Efeitos do aquecimento global sobre o metabolismo de algas e cianobactérias e as interações fitoplâncton–bacterioplâncton em ecossistemas aquáticos

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Rio Grande
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ATA DE DEFESA DE TESE DE DOUTORADO EM BIOLOGIA DE AMBIENTES AQUÁTICOS CONTINENTAIS – Nº 004/2026

Às 13h30 (treze horas e trinta minutos) do dia 04 (quatro) do mês de setembro de 2026 (dois mil e vinte e seis), no Laboratório de Bioinformática do ICB e via Webconferência no endereço (https://conferenciaweb.rnp.br/sala/pablo-guimaraes) reuniram-se docentes, discentes e comunidade em geral, para a Defesa Pública da Tese de Doutorado da acadêmica Manuela Passos Tourinho**.** A Tese intitulada **"Efeitos do aquecimento global sobre o metabolismo das algas e as interações fitoplâncton–bacterioplâncton em ecossistemas aquáticos"** foi avaliada pela Banca Examinadora composta pelo Prof. Dr. Danilo Giroldo (Orientador); Dr. Pablo Santos Guimarães (coorientador); Profª Dra. Marinês Garcia (UFRGS), Prof. Dr. Márcio Silva de Souza (UFPEL) e Profª Dra. Edélti Faria Albertoni (FURG). Após a defesa e arguição pública, a Banca Examinadora reuniu-se, para deliberação final, e considerou a acadêmica aprovada. Desta forma, a acadêmica concluiu mais uma das etapas necessárias para a obtenção do grau de **DOUTORA EM BIOLOGIA DE AMBIENTES AQUÁTICOS CONTINENTAIS**. Nada mais havendo a tratar, às 16h30min (dezesseis horas e trinta minutos) foi lavrada a presente ata, que lida e aprovada, foi assinada pelos membros da Banca Examinadora, pela Acadêmica e pela Coordenadora do Curso.

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Dedico esta tese ao meu filho Bento, minha mãe Sílvia
E meus tios Quico e Renata (*in memoriam*)

Bráulio Bessa - Recomece

Quando a vida bater forte e sua alma sangrar,
quando esse mundo pesado
lhe ferir, lhe esmagar…
É hora do recomeço. Recomece a **LUTAR**.

Quando tudo for escuro e nada iluminar,
quando tudo for incerto e você só duvidar…
É hora do recomeço. Recomece a **ACREDITAR**.

Quando a estrada for longa e seu corpo fraquejar,
quando não houver caminho nem um lugar pra chegar…
É hora do recomeço. Recomece a **CAMINHAR**.

Quando o mal for evidente e o amor se ocultar,
quando o peito for vazio, quando o abraço faltar…
É hora do recomeço. Recomece a **AMAR**.

Quando você cair e ninguém lhe aparar,
quando a força do que é ruim conseguir lhe derrubar…
É hora do recomeço. Recomece a **LEVANTAR**.

Quando a falta de esperança decidir lhe açoitar,
se tudo que for real for difícil suportar…
É hora do recomeço. Recomece a **SONHAR**.

Enfim,

É preciso de um final pra poder recomeçar, como é preciso cair pra poder se levantar.
Nem sempre engatar a ré significa voltar.

Remarque aquele encontro, reconquiste um amor,
reúna quem lhe quer bem, reconforte um sofredor,
reanime quem tá triste e reaprenda na dor.

Recomece, se refaça, relembre o que foi bom,
reconstrua cada sonho, redescubra algum dom,
reaprenda quando errar, rebole quando dançar,
e se um dia, lá na frente, a vida der uma ré,
recupere sua fé e **RECOMECE** novamente.

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RESUMO

As mudanças climáticas representam uma ameaça ao funcionamento dos ecossistemas aquáticos, e entre os organismos mais diretamente afetados estão as algas. Nesse contexto, esta tese investigou os efeitos das mudanças climáticas sobre o metabolismo algal e suas possíveis consequências para as interações entre produtores primários e comunidades bacterianas em ambientes aquáticos. Inicialmente, foi realizada uma revisão sistemática e análise cientométrica (*research weaving*) para avaliar o conhecimento disponível sobre os efeitos da temperatura e da acidificação na produção de metabólitos por algas. Os resultados evidenciaram maior concentração de estudos relacionados aos lipídios, enquanto carboidratos, proteínas e vitaminas permanecem relativamente pouco explorados. Além disso, identificou-se predominância de estudos conduzidos com organismos isolados, evidenciando lacunas relacionadas às respostas de comunidades algais e às interações entre diferentes níveis tróficos. A partir dessas lacunas, foi conduzido um experimento em microcosmos para avaliar os efeitos do aquecimento crônico e de ondas de calor sobre a dinâmica do fitoplâncton–bacterioplâncton e dos carboidratos dissolvidos em um ecossistema aquático subtropical raso. Foram comparadas três condições térmicas: controle (24 °C), aquecimento crônico (29 °C) e ondas de calor (24-29 °C). O aquecimento alterou a dinâmica da comunidade fitoplanctônica, promovendo senescência precoce e redução da riqueza taxonômica, com respostas das ondas de calor semelhantes às observadas sob aquecimento crônico. Também foram observadas redução da concentração final e mudanças temporais na composição de carboidratos dissolvidos. Em conjunto, os resultados demonstram que o aquecimento global pode modificar não apenas a produção e a composição de metabólitos algais, mas também sua disponibilidade para comunidades microbianas, alterando a dinâmica das interações fitoplâncton–bacterioplâncton e potencialmente o processamento do carbono em ecossistemas aquáticos subtropicais. A tese evidencia a necessidade de ampliar os estudos sobre respostas metabólicas de comunidades algais e suas interações ecológicas, especialmente diante da intensificação de eventos extremos de temperatura.

Palavras-chave: mudanças climáticas; carboidratos dissolvidos; ondas de calor; comunidades algais; interações microbianas; produção de metabólitos.

ABSTRACT

Climate change represents a threat to the functioning of aquatic ecosystems, with algae being among the organisms most directly affected. In this context, this thesis investigated the effects of climate change on algal metabolism and their potential consequences for interactions between primary producers and bacterial communities in aquatic environments. Initially, a systematic review and scientometric analysis (*research weaving*) were conducted to assess the available knowledge on the effects of temperature and acidification on algal metabolite production. The results revealed a greater concentration of studies related to lipids, whereas carbohydrates, proteins, and vitamins remain relatively underexplored. Furthermore, a predominance of studies conducted with isolated organisms was identified, highlighting knowledge gaps concerning the responses of algal communities and interactions among different trophic levels. Based on these gaps, a microcosm experiment was conducted to evaluate the effects of chronic warming and heat waves on phytoplankton–bacterioplankton dynamics and dissolved carbohydrates in a shallow subtropical aquatic ecosystem. Three thermal conditions were compared: control (24 °C), chronic warming (29 °C), and heat waves (24–29 °C). Warming altered phytoplankton community dynamics, promoting premature senescence and reducing taxonomic richness, with heat-wave responses similar to those observed under chronic warming. A reduction in final dissolved carbohydrate concentration and temporal changes in carbohydrate composition were also observed. Overall, the results demonstrate that global warming may modify not only the production and composition of algal metabolites but also their availability to microbial communities, altering phytoplankton–bacterioplankton interactions and potentially carbon processing in subtropical aquatic ecosystems. This thesis highlights the need for further research into the metabolic responses of algal communities and their ecological interactions, particularly in the context of the increasing intensity of extreme temperature events.

Keywords: climate change; dissolved carbohydrates; heat waves; algal communities; microbial interactions; metabolite production.

APRESENTAÇÃO

Esta tese, como pré-requisito para obtenção do título de doutorado em Biologia de Ambientes Aquáticos Continentais pela Universidade Federal do Rio Grande (FURG), foi estruturada em uma introdução geral seguida de dois capítulos, sendo eles um artigo de cienciometria e o outro artigo com experimento em microcosmo. As normas adotadas para formatação de cada sessão seguiram as orientações do Programa de Pós-Graduação. Para Introdução Geral e Considerações Finais, foram adotadas as normas da ABNT. Uma vez que os capítulos 1 e 2 são compostos por artigos submetidos à periódicos científicos, estes seguem as normas de formatação dos respectivos periódicos. O capítulo 1, intitulado “Global warming and metabolite biosynthesis by algae: A scientometric and systematic approach” (https://doi.org/10.1071/MF25247) foi publicado na Marine and Freshwater Research em março de 2026. O segundo capítulo, intitulado “Chronic warming and heat waves reshape phytoplankton–bacterioplankton dynamics and dissolved carbohydrate composition in a subtropical coastal lagoon” foi submetido na Hydrobiologia em agosto de 2026 e encontra-se sob análise do editor.

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INTRODUÇÃO GERAL

Aquecimento global

Desde 1750 as concentrações de gases de dióxido de carbono, metano e óxidos nitrosos têm aumentado consideravelmente (Moore et al., 2008; Allaf e Trick, 2024). Apesar de oscilar durante os anos, e dias da semana, é possível observar um aumento, sobretudo quando comparamos o período pré-industrial (280 ppm) com maio de 2026, onde chegou a atingir 428,73 ppm (Lan et al., 2026). Além disso, o CO_2 é considerado um dos principais catalisadores do aquecimento, e no Brasil os setores de maior produção e emissão estão associados às mudanças no uso da terra, atividades de silvicultura (Garofalo et al., 2022; Wang et al., 2024) e os departamentos industrial e de transporte terrestre (Olier e Coneo, 2026).

