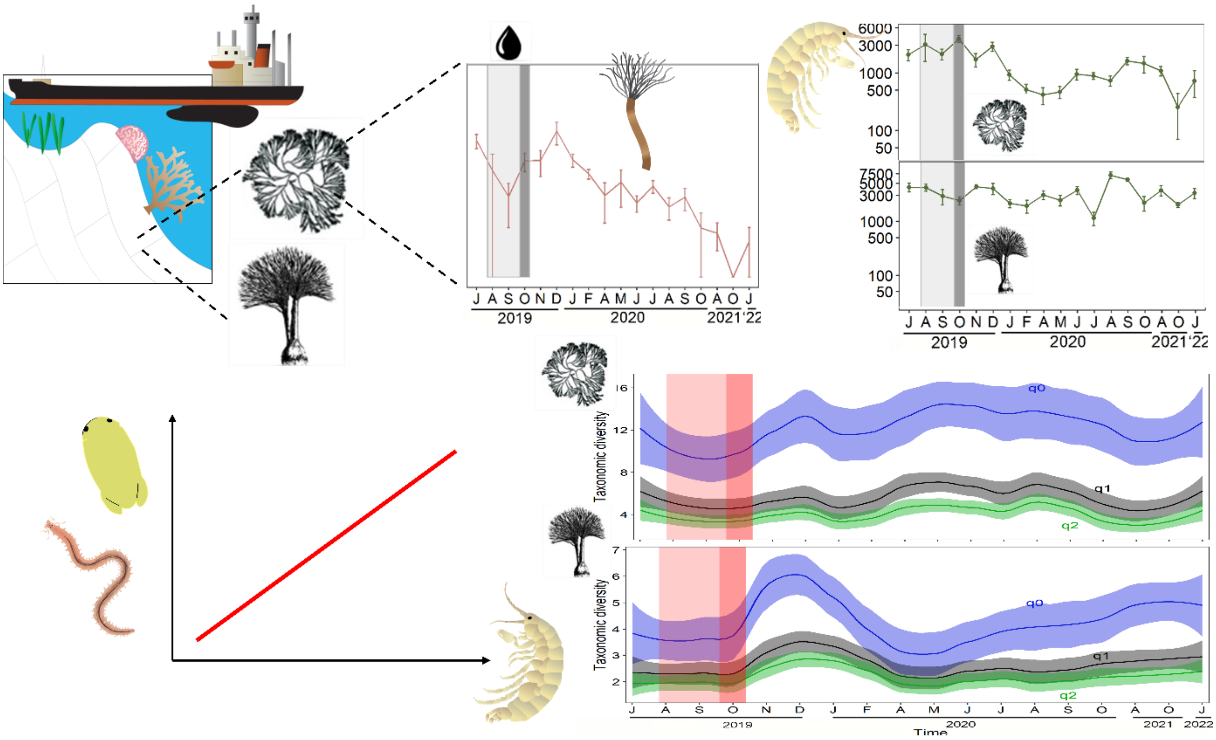
3 ARTIGO 2 - THE ROLE OF HABITAT HETEROGENEITY AND TIMESCALES ON THE RECOVERY OF REEF EPIFAUNAL COMMUNITIES AFFECTED BY A MASSIVE OIL SPILL IN THE TROPICS

A ser submetido ao periódico *Science of the Total Environment* (ISSN 0048-9697)

Highlights

- The unique Brazilian reefs were affected by a massive oil spill in 2019
- Epifaunal assemblages of two macroalgae had distinct responses to the impact
- Sensitive and tolerant taxa were found
- Probable buffering effect at landscape level due to distinct responses
- Need for long-term monitoring, especially for some key taxa

Graphical abstract



Abstract

From August 2019 to January 2020, the Brazilian Coast was impacted by the largest oil spill event in Tropical oceans so far. Paiva Beach, located in the northeast coast of Brazil, was one of the most affected regions by the oil spill in October 2019. Paiva Beach has important reef systems that harbor diverse macroalgal assemblages and their epifaunal communities. The present study aimed to evaluate the impacts of the Brazilian Oil Spill on epifauna associated with the seaweeds *Jania capillacea* and *Penicillus capitatus* collected in Paiva Beach from July 2019 to July 2022, and use the interaction macroalgae/epifauna/timescale as a proxy to quantify the effects of oil spills on community structure and recovery. The epifauna of both algae apparently did not suffer big changes in abundance immediately after the spill, however, taxa like echinoderms, sea spiders (Pycnogonida) and peracarid crustaceans had abundance drops during or soon after the event, whereas others like sabellid worms had increases in abundance possibly related to the spill. Both phytal assemblages also showed distinct temporal patterns in species diversity and abundance, the last one being positively correlated to amphipod abundance. The epifauna of *J. capillacea* showed an immediate decrease of taxonomic diversity, especially in rare species, whereas the epifaunal communities of *P. capitatus* actually gained a few taxa in the months immediately following the spill. The diversity profiles of both communities went back to normal levels within a few months; however, the tendency of abundance drop in *J. capillacea* might indicate a lasting effect. Abiotic variables and the maintenance of landscape heterogeneity, connectivity and keystone species (mainly amphipods) were possibly the main buffering factors for the phytal communities after the oil spill.

Keywords: Epifauna, Oil, Seaweed, Bioindication, Macrofauna.

1. Introduction

The Brazilian 2019 Oil Spill affected several coastal ecosystems (e.g., reefs, mangroves, sandy beaches, seagrass beds) and protected areas along nearly 3,000 km on the Brazilian coast and represented the most extensive oil spill ever recorded in the Tropical oceans (Magris and Giarrizzo, 2020; Soares et al., 2022). Since then, many studies have presented evidence of oil contamination in different compartments of the marine food web, like seagrasses (Magalhães et al., 2021), zooplankton (Campelo et al., 2021), filter feeders (Cerqueira et al., 2020), deposit feeders (Cerqueira, 2021), polychaetes (Lira et al., 2021), epifauna (Craveiro et al., 2021) and vertebrates (Soares et al., 2020). Despite the amount of evidence so far, relatively few studies (Craveiro et al., 2021; da Rosa, 2022; de Souza et al., 2022; Gusmao et al., 2021; Lira et al., 2021; J. L. Santana et al., 2022b) have quantified the direct and indirect effects of the oil spill on marine biota. Due to the recent nature of the event, the works published hitherto have focused on immediate to short-time impacts, with different levels of limitation due to the lack of baseline information about the affected species/assemblages.

The Brazilian northeast coast is characterized by the presence of beachrocks, intertidal reefs mainly formed by quartz and biogenic grains derived from algae and mollusks cemented by calcium carbonate (Laborel, 1970). These structures are either permanently exposed or submerged (at depths of 5–10 m), or exposed at alternate states depending on tide level (Bérgamo et al., 2022; Leão et al., 2016). Their morphology varies considerably, with a thickness of 3–5 m, width of up to 60 m, and a maximum extension of 10 km (Bérgamo et al., 2022; Laborel, 1970). These reefs play an important role in the maintenance of local marine biodiversity (Laborel, 1970; Leão et al., 2016) and provide a range of ecosystem services for nearby human populations, such as coastal protection, leisure areas and income generated by fishing and tourism (Leão et al., 2016). Although first described by Darwin (1841), the reefs of the Brazilian northeast coast are still relatively poorly studied. The beachrocks are covered by corals such as *Millepora alcicornis* (Linneaus, 1758), *Mussismilia hartii* (Verril, 1868), *Siderastrea* Blainville, 1830, *Montastrea cavernosa* (Linneaus, 1767) and *Porites astreoides* Lamarck, 1816 (Ferreira and Maida, 2006). However, the most representative sessile organisms in relative abundance are macroalgae and turf algae (Aued et al., 2018), whose assemblages are typically found in the tropical phycogeographic region (Horta et al., 2001).

“Macroalgal reefs”, defined as patches of carbonate reef with higher biogenic cover of fleshy algae than live coral (Fulton et al., 2019), are complex benthic environments that host abundant and diverse biological communities in tropical areas (Fulton et al., 2019; Tano et al., 2016). Seaweeds act as shelter against predators, reduce environmental stressors (e.g., wave action, dehydration, UV radiation), and act as important feeding, reproduction and foraging sites for multiple epifaunal species (Chen et al., 2021; Christie et al., 2009; Tano et al., 2016). Epifauna is dominated by small sized (usually 0.5 – 10 mm) animals such as peracarid crustaceans (e.g., amphipods, isopods, tanaids, cumaceans), gastropods and polychaete worms, being frequently found in high abundances in vegetated bottoms (Chen et al., 2021; Tano et al., 2016).

Despite its significance as an important link for secondary production in marine food webs, the epifauna has been often ignored or underestimated in many studies about oil spill impacts, especially in the Tropics (Roberts et al., 2008). These organisms can be particularly sensitive to pollution (Dauvin and Gentil, 1990; Rumbold et al., 2015) and their low mobility and diversified life histories are desirable features for model organisms in environmental impact studies (Lourenço et al., 2019). The variable degress of tolerance of macroinvertebrates facing organic pollutants have been the main aspect behind indexes based on sensitive/tolerant taxa ratios (Dauvin et al., 2016). Besides the intrinsic factors, spatial scales have been shown to play a role in the local responses of epifaunal communities, with significant changes in community structure and "vulnerability" even at relatively short distances (Grande et al., 2012; Tanaka & Leite, 2003). Altough mass mortality events and diversity losses of marine invertebrates are generally observed only in the first contact with the oil spill, its indirect impacts can last much longer (Suchaneck, 1993). This includes cascading effects like changes in community composition and zonation patterns, bioaccumulation, bioinvasions and disrupted succession processes (O'Brien and Dixon, 1976; Roberts et al., 2008; Suchaneck, 1993).

The present study aimed to evaluate the impacts of the 2019 Brazilian Oil Spill on seaweed epifaunal communities in the tropical coast of Brazil at short to medium timescales, and use the interaction macroalgae/epifauna/timescale as a proxy to quantify the effects of oil spills on community structure and recovery. This is also the first study to quantify the impacts of the 2019 Oil Spill using a relatively long (three years) timeseries. Our hypotheses were: 1) Different epifaunal groups will show distinct responses to the oil spill; 2) The characteristics of the algal microhabitat will interfere on epifaunal responses at the community and/or population level; 3) The effects of the oil spill will be more clearly noted at immediate to short timescales.

2. Material and methods

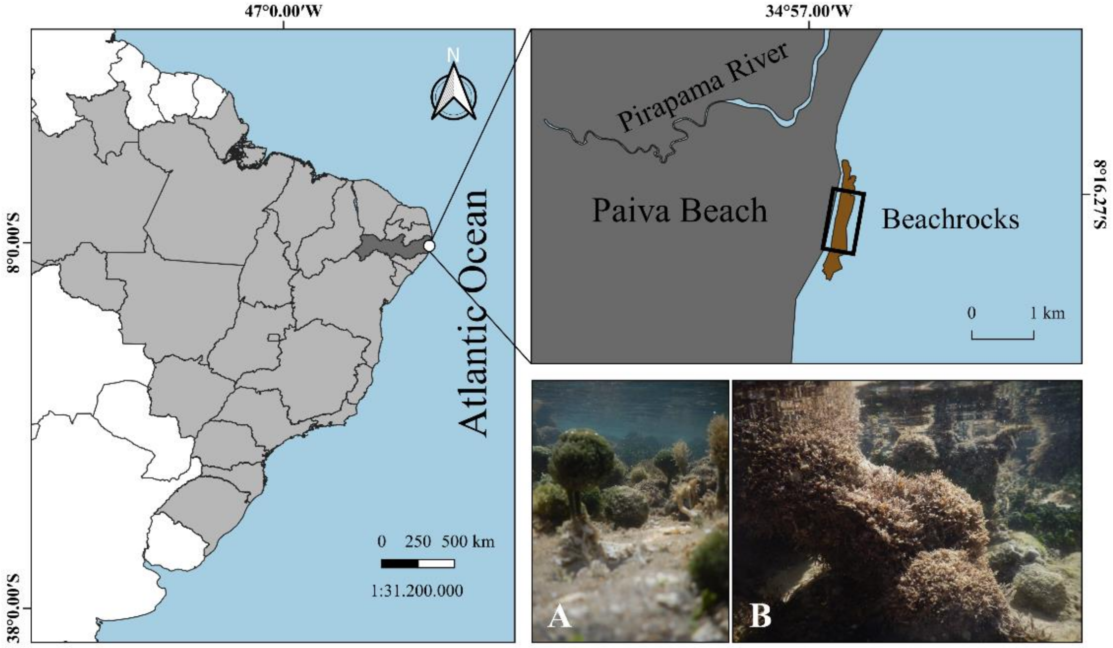
2.1. Study area

Paiva Beach (8°16'S; 34°56'W) is an open ocean tropical sandy beach approximately 7.8 km long located in Cabo de Santo Agostinho municipality (Pernambuco State, northeast Brazil) (Holanda et al., 2020). The climate is tropical hot/humid, with mean annual temperature above 25°C and precipitation averaging from 1800 mm to 2500 mm year^{-1}. The tidal regime is mesotidal semi-diurnal, with tide height varying between 0.7 m (neap tide) and

2.5 m (spring tide) (Domingues et al., 2017). The pluviometric regime can be divided into two seasons: a dry season (September – February, mean monthly rainfall 40 – 51 mm), and a rainy season (March – August, mean monthly rainfall 180 – 212 mm), with the majority of the rains typically occurring between April and June (400 mm month^{-1}) (Medeiros et al., 2001).

The shallow sandstone reefs of Paiva Beach are elongated rocky bodies parallel to the shoreline and densely covered by seaweeds (Craveiro et al., 2021; Laborel, 1970), with patchy beds of the perennial macroalgae *Jania capillacea* and *Penicillus capitatus* common in the intertidal zone (Figure 1). The region was the most affected by the 2019 oil spill (Bontempo Filho et al., 2022). In only one week (19-28 October 2019), more than 1,000 tons of crude oil were collected from Cabo de Santo Agostinho municipality alone (Craveiro et al., 2021). Although less perceptible, oil strains started appearing in Pernambuco's beaches by the end of August 2019 (Soares et al., 2020), months before the main sheet of crude oil arrived at Paiva Beach.

Figure 1. Location of the study area (Paiva Beach, Pernambuco State, Northeastern Brazil). Macroalgae collected in this study: A) *Jania capillacea* and B) *Penicillus capitatus*.



2.2. Sampling design and laboratory procedures

Sampling occurred monthly from July 2019 to October 2020 (except in March 2020, due to COVID-19 lockdown restrictions), and on three more occasions: April 2021 (1.5 years after the major spill), October 2021 (two years after the major spill), and July 2022. At each sampling occasion, ten fronds of the red seaweed *Jania capillacea* and ten fronds of the green seaweed *Penicillus capitatus* were collected within or close to tide pools. The fronds were wrapped with plastic bags to prevent motile animals from escaping and then removed from the substrate. Samples were fixed with 4% saline formalin. In the laboratory, the samples were sieved (0.3 mm mesh size) and the retained epifaunal organisms were sorted under the stereomicroscope. All specimens were identified to the lowest taxonomic level possible, counted and preserved in 70% ethanol. Algal dry weight (g) of each frond was measured using an analytical balance.

2.3. Statistical analysis

Abundance data (per 100 grams of algal dry weight) were weighted using the Morisita dispersion index (Morisita, 1962) in "*vegan*" package to downweigh highly aggregated taxa. Whenever aggregation was significant, we divided the abundance of each taxon by its index. Data were then square root transformed and used to calculate resemblance matrices with Bray-Curtis dissimilarity. Permutational analyses of Variance (Permanova) (Anderson, 2001) were used to compare community structure among sampling occasions and seasons in "*adonis*" package. For each algae, ordination plots were used to represent groups of samples from different occasions (before, during and after the oil spill) and the taxa which contributed the most for their separation ($p < 0.05$; $r > 0.3$) as vectors through Canonical Analyses of Principal Coordinates (CAP) (Anderson and Willis, 2003) using "*CAPdiscrim*" and "*envfit*" functions in "*BiodiversityR*" package. Sample completeness and diversity profiles using Hill numbers (Eq. 1) including rare (*q0* – species richness, Eq. 2), common (*q1* - Shannon exponential, Eq. 3) and dominant species (*q2* - Simpson's reciprocal, Eq. 4) were calculated for each month using the "four steps" method in "*iNEXT*" package (Hsieh et al., 2016).