Diante desse cenário de aumento das concentrações de gases de efeito estufa e de seus potenciais impactos sobre os sistemas naturais e a sociedade, tornou-se fundamental compreender e projetar os efeitos das mudanças climáticas em diferentes escalas. Nesse contexto, a fim de definir e sintetizar os impactos das mudanças climáticas nos diferentes âmbitos, sendo eles social, econômico e ambiental, foi criado, em 1988, após a Assembleia Geral da ONU, e com base no conhecimento científico e técnico, o Painel Intergovernamental de Mudanças Climáticas (IPCC).

Mais recentemente, o IPCC divulgou em seu sexto relatório de avaliação (AR6) estimativas da temperatura média global dos corpos d'água até 2100. Estes modelos geram simulações de cenários futuros climáticos com base no percentual de gases emitidos, e criam perspectivas de cenários pessimistas e otimistas baseadas nos níveis de emissão dos gases. O cenário otimista RCP 2.6, com baixas emissões de gases estufa, possui um acréscimo limitado na temperatura de no máximo 2,0 °C (IPCC, 2023). Já o cenário RCP 8.5, considerado pessimista a partir de concentrações de emissões muito altas de gases estufa, poderia exceder o aquecimento de 4 °C (IPCC, 2023). Dentre os impactos gerados estão alterações nos fluxos hidrológicos e nas precipitações, que podem influenciar a dinâmica dos ecossistemas aquáticos continentais a partir de alterações em parâmetros como temperatura e pH (Dudgeon, 2019), influenciando também a estrutura e a função das comunidades fitoplanctônicas.

Ecossistemas aquáticos continentais

Os ecossistemas aquáticos continentais são considerados recursos insubstituíveis pelo uso socioeconômico e pela biodiversidade (Dudgeon, 2019), além disso apresentam levada relevância social, ecológica, ambiental e econômica (Dudgeon et al., 2006, Dudgeon, 2019; Hughes et al., 2019). As ações de conservação têm maior probabilidade de serem eficazes quando se demonstra que a biodiversidade de água doce contribui para a oferta de serviços ecossistêmicos para os seres humanos. Estes ecossistemas são considerados *hotspots* globais de biodiversidade (Dudgeon, 2019), sendo o fitoplâncton responsável por aproximadamente 50% da produção primária global (Field et al., 1998).

Entretanto o ambiente e os organismos, são especialmente suscetíveis às mudanças, e as ameaças a esses ambientes intensificaram-se, sobretudo durante o Antropoceno (Dudgeon, 2019). Entre essas alterações, o aumento da temperatura pode alterar a estratificação térmica dos corpos d'água, influenciando a distribuição de calor em diferentes profundidades e potencialmente modificando os habitats dos organismos aquáticos. O derretimento das calotas polares e das geleiras contribui para a elevação do nível do mar, podendo afetar a salinidade de ambientes costeiros e estuarinos. Além disso, alterações nos níveis de salinidade nos estuários, em virtude das modificações no aporte fluvial, decorrentes de mudanças no regime de chuvas (Sugie et al., 2020; Thangaraj & Sun, 2023).

O aumento da precipitação e a ocorrência de eventos de chuva podem intensificar a conexão hidrológica entre solos e cursos d’água e, assim, alterar a exportação de materiais terrestres. Durante uma tempestade monitorada em bacias florestais, aumentaram as concentrações de carbono orgânico dissolvido e particulado nos cursos d’água (Fellman et al., 2020); em riachos boreais, a maior vazão durante o degelo concentrou grande parte da exportação anual de sedimentos (Naiman, 1982). Em ecossistemas de água doce, o brownification — ou escurecimento — corresponde ao aumento da cor da água, frequentemente associado ao aporte de matéria orgânica dissolvida e carbono orgânico dissolvido (COD) de origem terrestre (Blanchet et al., 2021). O aumento do COD pode reduzir a transparência e atenuar a penetração da luz, modificando também os perfis térmicos e de oxigênio dos lagos (Pilla & Couture, 2021). As respostas do fitoplâncton, contudo, variam conforme o balanço entre disponibilidade de luz e nutrientes; portanto, não se deve presumir que o escurecimento sempre reduza sua biomassa ou favoreça cianobactérias (Isles et al., 2021). Em experimentos e dados de lagos do norte da Europa, o escurecimento

esteve associado à supressão de cianobactérias e à mudança da comunidade para criptófitas mixotróficas (Lyche Solheim et al., 2023). Em determinadas condições, maior densidade de cianobactérias pode associar-se a menor riqueza fitoplanctônica; por sua vez, o escurecimento e a eutrofização podem reduzir a assimilação de algas de alta qualidade por zooplâncton, com possíveis repercussões sobre a transferência de energia aos níveis tróficos superiores (Bockwoldt et al., 2017; Taipale et al., 2019).

Comunidades fitoplanctônicas e bacterioplanctônicas: estrutura e interações

O fitoplâncton desempenha papel central no funcionamento dos ecossistemas aquáticos, contribuindo para produção primária e fluxo de matéria e energia nas cadeias alimentares (Field et al., 1998). Esses organismos constituem uma importante fonte de matéria orgânica autóctone e participam ativamente do ciclo do carbono, sustentando, direta ou indiretamente, diversos níveis tróficos (Marisol et al., 2018). Além de sustentar a produção de biomassa, esses organismos sintetizam diferentes classes de biomoléculas (Bel'kova et al., 2003). Porém são sensíveis às mudanças no ecossistema aquático (Hanashiro et al., 2023; Di Pane et al., 2024). As alterações nos índices de pH, temperatura e condições tróficas ambientais resultam em mudanças na composição bioquímica das células, alocação de carbono e metabolismo de comunidades fitoplanctônicas (Guimarães et al., 2013; Von Scheibner et al., 2014; Hanashiro et al., 2023)

Os organismos fotossintéticos utilizam compostos inorgânicos como fonte de nutrientes para o crescimento e para a síntese de diferentes metabólitos primários e secundários. Entre os principais grupos de metabólitos produzidos estão os lipídios, as proteínas, os carboidratos e as vitaminas, características que contribuem para o elevado valor de sua biomassa, tanto como fonte de alimento quanto como recurso para organismos de níveis tróficos superiores (Vidyarathna et al., 2024). Além de desempenharem funções essenciais no metabolismo celular, esses compostos podem variar em resposta às condições ambientais, refletindo alterações fisiológicas e diferentes estratégias de aclimatação dos organismos. Dessa forma, a composição e a quantidade de metabólitos produzidos podem ser utilizadas como indicadores das respostas dos organismos às mudanças no ambiente (Calderini et al., 2023; Mountourakis et al., 2023; Schiksnis, 2024; Xiao et al., 2024).

Mudanças climáticas podem influenciar no aumento da produção de carboidratos, e alterações no armazenamento e liberação destes para o meio extracelular pelo fitoplâncton (Smith & Underwood 2000; Giroldo et al., 2005). Uma vez que os carboidratos são considerados um elemento chave na relação bacterioplâncton e fitoplâncton, é comum observar uma maior atividade bacteriana associada ao aumento da produção de carboidratos nos meses mais quentes (Baines & Pace, 1991; Guimarães et al., 2013). Isso pode repercutir não apenas no crescimento dos produtores, mas também na estrutura e no funcionamento das comunidades aquáticas.

A composição quantitativa e qualitativa de carboidratos de um corpo d'água dependem da composição da comunidade fitoplanctônica, de seu estado fisiológico e fenológico, bem como das características físico-químicas do corpo d'água (Fogg 1983; Myklestad, 1995). A matéria orgânica associada ao fitoplâncton não constitui uma fração quimicamente homogênea, podendo apresentar diferentes características de composição, complexidade e disponibilidade para os organismos heterotróficos. Dentre os carboidratos liberados temos os monossacarídeos, dissacarídeos e polissacarídeos extracelulares (EPS) compondo parte importante do carboidrato liberado (Giroldo et al., 2005). Alguns estudos apontam um aumento na produção de glucose e manose/xylose em cultivos ou comunidades dominadas por cianobactérias e diatomáceas, respectivamente (Guimarães et al., 2013; Francis et al., 2021). O aumento da ocorrência e dominâncias destes dois grupos de microrganismos fotossintetizantes também têm sido previstos em futuros cenários de aquecimento global (Rasconi et al., 2015; Zhang et al., 2016). Sendo assim, não apenas a composição da comunidade fitoplanctônica pode ser alterada, mas também seus metabólitos, entre eles os carboidratos. Embora existam poucos estudos para ambientes aquáticos continentais, trabalhos com comunidades marinhas têm mostrado que a composição da matriz de polissacarídeos é capaz de selecionar a comunidade bacteriana e suas taxas metabólicas (Francis et al. 2021; Sidhu et al. 2023). Logo, a análise simultânea das comunidades fito e bacterioplanctônica permite uma compreensão acerca dos possíveis cenários futuros em consequência das alterações climáticas (Liu et al., 2015).