Eq. 1 Hill's numbers general equation

$$N_q = \left(\sum_{i=1}^{S} p_i^q\right)^{1/(1-q)}$$

Eq. 2. Hill's numbers q = 0, Species richness

$$N_0 = \sum_{i=1}^{S} p_i^0$$

Eq. 3. $q=\lim_{q\rightarrow 1}1$, exponential of Shannon's entropy

$$N_{lim\rightarrow 1} = \left(\sum_{i=1}^{S} p_i^{lim\rightarrow 1}\right)^{1/(1-lim\rightarrow 1)} \equiv exp\left(\sum_{i=1}^{S} p_i \, lnp_i\right)$$

Eq. 4. q = 2, Simpson's reciprocal index

$$N_2 = \left(\sum_{i=1}^{S} p_i^2\right)^{1/(1-2)} \equiv \frac{1}{\sum_{i=1}^{S} p_1^2}$$

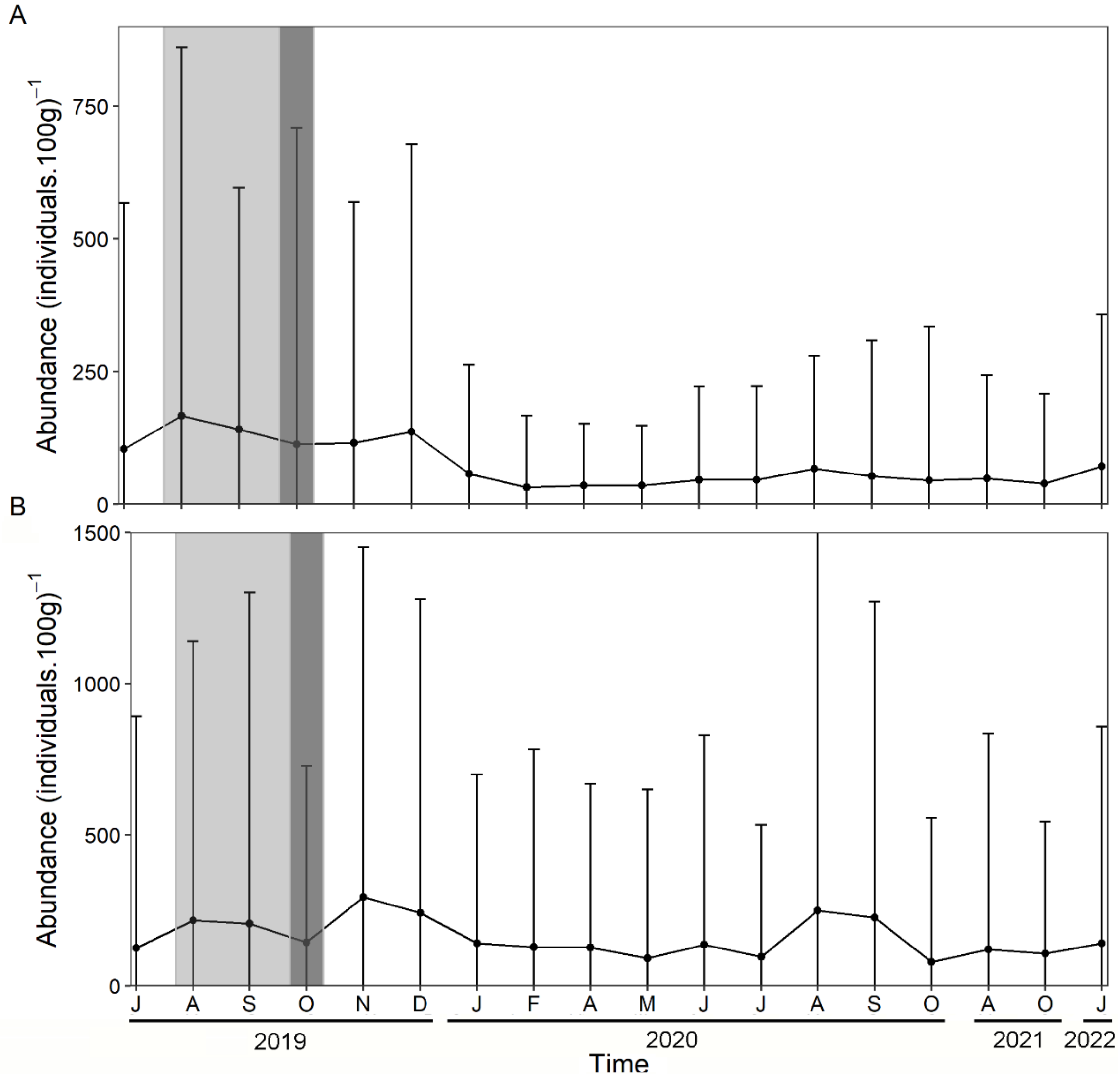
Where N_q is the diversity index, q is a parameter that represents the "weight" given to the relative abundance of the i-nth taxon (p_i). The q number never may be equal to 1, otherwise the equation would be unfeasible due to a division by zero. When $q = 0$, N_0 represents the total species richness (including rare species), when $q = \lim_{q \to 1}$, N_1 is the exponential of Shannon's index, due to common species' weight and when $q = 2$, N_2 is the inverse of Simpson's index with a higher "weight" attributed to dominant species.

The Generalised Additive Model (GAM) (Hastie and Tibshrani, 1990) was fitted as cubic regression splines (bs="cr") to estimate the expected effect of Amphipoda abundance variations on the other taxa (*Cymodoce* sp., Polychaeta, Syllidae and *Janaira gracilis*) abundance trends in two different algae species, *P. capitatus* and *J. capillacea*. The models were established for each taxon, considering their abundance log as the response variable and Amphipoda abundance as the predictor variable. The probability distribution model used was the Gaussian family with the logarithmic link function. All analyses were performed in R software (R Core Team, 2022) considering a significance level of 0.05.

3. Results

There were 40 and 50 taxa associated with *Penicillus capitatus* and *Jania capillacea*, respectively. There was strong evidence of temporal variation in the structure of epifaunal communities of *J. capillacea* (months - Pseudo-F: 8.87, $p < 0.01$; seasons - Pseudo-F: 10.21, $p <0.01$) and *P. capitatus* (months - Pseudo-F: 4.77, $p <0.01$; seasons - Pseudo-F: 3.46, $p <0.01$). In general, lower abundances occurred during the rainy season, with discrete peaks of abundance in dry months, which can be more easily seen in *P. capitatus*. There wasn't any drastic decrease in total abundance during the oil spill months on both algae, however, it is important to note the higher values of standard deviations during the period of oil arrival and soon after, especially in *J. capillacea*. A relative tendency of decrease in total abundance was also observed in *J. capillacea* during the years following the spill, which remained low after the subsequent rainy seasons (Figure 2).

Figure 2. Variation in mean abundance of the epifaunal communities of *Jania capillacea* (A) and *Penicillus capitatus* (B) from July 2019 to July 2022. Bars indicate standard deviations and the light grey and dark grey rectangles represent the periods of lower (August-September 2019) and strong oil arrival (October 2019), respectively.



The nine most abundant taxa in each alga (Figures 3 and 4) corresponded to more than 90% of their total abundances, with peracarid crustaceans such as amphipods, isopods (*Janaira gracilis*) and tanaids (*Chondrochelia dubia*) the most dominant taxa. In *J. capillacea* syllids were clearly affected by the oil spill, whereas some other groups had their lowest abundances in rainy months, probably not related to the spill. However, in *J. capillacea*, Amphipods, sabellid worms and the isopod *Janaira gracilis* had an overall tendency of decrease in abundance during the studied period (Figure 3). In *P. capitatus* the dominant taxa had apparent natural stochastic variations in abundance year-round, perhaps Pycnogonida (sea spiders) being the most affected by the spill (Figure 4). For some epifaunal groups, mainly those associated to *J. capillacea*, tendencies of populational growth were interrupted by the main spill, as observed in Podocopida (Ostracoda), Syllidae and *J. gracilis* (Figure 3).

Figure 3. Temporal variation in mean abundance of the most abundant epifaunal taxa of *Jania capillacea* from July 2019 to July 2022. Bars indicate standard errors and the light grey and dark grey rectangles represent the periods of lower (August-September 2019) and strong oil arrival (October 2019), respectively.

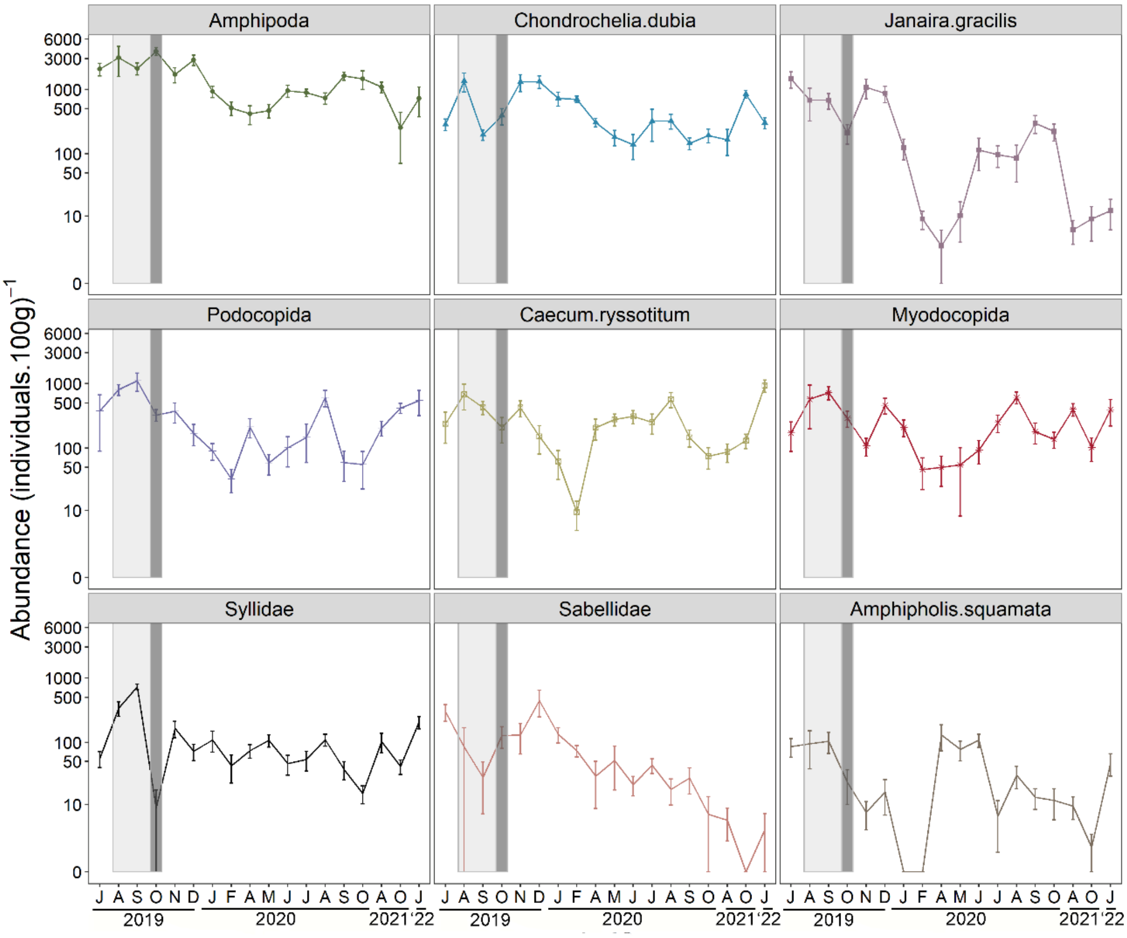
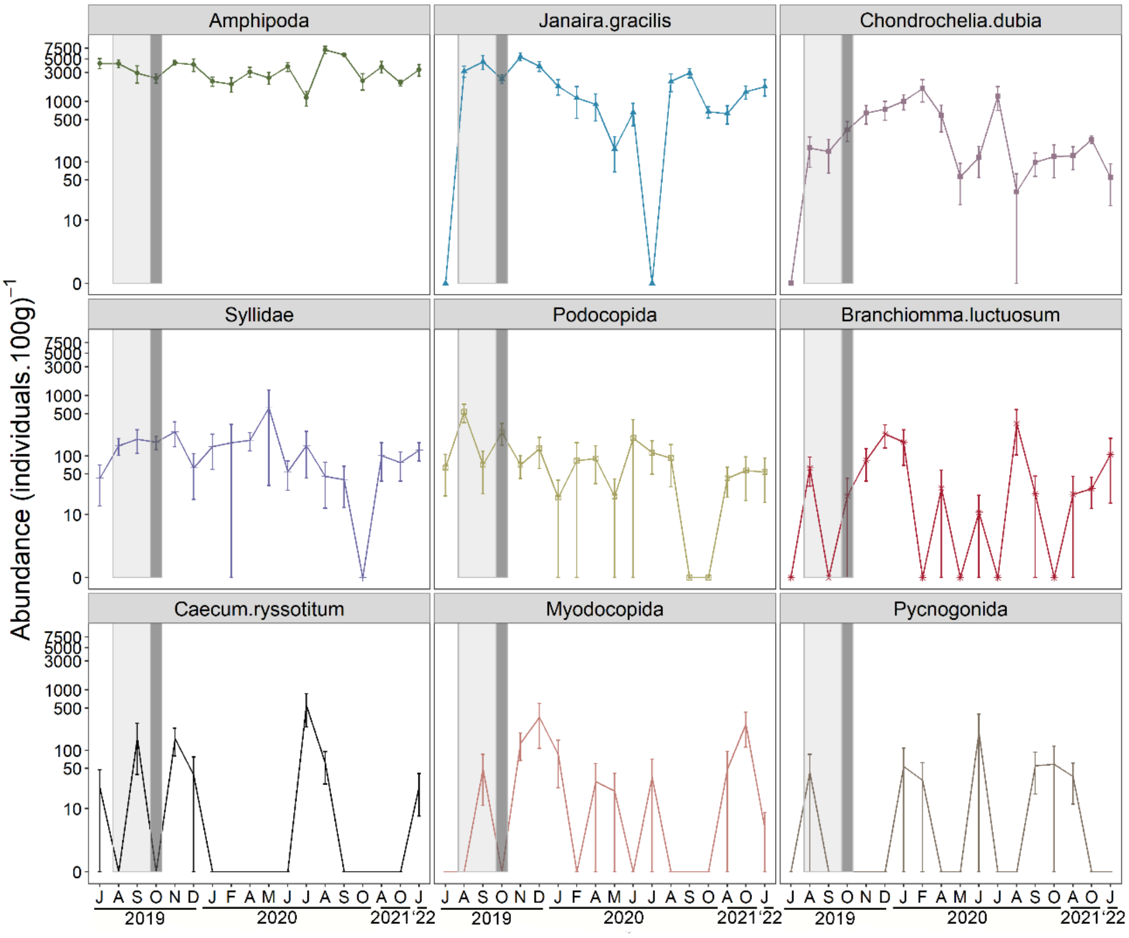


Figure 4. Temporal variation in mean abundance of the most abundant epifaunal taxa of *Penicillus capitatus* from July 2019 to July 2022. Bars indicate standard errors and the light grey and dark grey rectangles represent the periods of lower (August-September 2019) and strong oil arrival (October 2019), respectively.



Strong evidence of positive correlation was found between the abundance of amphipods and other taxa in both algae (Figure 5). In *J. capillacea*, the lowest richness (18 taxa) and evenness were found immediately after the oil spill (October 2019), whereas in *P. capitatus* evenness values showed a tendency of subtle decrease from the oil spill period (Figure 6). Sample completeness was 100% for both algae in all months, and the asymptotic values of species richness and Shannon diversity were equivalent to the estimated values.

Figure 5. GAM models showing the correlation between amphipod abundance (predictive variable) and other taxa abundance in both algae.