Fitoplâncton e o bacterioplâncton estão na base da teia trófica e compreendem parte significativa da biomassa dos corpos d'água, uma vez que são organismos-chave no ciclo do carbono (Chrost & Faust 1983; Vieira et al 2006). O fitoplâncton

constitui uma importante fonte de matéria orgânica autóctone nos ecossistemas aquáticos, liberando para o ambiente uma variedade de compostos orgânicos derivados da fotossíntese, entre estes compostos, estão os carboidratos, em especial na forma de EPS (Fogg, 1983; Wood & Van Valen 1990; Giroldo et al. 2003).

O mecanismo de liberação dos metabólitos depende de alguns fatores como desequilíbrio estequiométrico, estado trófico do ecossistema, vazamento passivo ou exsudação ativa das moléculas (*overflow*), através da sinalização, defesa (Smith & Underwood 2000; Giroldo et al. 2003; Vieira et al 2006). Além da exsudação de compostos durante o crescimento, a matéria orgânica fitoplanctônica também pode ser disponibilizada ao ambiente durante a senescência e a degradação das células, contribuindo para o suprimento de substratos para as comunidades bacterianas (Giroldo et al. 2003). Uma vez que o composto é liberado ou excretado das células fitoplanctônicas para o ambiente, as bactérias passam a assumir um papel importante e dominante na transformação deles. Bactérias heterotróficas podem degradar seletivamente os diferentes carboidratos dissolvidos, liberando compostos em partículas de menor peso molecular, utilizando parte deste carbono para seu crescimento e disponibilizando novamente para outros níveis tróficos (Giroldo et al. 2003). Esse conjunto de processos constitui um dos principais mecanismos da alça microbiana, pela qual a matéria orgânica dissolvida, anteriormente pouco acessível aos níveis tróficos superiores, é reincorporada à teia alimentar (Giroldo et al. 2003).

As bactérias heterotróficas constituem um dos principais grupos decompositores dos ecossistemas aquáticos e uma via central de utilização do carbono orgânico dissolvido (COD), sobretudo de suas frações biodisponíveis. Ao assimilarem e transformarem esses compostos, parte do carbono é incorporada à biomassa bacteriana e pode ser transferida a protozoários e zooplâncton pela alça microbiana, enquanto outra parte é remineralizada; as bactérias também podem produzir compostos orgânicos dissolvidos, influenciando a composição e o destino do COD no ambiente (Chróst & Rai, 1994; Sigee, 2005; Guillemette & del Giorgio, 2012). A maioria das bactérias possuem dimensão numa faixa de picoplâncton (0,2 – 2 um) a nanoplâncton (2 – 20 um), porém este tamanho pode variar de acordo com o estado nutritivo, e podem apresentar diferentes formas como helicoidal, haste, vibrióide (curva), e algumas formas cocóides (esféricas) (Sigee, 2005). Além da composição taxonômica, características estruturais podem fornecer informações sobre a resposta da comunidade às condições ambientais (Young, 2006). Sendo assim, a utilização de

imagens digitais de microscopia pode auxiliar em um dos desafios da ecologia microbiana, uma vez que Liu et al., (2001) descreveram um sistema interativo através de uma ferramenta ecológica para analisar a morfologia dos organismos da comunidade através de imagens. Esta caracterização dos organismos bacterianos e a resposta frente a condições ambientais a partir de um método mais barato (Young, 2006).

As bactérias podem ser classificas em 11 morfotipos a partir de características como perímetro, área e comprimento dos eixos (Liu et al., 2001). Embora essa classificação seja prática, ela não reflete a diversidade presente na natureza, tampouco pode ser comparada à precisão de uma classificação filogenética, não podendo, portanto, ser utilizada para identificação. Entretanto, pode ser utilizada como um preditor ecológico, uma vez que a forma determina alguns aspectos metabólicos, podendo caracterizar grupos ou indivíduos (Massana et al., 1997).

A classificação dos morfotipos também podem refletir estratégias ecológicas, uma vez que Kuznetsova et al. (2020) observaram, em um reservatório, a predominância de cocos pequenos e cocobacilos de tamanho médio, enquanto bastonetes de diferentes tamanhos também se destacaram em determinados ambientes. Esse padrão pode estar relacionado tanto à competição por recursos quanto à predação, uma vez que bactérias maiores e mais ativas tendem a ser consumidas seletivamente por nanoflagelados heterotróficos, favorecendo a predominância de formas menores (Kuznetsova et al., 2020). Sendo assim, a distribuição e classificação dos morfotipos pode refletir a influência conjunta acerca da disponibilidade de recursosl, interações biológicas e condições ambientais.

Nesse contexto, a análise integrada das comunidades fitoplanctônicas e bacterioplanctônicas permite compreender como alterações na estrutura e no metabolismo dos produtores primários podem repercutir sobre a disponibilidade de matéria orgânica e, consequentemente, sobre a composição e a atividade das comunidades bacterianas, com implicações para a transformação e a remineralização do carbono e dos nutrientes. A compreensão dessas relações também pode contribuir para o desenvolvimento de abordagens capazes de relacionar padrões de alocação de carbono às taxas de crescimento celular em comunidades naturais, um desafio ainda relevante para a ecologia microbiana (Wagner, 2016). Dessa forma, o estudo conjunto dessas comunidades constitui uma abordagem importante para compreender como alterações nas condições ambientais podem modificar o fluxo de

matéria e energia e, consequentemente, o funcionamento dos ecossistemas aquáticos.

Ambiente estudado

A lagoa Mirim contempla dois países Uruguai e Brasil, do lado brasileiro, encontra-se parcialmente dentro da Estação Ecológica do Taim, juntamente com outras lagoas e áreas úmidas (Vieira & Rangel, 1988). Possui área de 3748 km2 e profundidade máxima de 7 m e o clima regional é subtropical úmido (Fragoso et al., 2008), o nível d'água é influenciado pela direção e intensidade dos ventos. Essas variações podem favorecer o alagamento das planícies aluviais adjacentes, contribuindo para a dinâmica hidrológica e ecológica do sistema.

A Lagoa Mirim é considerada menos eutrofizada que a Lagoa dos Patos (Yunes et al., 1996; Pérez & Odebrecht, 2005), à qual está conectada por meio do canal São Gonçalo. A Lagoa dos Patos, por sua vez, é classificada entre as condições mesotrófica e eutrófica (Torgan, Pillar & Niencheski, 2004). Embora a Lagoa Mirim esteja conectada a esse sistema lagunar, a salinização deixou de ocorrer após 1977, quando foi construída uma eclusa no canal São Gonçalo, que passou a limitar a intrusão de águas salobras provenientes da Lagoa dos Patos (Vieira & Rangel, 1988).

Estudos que relacionam a produção de carboidratos com a dinâmica das populações fitoplanctônicas são bastante raros, inclusive na região subtropical brasileira, onde se encontra a estação ecológica do Taim. Como contribuição ao conhecimento da dinâmica fitoplanctônica e das interações entre fitoplâncton, bacterioplâncton e carboidratos dissolvidos na Lagoa Mirim, Guimarães et al. (2013) realizaram um estudo mensal entre setembro de 2009 e agosto de 2010, avaliando as comunidades planctônicas, as características físicas e químicas da água e a composição dos carboidratos dissolvidos. Foram identificadas oito classes fitoplanctônicas, sendo Chlorophyceae a classe com maior riqueza, seguida por Bacillariophyceae, Cyanophyceae e Zygnematophyceae. Entretanto, as maiores densidades foram registradas para Bacillariophyceae e Cyanophyceae, principalmente devido à ocorrência de *Aulacoseira cf. muzzanensis*, *Planktolyngbya cf. contorta* e *Planktolyngbya limnetica*, que foram abundantes ao longo do período estudado (Guimarães et al., 2013; Moraes, 2022). A maior densidade fitoplanctônica ocorreu em dezembro e março, enquanto setembro apresentou os menores valores,

evidenciando uma marcada variação sazonal da comunidade. Os autores também observaram que a densidade do fitoplâncton esteve principalmente relacionada à temperatura, condutividade específica, fosfato e duração do brilho solar, enquanto a comunidade bacterioplanctônica apresentou forte correlação positiva com o fitoplâncton. Em relação aos carboidratos dissolvidos, foram encontrados exclusivamente carboidratos dissolvidos combinados, constituídos por oligossacarídeos e polissacarídeos, com maiores concentrações em novembro, março-abril e setembro e menores valores em dezembro-janeiro e julho-agosto. A glicose foi o principal componente, seguida por manose/xilose, ribose, arabinose e ácido galacturônico. De modo geral, os resultados indicaram que a composição e a densidade do fitoplâncton, associadas às condições ambientais, influenciam a disponibilidade de carboidratos dissolvidos, os quais, por sua vez, constituem uma importante fonte de carbono para o bacterioplâncton na Lagoa Mirim (Guimarães et al., 2013). A partir do exposto, hipotetisamos que as alterações ambientais associadas às mudanças climáticas, particularmente o aumento da temperatura e ondas de calor, modificam a produção e a composição dos metabólitos fitoplanctônicos, alterando a disponibilidade de matéria orgânica e, consequentemente, a dinâmica e as interações entre as comunidades fitoplanctônica e bacterioplanctônica.

Hipóteses específicas

(I) O aumento da temperatura altera a concentração e a composição dos carboidratos associados ao fitoplâncton.

(II) O aquecimento crônico e os eventos de onda de calor produzem respostas distintas na produção e composição dos carboidratos fitoplanctônicos.