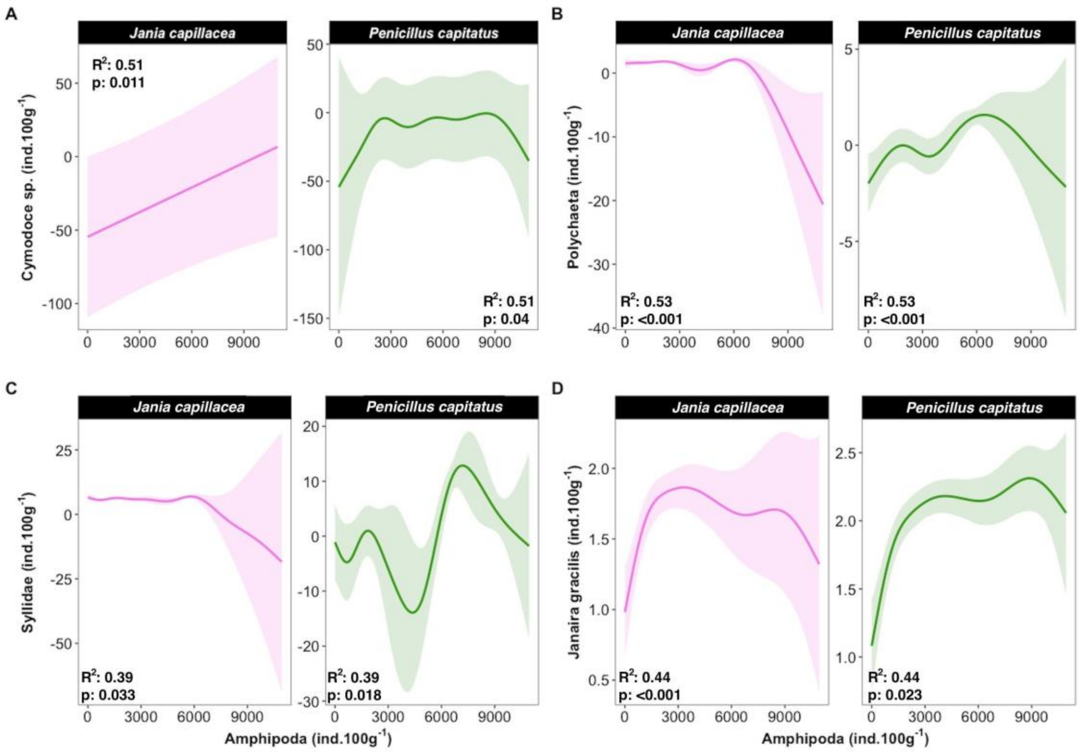
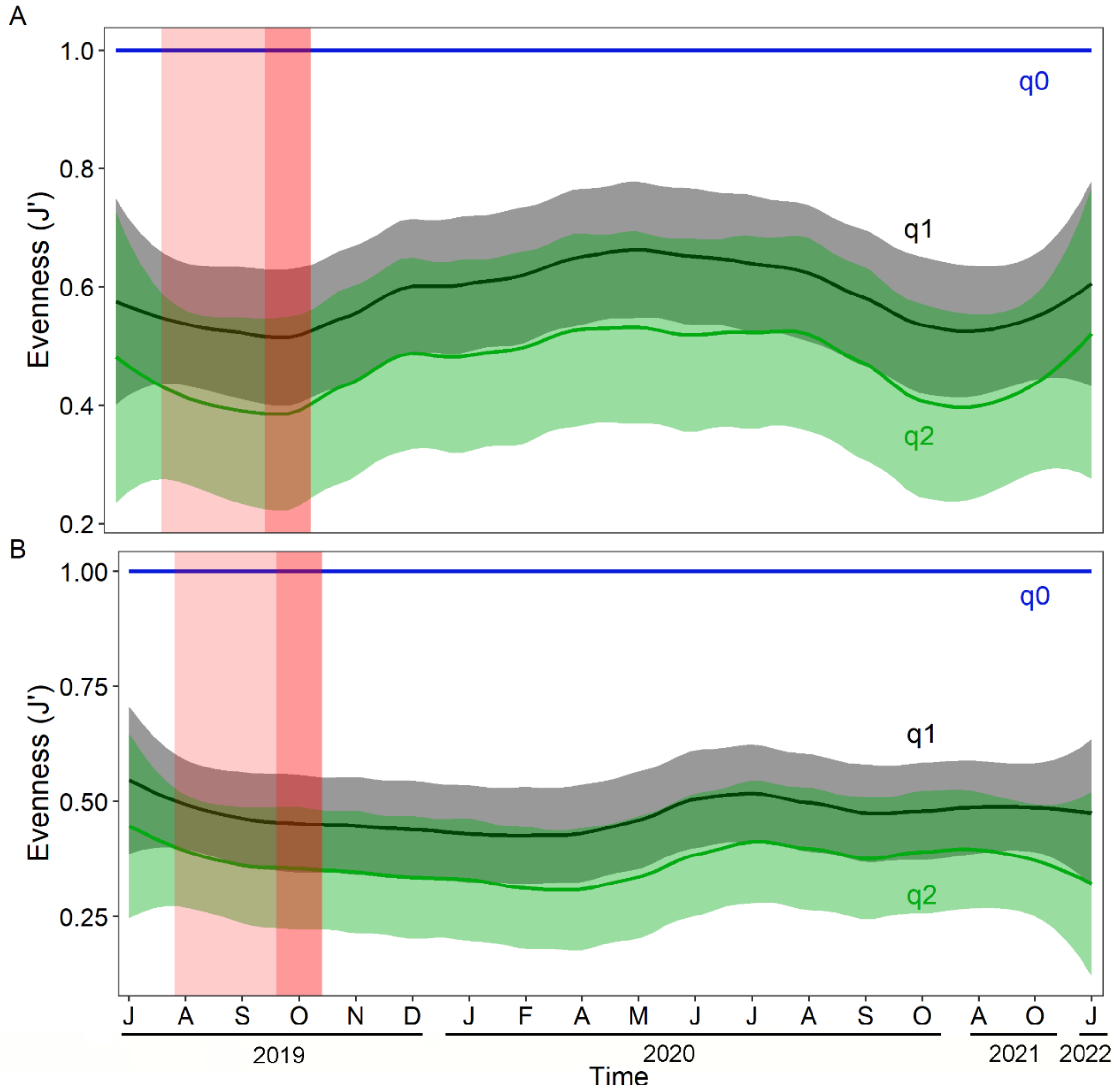
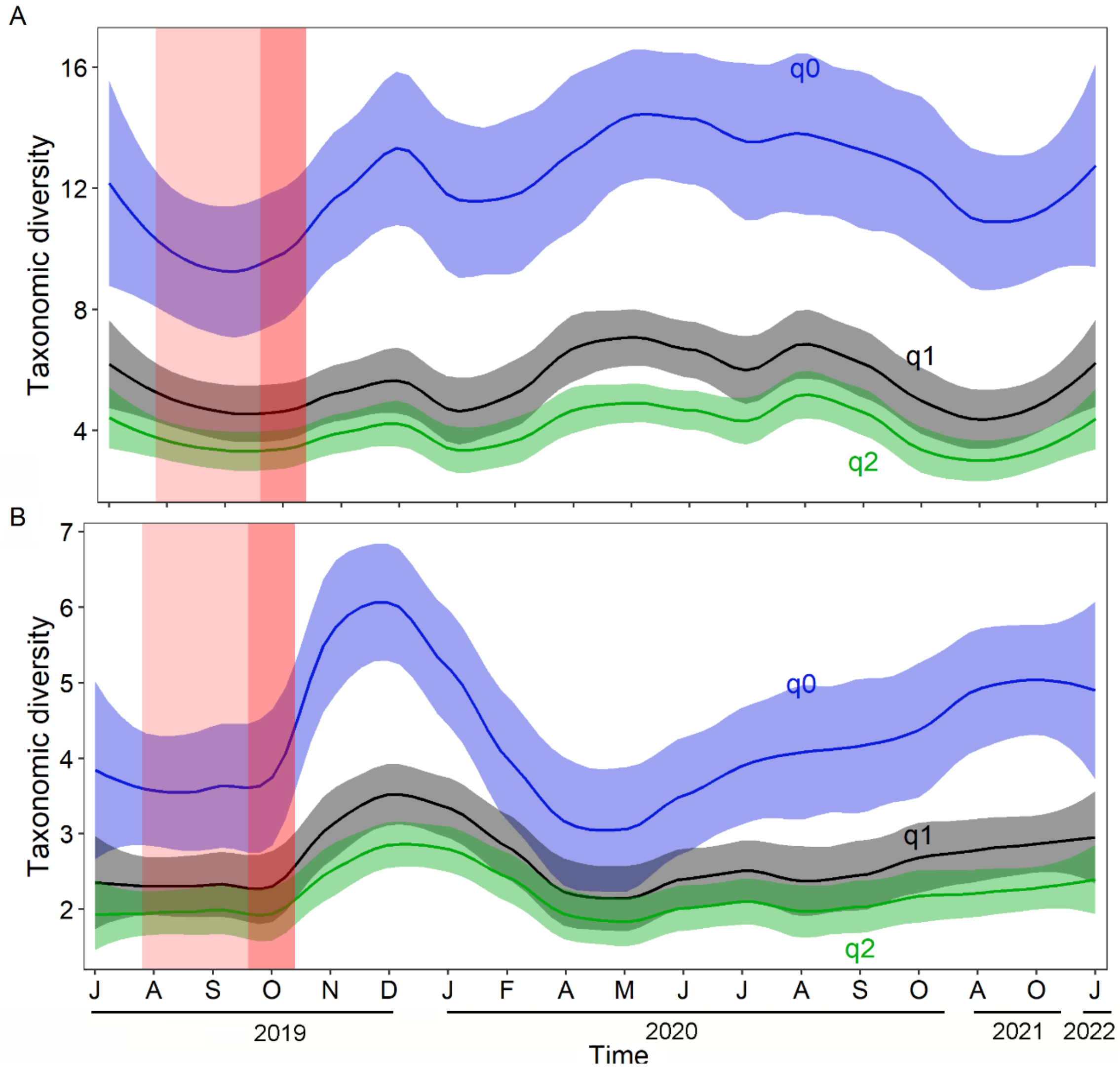


Figure 6. Temporal variation in the evenness (J') profiles of each *q* order (Hill's numbers) in the epifauna of *Jania capillacea* (A) and *Penicillus capitatus* (B) from July 2019 to July 2022. The light red and red rectangles represent the periods of lower (August-September 2019) and strong oil arrival (October 2019), respectively.



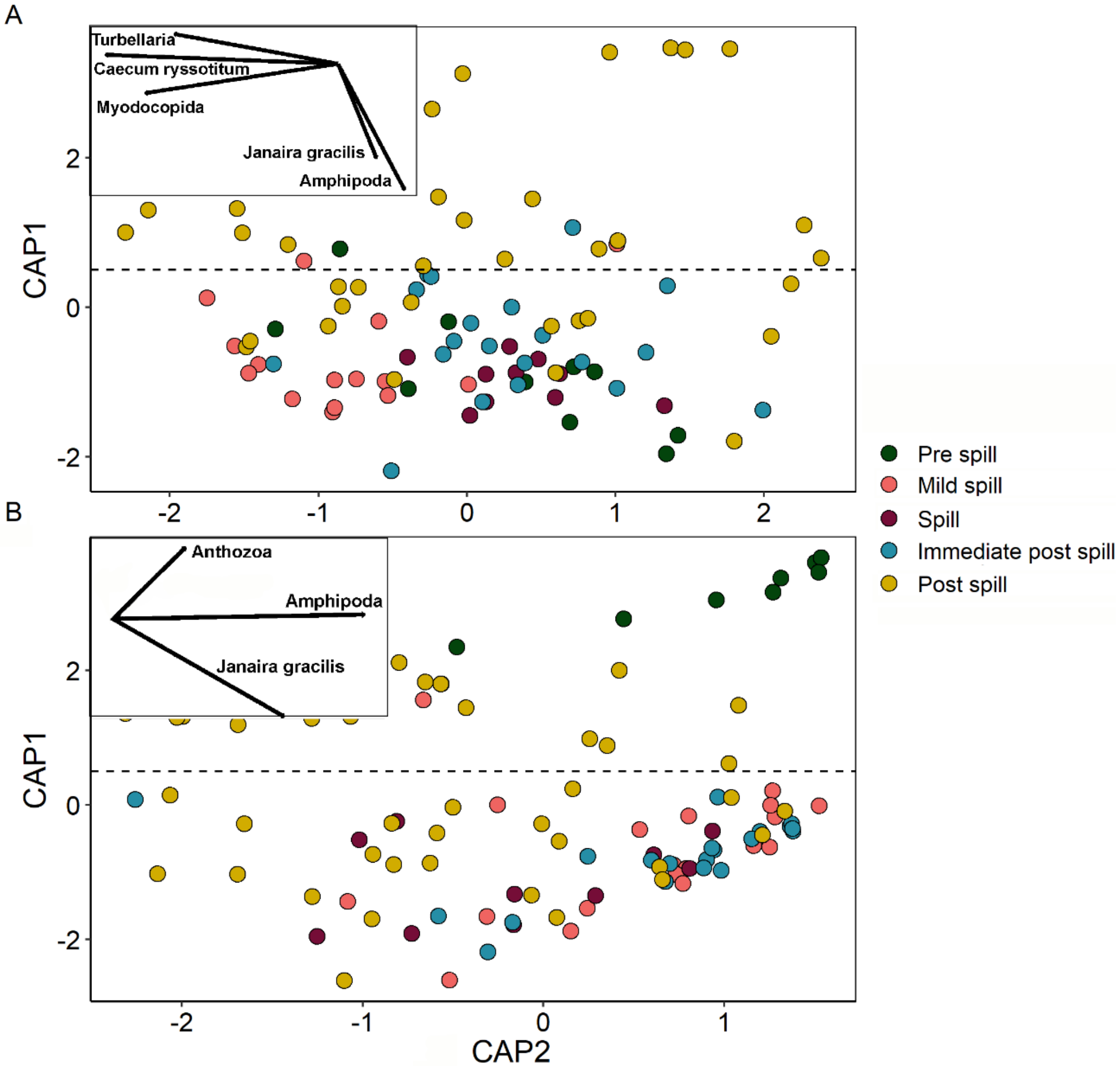
Most taxa that disappeared during the oil spill in *J. capillacea* were rare species (Figure 7), such as Echnoidea (juvenile sea urchins), Pycnogonida, Anthozoa (anemones) and Turbellaria (flatworms). In contrast, richness in *P. capitatus* increased (either in rare, abundant and dominant taxa) from 12 taxa (July 2019) to 17 taxa (December 2019) during the months immediately after the spill, returning to pre-spill levels soon after (Figure 7).

Figure 7. Temporal variation in diversity profiles of each *q* order (Hill's numbers) in the epifauna of *Jania capillacea* (A) and *Penicillus capitatus* (B) from July 2019 to July 2022. The light red and red rectangles represent the periods of lower (August-September 2019) and strong oil arrival (October 2019), respectively.



Some of these "new" taxa found temporally in *P. capitatus* were Turbellaria, Polyplacophora (chitons), Orbinidae and *Caecum brasilicum*. The ordination plots showed a separation of samples of the post spill period from other periods in *J. capillacea*, mainly caused by Amphipoda and *J. gracilis*, whereas in *P. capitatus* post and pre spill samples were at the same side of the ordination, the last ones distinguished by Anthozoa (Figure 8).

Figure 8. Ordination plots representing samples from pre spill (July 2019), mild (August-September 2019), main (October 2019) immediate post (November-December 2019) and post spill (July 2020, October 2020, October 2021 and July 2022) occasions. Vectors indicate the taxa which contributed the most for group separation ($p < 0.05$; $r > 0.3$) in *Jania capillacea* (A) and *Penicillus capitatus* (B).



4. Discussion

The epifauna of both algae apparently did not suffer big changes in abundance immediately after the spill, however, some taxa had abundance drops during or soon after the event. Both phytal assemblages also showed distinct temporal patterns in species diversity and abundance, the last one being significantly correlated to amphipod abundance. The higher standard deviations and mean abundance values during the spill period especially in *J. capillacea* might be a sign of contamination, since organisms tend to become more aggregated in stressed environments (Warwick and Clarke, 1993). However, phytal organisms, especially those with direct or sessile development, have naturally aggregated distributions (Tanaka and Leite, 2003), which means that such pattern might be related to dry season instead, when some tropical marine species usually have their highest abundances (Alves et al., 2023; Santos et al., 2019).