(III) As alterações na quantidade e composição dos carboidratos sob diferentes condições de temperatura modificam a dinâmica e a utilização desses compostos pelo bacterioplâncton.

(IV) O aumento da temperatura altera a estrutura e a dinâmica das comunidades fitoplanctônica e bacterioplanctônica, afetando riqueza, abundância e composição das comunidades.

(V) As alterações na matéria orgânica produzida pelo fitoplâncton alteram as relações tróficas e a ciclagem da matéria orgânica;

(VI) A literatura científica sobre mudanças climáticas e metabólitos fitoplanctônicos é predominantemente direcionada aos efeitos da temperatura e ecossistemas marinhos;

Objetivo geral

Avaliar por meio deuma abordagem cienciométrica e experimental, os efeitos das alterações ambientais associadas às mudanças climáticas sobre a produção de metabólitos pelos fitoplâncton e suas implicações sobre a dinâmica e interações entre as comunidades fitoplanctônica e bacterioplanctônica.

Objetivo Específicos

(i) Caracterizar o conhecimento científico sobre o efeito ta temperatura e mudanças no pH na produção de metabólitos produzidos pelo fitoplâncton, identificando tendências, lacunas;
(ii) Identificar quais os principais metabólitos analisados, quais ecossistemas tem maior predomínio de publicação;
(iii) Avaliar experimentalmente os efeitos das mudanças de temperatura sobre a produção, composição e disponibilidade de carboidratos associados ao fitoplâncton,
(iv) Analisar as possíveis alterações na utilização dos carboidratos pelo bacterioplâncton sob diferentes condições de temperatura;
(v) Investigar os efeitos da temperatura na dinâmica das comunidades fitoplactônicas e bacterioplanctônicas e integrar as respostas das comunidades a fim de compreender as consequências das mudanças na dinâmica da matéria orgânica nos ecossistemas aquáticos continentais.

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CAPÍTULO 1

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Global warming and metabolite biosynthesis by algae: A scientometric and systematic approach

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Abstract

The Intergovernmental Panel on Climate Change (IPCC) has projected an increase in greenhouse gas emissions. Among the consequences are changes in temperature and atmospheric CO_2 levels, which can impact hydrological flows, biodiversity, and primary production in aquatic ecosystems. Moreover, these factors may influence, either individually or in combination, the metabolic composition as well as the production and extracellular release of metabolites by algae. This study combines a systematic review with a scientometric analysis (research weaving) to investigate the effects of temperature and acidification on metabolite production by algae. We analyzed publication trends, the most studied environmental factors, the ecosystems most frequently addressed, taxonomic groups, and existing knowledge gaps. Among the

metabolites, a greater research interest is observed in lipid-related studies, while carbohydrates, proteins, and vitamins remain underexplored. Furthermore, many studies focus on the responses of isolated organisms, highlighting the need for research on the effects of climate change on microalgal communities and their interactions with organisms from other trophic levels. Our findings highlight critical gaps in the literature and provide a solid foundation to guide future research on the effects of climate change on metabolite production by algae, with relevant ecological and biotechnological implications.

Keywords: Carbohydrates, Climate change, Lipids, Protein, Phytoplankton, Vitamin, Gaps.

1. Introduction

Global warming and its consequences, as detailed in the Intergovernmental Panel on Climate Change's Sixth Assessment Report (AR6), represent the greatest environmental challenge of the century (IPCC 2023). The pessimistic scenario (RCP 8.5) assumes high concentrations of greenhouse gases and projects a temperature rise of over 4 °C. In contrast, the optimistic scenario requires immediate and drastic emission reductions and estimates an increase of up to 2 °C by 2100 (IPCC 2023). Rising temperatures influence precipitation patterns, alter hydrological flows and water levels in aquatic systems, and affect connectivity between aquatic environments (IPCC 2021; Pratap and Markonis 2022). The warming of the water column intensifies changes in oxygen solubility, biogeochemical cycles, and decomposition processes,

directly affecting primary productivity (O'Reilly *et al*. 2015; Wetzel 2001). These changes lead to alterations in the dynamics of inland aquatic ecosystems and in parameters such as temperature and pH (Dudgeon 2019).

Aquatic environments respond differently to changes in temperature patterns, pH, and atmospheric CO_2 concentrations. The ocean, due to its vast surface area and the abundance of autotrophic organisms, acts as an important CO_2 sink (Sabine *et al.* 2004); however, it is also subject to the impacts of acidification (Doney *et al*. 2020). In inland aquatic ecosystems, there is a complex interplay of factors and variables related to environmental conditions, which makes it difficult to generalize patterns (Hasler *et al.* 2016). Nevertheless, projections based on modeling (Phillips *et al.* 2015) and long-term monitoring studies in freshwater environments indicate a trend of decreasing pH due to the rising partial pressure of CO_2 leading to acidification (Weiss *et al.* 2018), which would affect growth rates and the production of reactive oxygen species in microalgae (Liu *et al.* 2021). Algae are responsible for a large portion of primary production in these ecosystems (Wetzel 2001). In addition to their role in primary productivity, algae synthesize and release several metabolites, the production of which can be significantly modulated by these environmental changes.

Photosynthetic organisms use inorganic compounds for growth and the production of primary and secondary metabolites. Algae, in particular, are capable of producing different classes of these metabolites, such as lipids, proteins, carbohydrates, and vitamins, which gives them high value as biomass, either as food or as a substrate for higher trophic level organisms. Moreover, these metabolites are also important indicators of adaptation or stress in response to environmental conditions (Calderini *et al.* 2023; Mountourakis *et al.* 2023; Schiksnis, 2024; Xiao *et al.* 2024). In addition to phylogenetic differences, the metabolic profile of algae is strongly influenced by environmental factors and nutrient availability (Park *et al.* 2023). Therefore, both thermal stress and acidification may influence, either individually or synergistically, the metabolic composition and extracellular release. As a result, algae may alter the production, storage, and extracellular release of metabolites (Giroldo *et al.* 2005; Smith and Underwood 2000). Consequently, the nutritional quality of phytoplankton and macroalgae for higher trophic levels tends to change (Hixson and Arts 2016), causing impacts on the food chain (Benítez *et al*. 2023).

It is worth noting that the changes driven by global warming also affect ecosystem services, biodiversity, species distribution, and the metabolism of aquatic

organisms such as microalgae and macroalgae (Di Pane *et al*. 2024; Dudgeon 2019; Hanashiro *et al.* 2023; IPCC 2021; Von Scheibner *et al.* 2014). In this context, understanding the composition of these organisms and the metabolic pathways and metabolites they produce under environmental stress conditions, such as warming and acidification, is essential. However, the lack of research on the influence of global warming on organisms at the base of the food web, especially those present in freshwater environments, poses a challenge for understanding how interactions will be affected. In this context, scientometric studies become essential tools for mapping existing knowledge, identifying gaps and emerging trends, and providing guidelines for future research addressing the impacts of global warming on algal metabolite biosynthesis. (Machado *et al*. 2023).

In this study, we conducted a combination of systematic review and scientometric analysis, a method known as *research weaving* (Nakagawa *et al.* 2019), which enables a detailed assessment of the investigated knowledge gap (Castro *et al.* 2025). Specifically, we examined the influence of temperature and acidification on algal metabolite production and composition to address the following objectives:

(1) the number of articles published over the years;

(2) which journals publish most frequently on this topic;

(3) which countries have contributed most to the literature;

(4) which factor, temperature or pH/acidification, has been more frequently analyzed;

(5) which ecosystem (marine, freshwater, or transitional environments) has attracted greater scientific interest;

(6) which metabolites have been evaluated in response to climate change;

(7) which taxonomic groups are most commonly used to assess the influence of temperature and acidification on metabolite production; and

(8) to identify research trends and knowledge gaps to guide future investigations.

2. Materials and methods

We used the Web of Science Core Collection (WoS) from Clarivate Analytics and the Scopus (SC) database to conduct the scientometric analysis. The systematic mapping was carried out following the Reporting Standards for Systematic Evidence Synthesis (Fig.1) (Haddaway *et al.* 2018; checklist available in Supplementary File 1).

The compilation was limited to articles published in English between 1988 and 2024. The year 1988 was chosen because it marks the establishment of the Intergovernmental Panel on Climate Change (IPCC).

The advanced searches focused on terms related to algal taxa, their physiological/biochemical responses, stressors associated with climate change, and the consequences of global warming. To perform the search, we used the following keyword combinations: ("*alga*" OR "phytoplank*" OR "cyanobac*") AND (“response” OR "physiolog*" OR "biochem*") AND ("climatic change" OR "warming" OR "global change" OR "Intergovernmental Panel on Climate Change" OR "global warming") AND (“temperature” OR “acidification” OR “pH”). We apply the following filters to the searches performed:

(i) articles published in English only,

(ii) publication period from January 1988 to December 2024,

(iii) research articles only.

Of the 4,171 articles retrieved (2,226 from WoS and 1,945 from Scopus), 4,066 were excluded based on the following criteria:

(1) duplicate records,

(2) articles not aligned with the study objectives,

(3) use of organisms outside the scope of interest,

(4) review articles, meta-analyses, conference abstracts, book chapters, and books.

As a result, 105 articles were included (Table SM1 – Supplementary File 2). We extracted information such as (1) year of publication,

(2) journal of publication,

(3) most commonly used keywords across the articles, and

(4) geographical distribution (based on the corresponding author's postal code) from the metadata downloaded from the WoS and SC platforms in BibTeX format. These data were analyzed in the R environment (R Core Team 2023) using the bibliometrix package (Aria and Cuccurullo 2017). To assess the impact factor (IF) of each journal, we used data from the Journal Citation Reports (2023).

Additionally, to construct a keyword co-occurrence network, files were downloaded in RIS format from both databases (WoS and Scopus), and the fractional counting method was applied using VOSviewer (Van Eck and Waltman 2010). From the analysis, 16 terms were extracted from the dataset, and to be included, each keyword had to appear at least eight times in the articles. It is also important to note

that keywords related to the original search terms were excluded from the analysis, as they are expected to be among the most frequent (Barbosa and Lanari 2022). Additionally, it is worth noting that this type of analysis may filter out some of the oldest or most recent years, as the method tends to highlight terms that occur at least eight times, pulling them toward the center of the distribution.

Subsequently, for in-depth analysis, we extracted the following information through article reading:

(i) the methodological approach used (i.e., *in situ*, *ex situ*, or a combination of both),

(ii) the ecosystem in which the study was conducted,

(iii) variables assessed (temperature and pH),

(iv) the metabolites studied,

(v) the target organisms, which were later taxonomically categorized (according to Adl *et al*. 2019).

The evaluation was conducted as follows: when a study addressed multiple organisms, metabolites, or parameters, each was counted and analyzed individually. Therefore, a single article could be counted multiple times in the analysis, e.g., once for each distinct organism studied. Throughout the text, we refer to the mangrove ecosystem, as this was the only transitional environment identified during the analysis/reading of the articles. The classification of studies as mangrove, freshwater, or marine refers to the ecosystem in which the experiment was conducted or to the origin of the algal strains when experiments were carried out under laboratory conditions. All articles that analyzed lipids, saturated and/or unsaturated fatty acids, were grouped under the fatty acids category. These molecules, derived from sugars and structurally similar compounds, were classified as carbohydrates. Studies that performed a systematic analysis of the metabolites present in algae were categorized under metabolomics. This classification allowed for comparisons among different metabolite classes, highlighting those most frequently analyzed in the selected publications. Furthermore, the studies were also categorized based on the type of experiment. They were classified as "*in situ*" when the experiment or analysis was conducted directly in the natural environment; "*ex situ"* when the material was collected from the environment and developed in a different location; and experimental when the study was conducted exclusively in the laboratory. Additionally, some classifications encompassed more than one category, such as "in situ and ex situ" or "in situ and experimental", reflecting studies that integrated both field and laboratory approaches.

Experiments were classified as single-stressor or multi-stressor, or combined stress condition studies. This classification was consistently applied throughout the analysis and discussion to clearly indicate the experimental framework of each study and to facilitate the interpretation and comparison of results.

To assess the geographical distribution of the studies, a table was created representing the collaboration between the corresponding author's country and the co-authors' countries. Articles with authors from different nationalities were classified as "multiple-country publications" (MCP), while those with authorship and collaboration exclusively within a single country were classified as "single-country publications" (SCP).

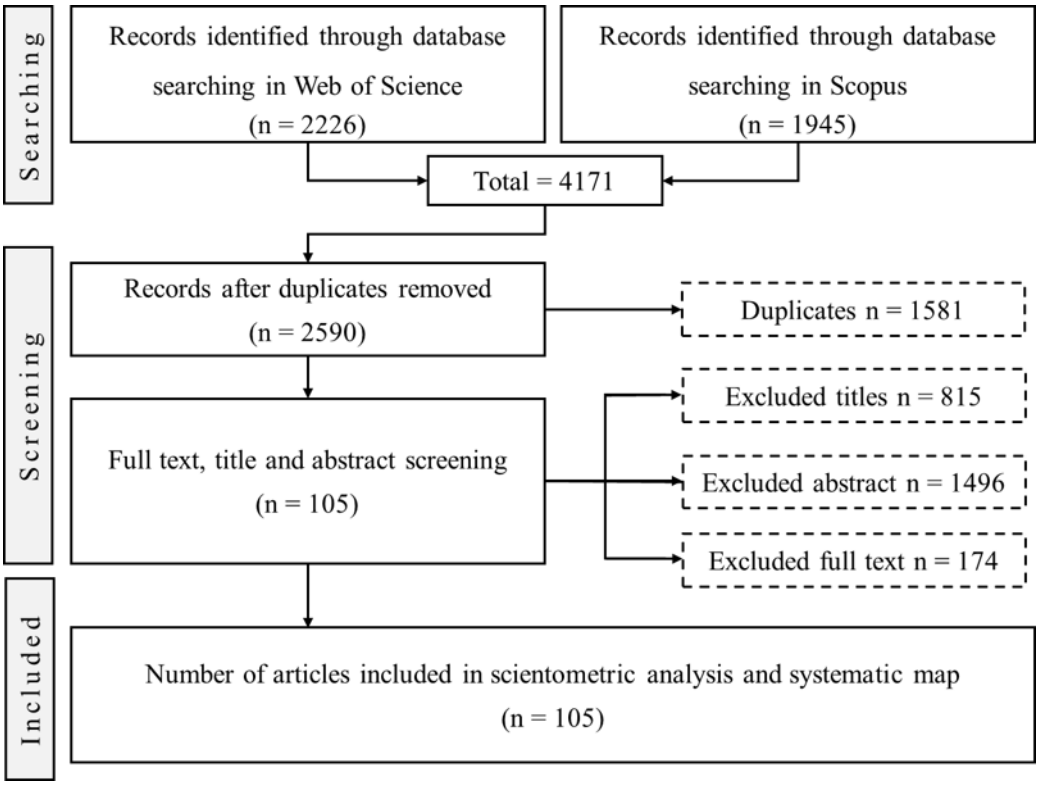


Fig. 1 Methodological process for the scientometric review and systematic mapping. The dotted blocks represent the excluded articles

3. Results and discussion

3.1 Temporal overview

Based on the systematic and scientometric survey, during the analyzed period (1988–2024), we selected articles that specifically addressed the influence of temperature

and pH variations on metabolite production in microalgae and macroalgae. As illustrated in Figure 2 (Fig. 2), the scientific development in this area was considered slow, especially in the early years of research. Despite its ecological importance, records in the literature from the evaluated databases only began in 1994, when the first article was published, assessing the influence of pH and temperature on the metabolism of the freshwater microalga *Cyanidium caldarium* (Akimoto *et al,* 1994).

After this initial publication, there was a ten-year hiatus, followed by a gradual increase beginning in 2013, culminating in a peak between 2023 and 2024. This peak accounted for more than 30% of the total scientific output on the topic, classifying it as an emerging focus of scientific interest (Bornmann and Mutz 2015). It is worth noting that the increase in scientific production reflects, above all, the growth of studies conducted in marine environments and ecosystems. However, this growth and consolidation are considered late when compared to the overall development of climate change research on phytoplankton, which began around 2007 (Machado *et al.* 2023). In contrast, articles evaluating the impact of warming and acidification on pesticide toxicity began to increase in number around 2006/2008 (Castro *et al*. 2025). Although studies on climate change date back to the 19th century (e.g., Arrhenius 1896), it was only after the establishment of the Intergovernmental Panel on Climate Change (IPCC) in 1988 that research on the subject began to receive greater attention (Hulme and Mahony 2010).

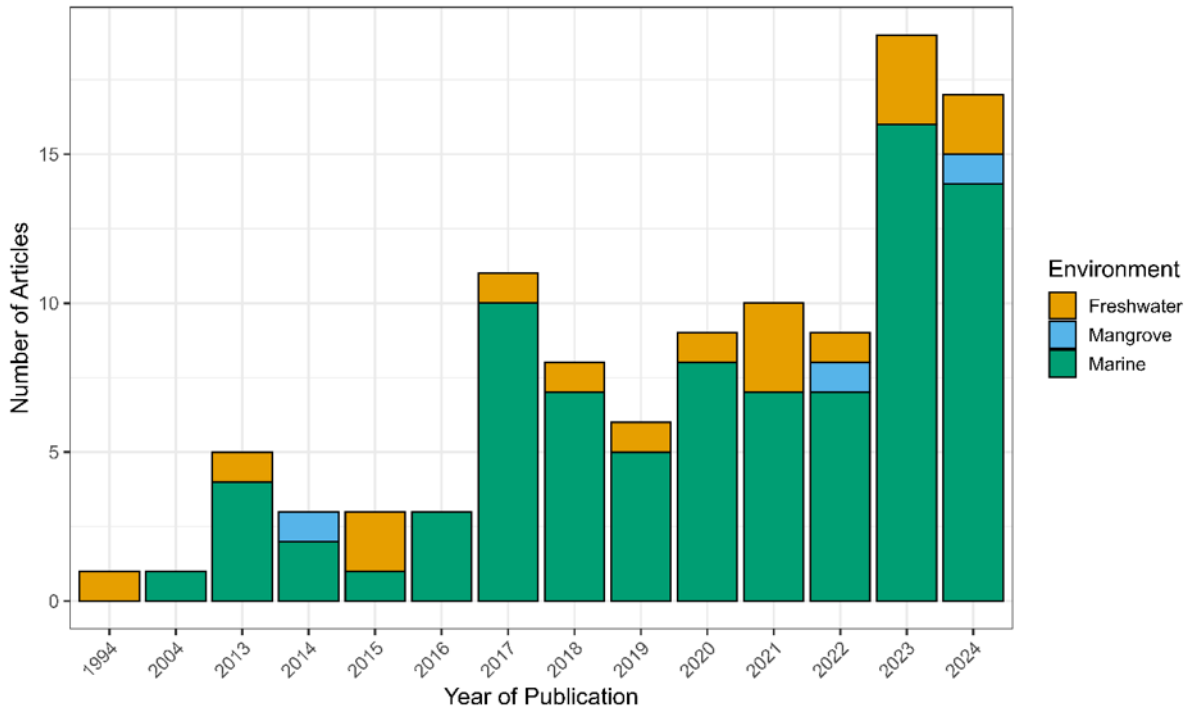


Fig. 2 Distribution of the number of articles published between 1994 and 2024 on the influence of temperature and/or pH on algal metabolite analysis