However, in *J. capillacea*, these peaks were not as strong in the following dry months after the spill during the studied period. This might be a reflex of the extreme rain events in recent years or broader seasonal cycles, since phenological changes in thallus growth and decay has been shown to cause migrations of phytal amphipods due to decrease of habitable spaces and habitat quality (Kodama et al., 2022). The Coast of Pernambuco is susceptible to strong wave action, storms, and high sedimentation rate in the rainy season (Medeiros et al., 2001), which may cause important qualitative and quantitative changes in the biogenic cover of the reefs (Piazzi et al., 2021; Santana et al., 2022a), like community simplification and decrease of thallus height in some algal species (author's unpublished data). Such changes could be even more disruptive than the oil spill itself. It is also possible that the oil spill and the rainy season had acted synergically: the oil lowered the growth rate of some epifaunal populations below a threshold, causing the expected decreases in rainy season to be more severe and have a lasting effect upon epifaunal abundance in *J. capillacea*. However, the lack of baseline studies in the area limit our conclusions.

In general, the abundance of molluscs like *Caecum ryssotitum*, echinoderms, cnidarians (Anthozoa), sea spiders (Pycnogonida) and polychaetes (Syllidae) reduced after the disaster, revealing their sensitivity to oil. Some of these organisms, such as gastropods and echinoderms, are well known to be sensitive to oil pollution (Suchaneck, 1993). In contrast, some taxa like sabellid worms (mainly the r-strategist *Branchiomma luctuosum*) and chitons were favored or at least not immediately affected by the oil arrival, confirming our first hypothesis that different taxa had distinct responses to the event. Such variable degrees of tolerance depend on the physiology, mobility, life histories and feeding habits of the organisms (Grande et al., 2012; Hamacher et al., 2022; Lourenço et al., 2019).

The increase of opportunistic taxa (e.g., *B. luctuosum* in this study) might occur when there is a significant disruptive impact (Suchaneck, 1993), as observed in Paiva beach from August 2019. *Branchiomma luctuosum* is a filter-feeding species that can become widespread in stressed environments, with a well-known colonizing potential (Lezzi et al., 2016). However, the abundance of Sabellidae in *J. capillacea* had a tendency of decrease during the months after the spill, probably due to its ephemerous life strategy facing a changing environment. Since some specimens were not identified to species level, the real diversity of taxa and responses of these phytal communities can have been understimated, however, the benefits of studying the whole community might compensate the losses of information caused by poor taxonomic resolution.

The abundance of some taxa was strongly correlated to the abundance of amphipods in the present study. Some species such as the so-called “ecosystem engineers” have strong impacts on community structure and might determine the rate of recovery after oil spill impacts (Fleeger et al., 2020). When the eliminated species are essential for the community (e.g., the seaweed that forms the biogenic habitat from which other species depend upon), then a quick recovery is much less likely (Suchaneck, 1993). For example, in salt marshes affected by the Deepwater Horizon oil spill in the Gulf Coast of the United States, the abundances of some macrofaunal groups were positively correlated with the abundance of an ecosystem engineer, the bioturbator amphipod *Apocorophium louisianum* (Fleeger et al., 2021). This species might have stimulated the recovery of the affected assemblages by increasing benthic microalgae production/availability, and/or resuspension of organic matter to surface- and suspension-feeding invertebrates (Fleeger et al., 2021). The tendency of decrease in abundance observed in *J. capillacea* for the two most numerous taxa, Amphipoda and *Janaira gracilis*, although in part coincide with rainy season, remained lower than expected in the following periods. The fall of these taxa, especially Amphipoda, likely accounted for the overall decrease of abundance of the epifauna in *J. capillacea*.

In contrast, amphipods are also usually considered sensitive to oil pollution (Dauvin and Gentil, 1990; Dauvin et al., 2016; Grande et al., 2012), and there is evidence of oil ingestion by sponge-dwelling polychaetes (*Branchiosyllis* spp.) collected in the study area (Lira et al., 2021), therefore, it is possible that toxic compounds have persisted in the food web, although inconclusive. Gammarid amphipods, besides usually being the most abundant group found in marine macrofauna (Carvalho et al., 2018; Jacobucci and Leite, 2008), are also very diverse in life histories and feeding strategies (Hughes and Ahyong, 2016), and consequently can have different ecosystem roles and responses to chemical pollution. For example, Lourenço et al. (2019) have found higher concentrations of hydrocarbons in omnivore families (Hyallidae) than herbivore (Ampithoidae) and detritivorous (Caprellidae) families, whereas Bellan-Santini (1980) observed that populations of some amphipod species have increased in polluted sites.

The epifauna of *Jania capillacea* suffered a visible effect upon the oil arrival, with the immediate overall decrease of taxonomic diversity, whereas the epifaunal communities of *P. capitatus* gained a few taxa in the months immediately following the spill. This difference is particularly interesting, since both algae cohabit the same reef only meters apart, share epifaunal taxa and were simultaneously affected by the same spill. It is possible to hypothesize that factors related to thallus morphology/complexity, micro-scale spatial distribution, and chemical composition of algae may be the main drivers of different responses of macrofauna to the oil spill. The two algae have very different architectures, with *J. capillacea* being more ramified and complex, which can host not only a higher number of taxa, but also trap more sediment and, possibly, oil fragments. Also, both algae occupy different zones within the studied reef system. While *P. capitatus* usually occur in sand bottoms inside tide pools, *J. capillacea* is more common in exposed areas in the borders of tide pools or reef crests. These features make *J. capillacea* more exposed to the suspended oil and its location and complex structure might difficult the physical removal of the oil (O'Brien and Dixon, 1976). Differences in chemical properties of the algae might also have influenced the distinct responses of their epifauna. Some algal thalli are more vulnerable to the contact with oil, whereas others can even produce mucilaginous compounds that "clean up" the algal surface (Grande et al., 2012; O'Brien and Dixon, 1976).

Many studies have highlighted the importance of algal identity on the structure of epifaunal communities (e.g., Bates, 2009; Gestoso et al., 2012; Holmlund et al., 1990). This can be explained by several intrinsic factors such as thallus morphology, toughness and complexity, chemical defenses, composition, interstitial size, epiphyte load and preferences of the epifauna (Bates, 2009; Carvalho et al., 2018; Gestoso et al., 2012). According to Olabarria et al. (2002), the spatial distribution of small organisms can be explained by the interactions of three main factors: 1) differential rate of larval/juvenile settlement; 2) differential survival rate; and 3) active habitat selection by adults. The richness gain in *P. capitatus* soon after the spill, for example, might be a consequence of habitat selection of some organisms that found a transitory refuge in this alga while seeking more suitable substrata. Besides, the stochastic oscillations in many taxa inhabiting *P. capitatus* might be a consequence of a more dynamic environment within its canopy compared to *J. capillacea*, with variable rates of survival and recruitment of individuals. This supports our second hyphotesis, that the algal microhabitat likely influences the epifauna's responses to environmental drivers at the community and/or population level.

Few months after the main oil spill, the communities already had signs of recovery, like the return of species richness and diversity profiles back to pre-disaster levels. Epifauna tends to recover relatively fast after oil spill impacts (Roberts et al., 2008), however, other abiotic factors might help to understand this recovery. First, the oil was transported for long distances in the sea, which might have caused the dissolution of light and toxic compounds before reaching the coast (Hamacher et al., 2022). Second, most of the oil was quickly removed upon reaching Paiva Beach by the work of authorities and especially volunteers (Bontempo Filho et al., 2022; Craveiro et al., 2021). Third, the high temperatures and strong hydrodynamics of the area, combined with weathering processes (e.g., evaporation, oxidation, biodegradation) probably caused much of the oil to be vanished in the area (Bontempo Filho et al., 2022; Craveiro et al., 2021; Lira et al., 2021). However, tar balls (compact oil residuals mixed with sand) have been found in the surf zone of Paiva Beach many months after the main spill, showing that some of the oil remained in the environment and was buried and reworked periodically (Bontempo Filho et al., 2022). Storms also have caused oil strains to reappear in many beaches of the Brazilian Northeast Coast since then, probably due to resuspension of sediments (Bontempo Filho et al., 2022). Besides, evidences of oil strains from other, possibly chronic, spill events have been found among the recent reappearances of oil in Brazilian beaches (de Azevedo et al., 2022; Lobão et al., 2022). Oil fragments incrusted onto hard substrates like the sandstone reefs of Paiva Beach might persist in the environment for even more time, even decades, until full degradation (Bontempo Filho et al., 2022).

The high spread of samples from the post spill period in the ordination analysis might be a consequence of their larger number of samples compared to other periods, however, a separation is still noticeable between the post spill and the other periods in *J. capillacea*, suggesting a community shift in some level. Our third hypothesis, that the effects of the oil spill would be more visible in immediate to short timescales, might be true considering the rapid changes in species richness and diversity profiles in both algae during the first months of the oil spill period; however, we don’t completely discard the possibility of a lasting effect of the oil spill enhanced by rainy season upon epifaunal abundance and community structure, especially in *J. capillacea*. Therefore, the continued and more detailed monitoring of these organisms for longer timescales will be necessary for more certain conclusions about the oil spill event.

Despite the relatively short distances, phytal assemblages only meters apart from each other can differ significantly within the same shore (Tanaka and Leite, 2003). The distinct local “behaviors” of the two phytal communities studied, being the epifauna of *J. capillacea* the more affected, might be a positive feature against environmental impacts. After an impact, heterogenous spaces have a mixture of more and less contaminated microhabitats to where organisms can migrate and recolonize (Grande et al., 2012; Roberts et al., 2008). Highly synchronized communities in homogenous habitats, in the other hand, can suffer a widespread impact and higher risk of extinction (Walter et al., 2021). The presence of diverse algal assemblages within the studied region might have a buffering effect upon epifaunal oscillations on the landscape level, although changes in smaller, local scales might occur. This reinforces the importance of habitat complexity and connectivity and the need to preserve these features to increase resilience and stability in reef systems.

5. Conclusions

The epifaunal communities associated with *Jania capillacea* and *Penicillus capitatus* had distinct responses to the oil spill, with stronger effects on the epifauna of *J. capillacea*. Abiotic variables and other factors such as landscape heterogeneity (i.e., diverse reef topography with distinct algal communities that, consequently, harbor asynchronous epifaunal assemblages), connectivity and possible "keystone species" (mainly amphipods) were possibly the main buffering factors for the phytal communities after the oil spill. Therefore, the preservation of spatial features like structural complexity might be of greater importance for reef conservation and resilience after environmental impacts. The increase of taxonomic resolution for some taxa and the continued monitoring of these communities will be essential to generate baseline information about epifaunal assemblages in the studied area and quantify in detail natural and/or anthropogenic oscillation patterns for longer timescales. This study might also be a reference within the scarce literature on oil spills' effects on coastal tropical environments and reef biota.

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4 CONSIDERAÇÕES FINAIS

O desastre de derramamento de petróleo que atingiu a Praia do Paiva em 2019 causou impactos diretos e possivelmente indiretos na macrofauna recifal costeira, com diferentes respostas dos grupos epifaunais. O crustáceo *Chondrochelia dubia*, por exemplo, demonstrou ser um dos táxons relativamente tolerantes, observação possivelmente relacionada à construção de tubos. Os parâmetros de crescimento, estimados pela primeira vez para a espécie, indicam uma história de vida oportunista e de crescimento relativamente rápido comparado a outras espécies de Tanaidacea. Por outro lado, táxons como *Amphipholis squamata*, Pycnogonida, *J. gracilis* e alguns moluscos e poliquetas demonstraram ser aparentemente sensíveis aos efeitos do óleo, em diferentes graus. A nível de comunidades, as assembleias associadas às algas *Jania capillacea* e *Penicillus capitatus*, respectivamente, comportarem-se de maneiras distintas no período estudado, sendo a primeira a mais afetada.

A complexidade topográfica do recife, que abriga comunidades algais distintas e, por conseguinte, permite epifaunas com alto grau de assincronicidade, somada à conectividade e à presença de “espécies-chave” (especialmente anfípodes), são fatores aparentemente fundamentais para o possível “tamponamento” da epifauna no recife como um todo, ainda que diferenças locais tenham ocorrido. Tais fatores reforçam o potencial da macrofauna fital em estudos de bioindicação e diagnóstico ambiental, e a importância de preservar a complexidade estrutural dos recifes a fim de aumentar a resiliência e estabilidade frente a impactos ambientais. O monitoramento continuado da epifauna pode ser uma importante ferramenta para quantificar os efeitos do derramamento de petróleo na área e melhor distinguí-los dos efeitos naturais e outros possíveis impactos antrópicos a longo prazo, além da geração de conhecimento de base sobre a biota recifal em ambientes tropicais.

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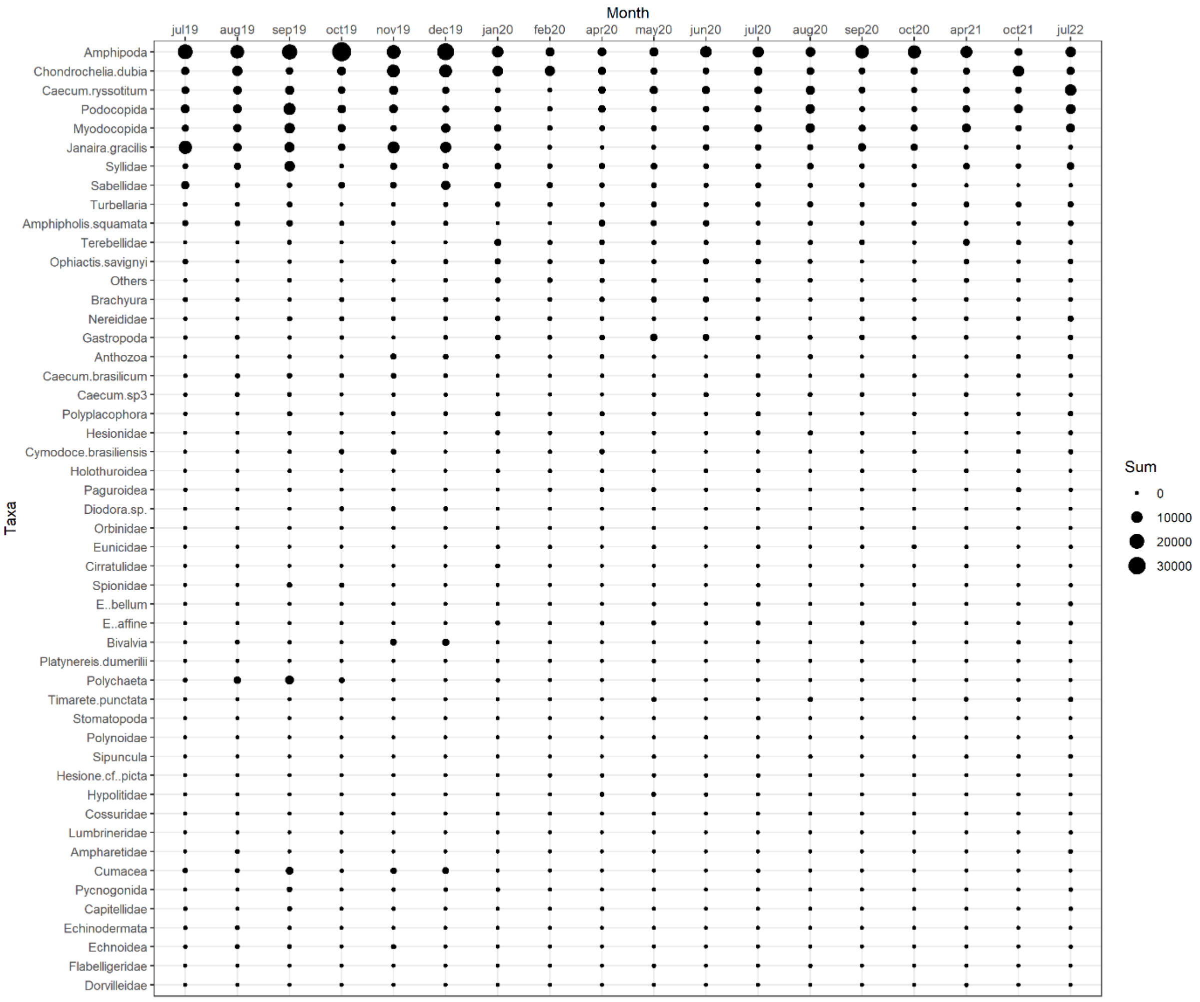
APÊNDICE A – ABUNDÂNCIA TOTAL DE CADA TÁXON (INDIVÍDUOS/100g DE ALGA) ASSOCIADO À JANIA CAPILLACEA POR MÊS



APÊNDICE B – ABUNDÂNCIA TOTAL DE CADA TÁXON (INDIVÍDUOS/100g DE ALGA) ASSOCIADO À *PENICILLUS CAPITATUS* POR MÊS