3.2 Journals

The articles were published in 52 journals indexed in the Web of Science and Scopus platforms (Fig. 3). Among these, 36 journals published fewer than three articles, and only three journals published at least six articles. This pattern reflects Bradford's Law, which states that a small number of journals account for the majority of publications (Bradford 1934). *Frontiers in Microbiology* and the *Journal of Applied Phycology* stood out as the most prolific journals, with eight articles each (Fig. 3). Both journals have scopes closely aligned with the investigated topic and present relevant impact indicators, with impact factors of 4.0 and 2.8, respectively, according to the 2023 Journal Citation Reports. Following these, other noteworthy journals include *Science of the Total Environment* (n = 6; IF = 8.2), *Algal Research – Biomass, Biofuels, and Bioproducts* (n = 5; IF = 4.6), and the *Journal of Phycology* (n = 5; IF = 2.8).

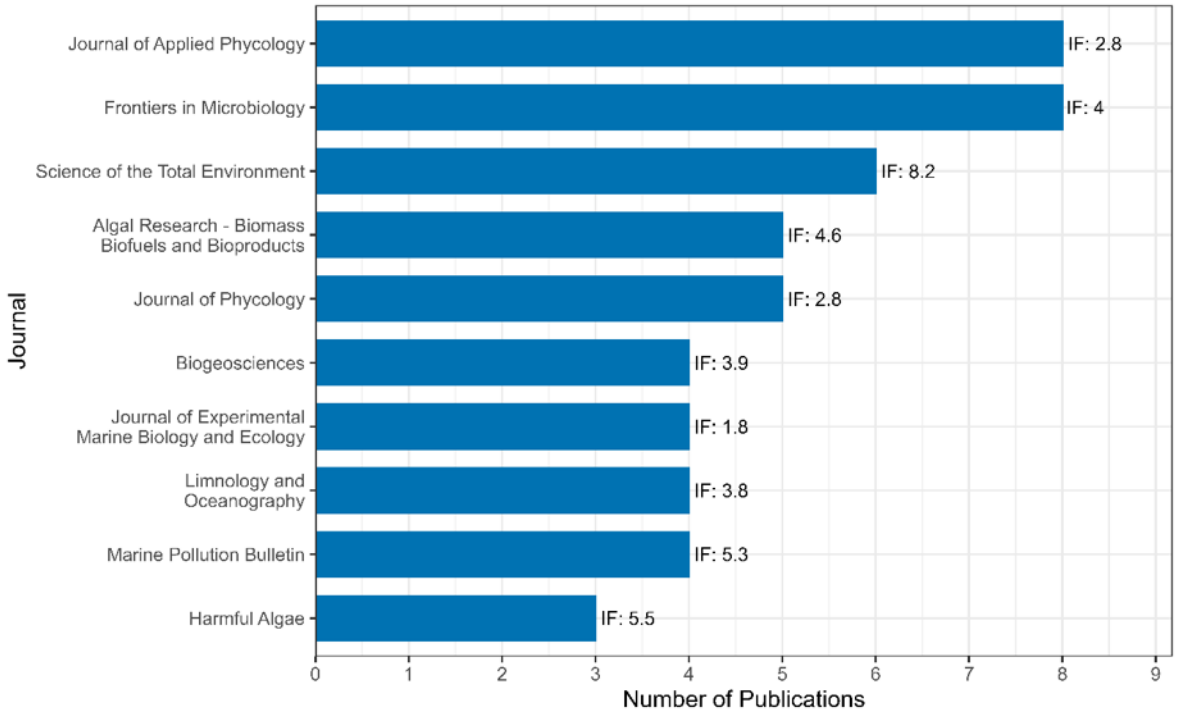


Fig. 3 Ranking of the top 10 journals with the highest number of publications indexed in the Web of Science and Scopus databases, from 1994 to 2024, related to algal metabolite analyses in aquatic environments under the influence of factors related to climate change

Approximately 30% of the total publications analyzed were concentrated in *Frontiers in Microbiology*, *Journal of Applied Phycology*, *Science of the Total Environment*, *Algal Research – Biomass, Biofuels and Bioproducts*, and *Journal of Phycology*. This concentration reflects the alignment of the editorial scopes of these journals with the subject addressed in the study. Although the research focuses on environmental and ecological issues, many publications also emphasize the biotechnological potential of algal-derived compounds, with a focus on technological advancements (Chisti 2007; Hu *et al*. 2008). Moreover, these journals have high impact factors (ranging from 2.8 to 8.2, according to Journal Citation Reports, Clarivate, 2023) and are recognized for their significant scientific contributions.

3.3 Keywords co-occurrence analysis

Keywords function as tools to identify the most recurrent themes within a research field (Ellegaard and Wallin 2015). In total, 920 terms were used across the analyzed articles (Fig. 4). Among them, the most central terms are strongly associated with the core of each cluster and show high levels of co-occurrence. “Growth” was the most frequent keyword, with 47 occurrences and 86 connections, emerging as the central node in the network. This reinforces its prominence in studies evaluating the adaptation and development of organisms under stress conditions (Borowitzka 2013; Chisti 2007).

The terms “photosynthesis” (25 occurrences and 59 connections) and “fatty acids” (20 occurrences and 36 connections) also highlight their relevance within the conceptual framework of the field and their coherence with the topic addressed. Photosynthesis is a fundamental process whose products are often used as indirect indicators of biomass, given their close relationship with cellular growth (Huot *et al*. 2007). Meanwhile, fatty acids, which are widely studied for their energetic, industrial, and pharmaceutical potential (Hu *et al*. 2008), also appear in ecological studies as indicators of algal biomass quality as a food source for higher trophic levels (Hixson and Arts 2016). Due to growing interest in the topic, “fatty acids” also ranked among the most frequently cited keywords in our analysis.

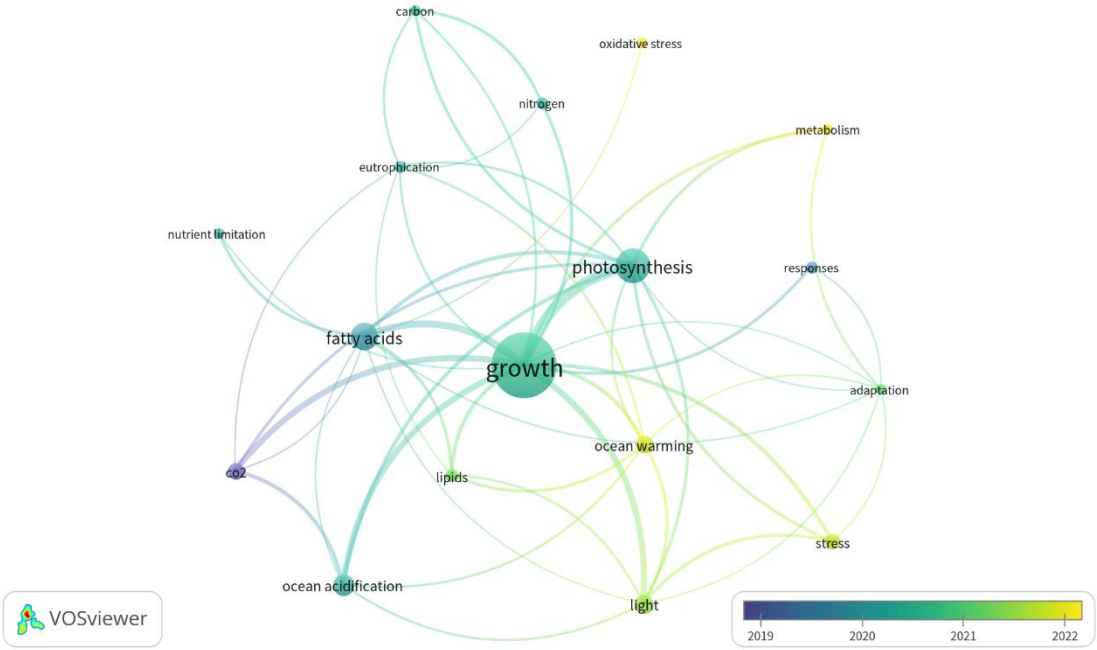


Fig. 4 Keywords co-occurrence network of articles published and indexed in the Web of Science and Scopus databases, from 1994 to 2024, on micro and macroalgae, their physiological or biochemical response to stressors (pH and temperature), consequences of global warming, and climate change. The size of the nodes and the thickness of the lines between them correspond to the frequency with which the keywords appear in the articles. The colors represent the year in which the keywords appeared most frequently in the articles

3.4 Geographical Distribution and Research Collaborations

The geographic distribution of publications highlights a broad interest in the topic, spread across various countries and continents, with emphasis on China, followed by Australia and Germany (table 1). Our results indicate a high rate of single-country publications (SCP), which may reflect well-established national research structures or scientific policies that favor domestic production (Glänzel 2001). China's dominance in absolute numbers and its high SCP percentage may be attributed to substantial investments in science and technology from both government and private sectors (Zhou and Leydesdorff 2006). The country operates China's National Key R&D Program, which focuses on climate change, environmental sustainability, ecological

studies, and biotechnological applications research involving phytoplankton and macroalgae (Zhang *et al*. 2023).

In contrast, a higher proportion of multi-country publications (MCP) was observed in studies addressing algal metabolites in the context of global climate change, particularly in articles from Argentina, Australia, Malaysia, Germany, the United States, and Brazil. This trend reflects this strong international engagement and a pursuit of cross-border collaborations, which tend to receive greater visibility and citation rates (Puuska *et al.* 2014). Such partnerships are especially valuable for scientists in developing countries or those affiliated with smaller institutions (Goldfinch *et al.* 2003).

3.5 Trends and thematic evolution

A total of 91.4% of the articles evaluated the influence of temperature (single or multi-stressor experiments) on the metabolites of aquatic micro- and macroalgae, indicating that temperature has been prioritized as a determining factor (Fig. 5). Most studies assessed static temperatures, while one article conducted an experiment involving heatwaves. The pH was evaluated in 33.3% of the selected studies (single or multi-stressor experiments). The combined analysis of temperature and pH (multi-stressor experiments) remains underexplored, representing only 24.7% of the studies. In addition to these factors, the articles also examined other concomitant variables, the most frequently assessed being nutrient concentrations (indicating different trophic levels), followed by salinity and the influence of light and radiation. These factors were evaluated across all types of environments, although they were more commonly studied in marine ecosystems.

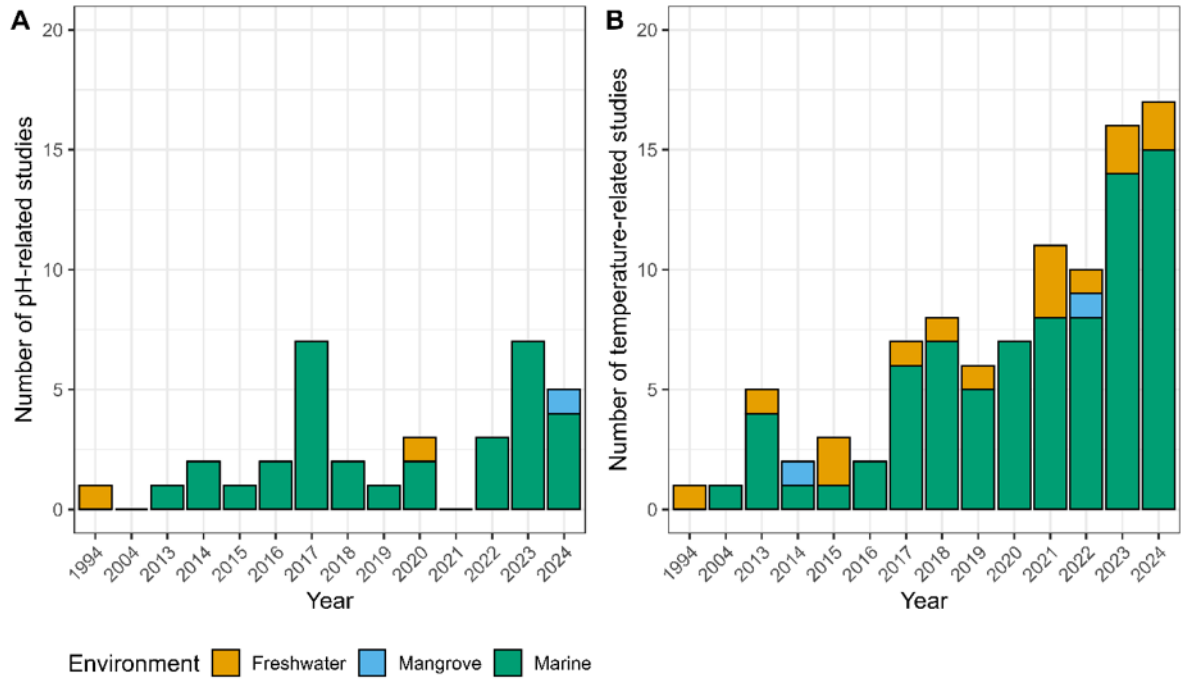


Fig. 5 Temporal trend of articles published between 1994 and 2024 on the influence of temperature (A) and pH (B) on the production of metabolites by microalgae and macroalgae, based on data from the Web of Science and Scopus databases

3.6 Influence of Environmental Factors on Algal Metabolites

During the analyzed period, 105 articles investigated the metabolic responses of phytoplankton and macroalgae related to lipids, carbohydrates, proteins, and vitamins. Most of these studies focused on a single type of biochemical analysis, with lipid analysis being the most frequent, accounting for 40.74% of the total publications (Fig. 6), followed by protein (25%) and carbohydrate (7.41%) analyses. Less frequent approaches included metabolomics (3.7%) and vitamin analysis (0.93%). Marine environments have been the focus of over 40 studies on lipids and proteins, and 19 on carbohydrates. In comparison, studies conducted in freshwater environments reveal a clear knowledge gap: lipids were addressed in only 11 articles, and proteins and carbohydrates in just 3 articles each (Fig. 6).

The predominance of studies evaluating lipid production reflects a greater scientific interest in this metabolite class, suggesting a gap in the broader biochemical characterization of algal biomass. This underrepresentation may hinder a more comprehensive understanding of trophic interactions and ecosystem functioning, as

884 the biochemical composition of organisms is directly linked to their nutritional quality
885 as a food source (Benítez *et al*. 2023).

886 Among the less frequently analyzed metabolites are carbohydrates. Dong *et al.*
887 (2015) observed that increased temperature, when analyzed in isolation, can enhance
888 the accumulation of soluble carbohydrates as an energy reserve under extreme
889 conditions. However, Mountourakis *et al*. (2023) reported increased carbohydrate
890 production in *Chlorella vulgaris* when temperature was assessed in combination with
891 other factors associated with global warming (multi-stressor experiment), such as
892 salinity stress and elevated CO_2. This increase in carbohydrate production may
893 function as an osmoprotective mechanism.

894 On the other hand, some species commonly found in eutrophic environments
895 have demonstrated adaptation to conditions projected under future global warming
896 scenarios. Among them, *Ulva lactuca*, a macroalga occurring in marine environments,
897 exhibited stimulated growth and increased carbohydrate production under elevated
898 carbon dioxide conditions alone; however, the opposite pattern was observed when
899 the interactive effects of elevated CO_2 combined with high temperature and nitrogen
900 levels were evaluated (Majumder et al., 2024). Dong et al. (2015) reported distinct
901 temperature-dependent responses in *Microcystis* spp. during winter, concluding that
902 low temperatures reduced cellular density while promoting intracellular carbohydrate
903 accumulation, whereas the opposite occurred at higher temperatures. Considering that
904 these species have the potential to dominate ecosystems under global warming
905 scenarios, the production of their metabolites is expected to be a key element in
906 understanding the systemic impacts of climate change.

907 Most of the articles that used protein analysis observed multiple environmental
908 stressors linked to warming, including associated with warming, phosphorus limitation
909 (Li *et al*. 2024; Spungin 2014), iron (Schiksnis 2024), copper (Bao *et al*. 2022),
910 acidification (Benítez *et al*. 2023; Bermúdez *et al*. 2015), and eutrophication (Bao *et al*.
911 2023). Total protein content and alterations in metabolic pathways such as glycolysis,
912 photosynthesis, carbon, phosphorus, and nitrogen metabolism are frequently
913 evaluated (Boyd and Hutchins 2012; Liu *et al*. 2021). In addition, some studies assess
914 the influence and ecological consequences, such as potential changes in food webs,
915 as there is a change in the nutritional quality of organisms (Benítez *et al*, 2023;
916 Bermúdez *et al*. 2015; Pierangelini *et al*. 2017). Although Benítez *et al*. (2023) did not
917 observe significant changes in total protein content in *Lessonia spicata* under elevated

temperature and pCO_2 (multi-stressor experiment), their results showed a reduction in organic matter and an increase in phenolic compounds. These biochemical shifts influenced trophic interactions, as the herbivorous snail *Tegula atra* preferred macroalgae not exposed to these stressors, likely due to their higher nutritional quality. This finding reinforces that even when protein levels remain stable, environmental stressors can alter other metabolic pathways with ecological consequences.

Differential protein production, although underexplored according to our results, is an important tool for investigating thermotolerance in microalgae, cyanobacteria, and macroalgae (Dedman *et al*. 2024; Liu *et al*. 2021; Schiksnis *et al*. 2024). The use of quantitative proteomic analysis based on iTRAQ (Isobaric Tags for Relative and Absolute Quantification) can be used to quantify and identify proteins, and changes in the pattern of protein production under stress can indicate the most impacted metabolic pathways (Liu *et al*. 2021). Some studies using this method have shown that proteins related to the photosynthetic system, synthesis and degradation, defense response, energy metabolism, and carbohydrates are differentially produced under climate change-related stress.

We identified only one study relating vitamin production to climate change factors, specifically concerning the effect of increased ocean temperature (single-stressor experiment) on the green alga *Symbiochlorum hainanensis* and the zooxanthellae *Effrenium sp.*, both symbiotic with corals. Vitamin analyses showed that thiamine and thiamine phosphate play an antioxidant role, reducing the effects caused by thermal stress. They also act as essential cofactors in the synthesis of metabolic processes in *Effrenium sp.* and *Symbiochlorum hainanensis* and may be linked to thermal tolerance (Xiao *et al*. 2024).

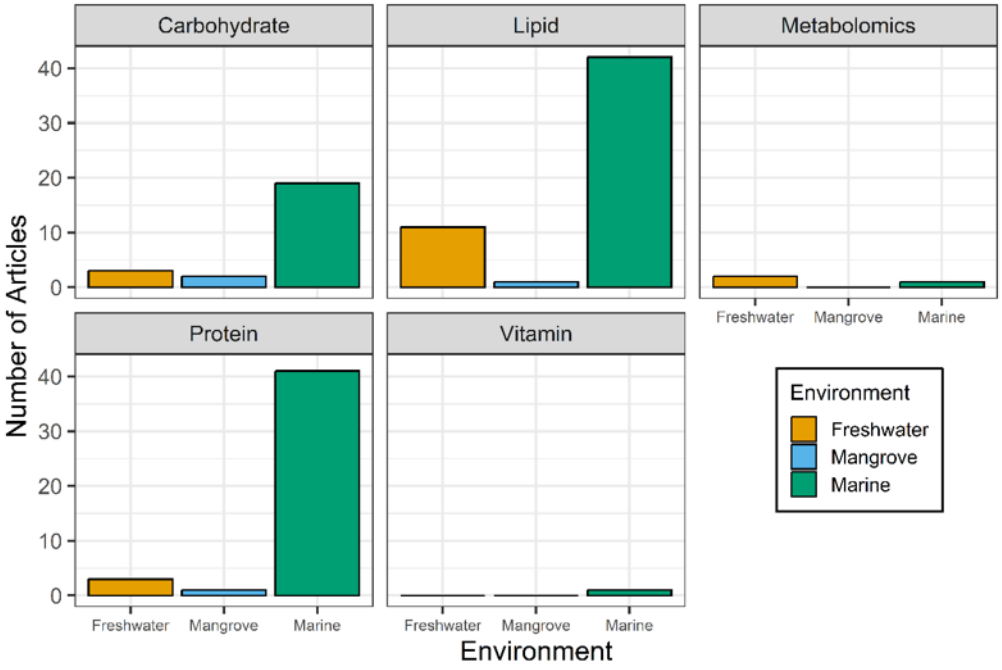


Fig. 6 Number of articles published on the influence of environmental variables (pH and temperature) on metabolite production by microalgae and macroalgae in marine, freshwater, and transitional (mangrove) environments, between 1994 and 2024, indexed in the Web of Science and Scopus databases

Organisms

It was observed that studies on microalgae predominated (78.1%) compared to macroalgae (21.9%). Additionally, the research has been concentrated on laboratory experiments using cultured species (84,76%). In contrast, only 9% of the articles investigated natural communities. Among the studied organisms, the most common taxon was Diatomista and Chlorophyta with 35 articles (33,3%), followed by Cyanobacteria, Dynophyceae, and Rodophyceae appeared in 19 articles (18,1%) (Fig. 7). Only seven articles evaluated interactions between freshwater species, and all of them specifically examined the influence of temperature (single-stressor experiment) on interactions between organisms from different trophic levels and on metabolite production.

These studies with isolated algae have shown that temperature and pH can modulate the production of metabolites by microalgae, especially as adaptation strategies to environmental variations. However, studies with communities have shown that these variables impact the production of metabolites mainly by altering the patterns of dominance in phytoplankton communities, favoring the occurrence of certain groups, especially cyanobacteria and diatoms, to the detriment of others (Dong et al., 2015; Hardenbicker et al., 2015; Sett et al., 2018), and that the impact on the trophic chain is not only related to the quantity of metabolites produced, but also to their quality (Calderini et al., 2023).

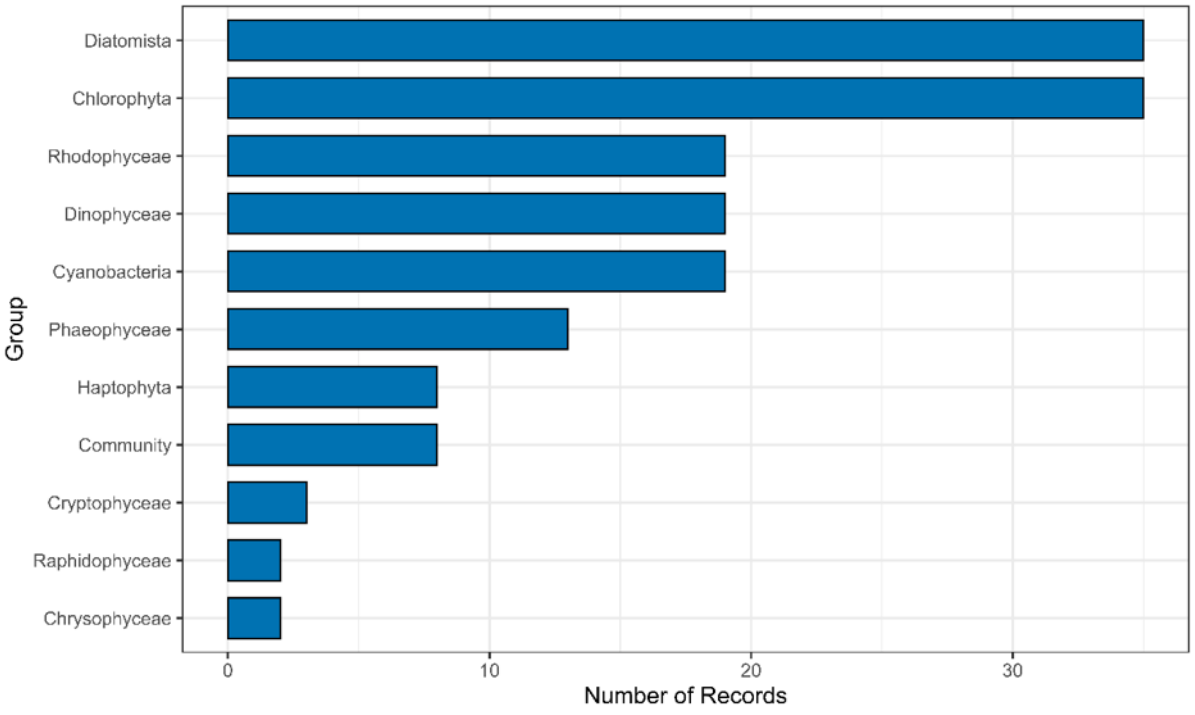


Fig. 7 Most frequently studied groups in articles assessing metabolite production by algae in response to stressors associated with climate change (acidification and temperature). Articles published and indexed in the Web of Science and Scopus databases between 1988 and 2024

Focus on Freshwater Ecosystems

The frequency of articles published (Fig. 2) in freshwater environments was significantly lower compared to marine ecosystems, not exceeding three publications per year. It was only in the last two decades that a subtle increase in interest was observed regarding changes in pH, temperature, or the combination of these factors

and their impact on metabolite production by microalgae. When analyzing exclusively studies on continental phytoplankton, a stronger ecological and ecotoxicological focus is observed (11 articles out of 14 selected). Most of these studies present experimental designs that consider environmental variations with fluctuations predicted by global warming models such as the IPCC. These studies have shown concern about the changes that global warming may induce in continental phytoplankton communities. The study by Yong et al. (2018) with green microalgae has indicated that the synergistic effect of temperature and anthropogenic activities (multi-stressor experiment) can probably exacerbate existing threats to primary producers.

Among the most studied metabolites in freshwater environments, lipid production by phytoplankton receives the most attention. There is a greater interest in research on lipid production by phytoplankton. Some studies have analyzed total lipid production (Mountourakis et al., 2023), but there is also growing interest in the production content of different fatty acid fractions (Abonyi et al., 2023), particularly polyunsaturated fatty acids (PUFAs) (Calderini et al., 2023), and how this production impacts the trophic relationships between phytoplankton and other herbivorous and parasitic organisms. The main factor influencing PUFA production is the composition of the phytoplankton community (Calderini et al. 2023), which in turn is directly affected by rising temperature and CO_2 levels, especially through an increased occurrence of cyanobacteria (Dong et al., 2015; Hardenbicker et al., 2015; Niu et al., 2020; Strandberg et al., 2022). However, while eukaryotic algae such as diatoms, dinoflagellates, and cryptophytes produce long-chain fatty acids (eicosapentaenoic acid and docosahexaenoic acid), cyanobacteria produce short-chain fatty acids (e.g., linolenic acid and alpha-linolenic acid), which may not meet the nutritional needs of consumers. Additionally, their colonies and filaments can be more difficult to ingest (Strandberg et al., 2022; Calderini et al., 2023; De la Rosa et al., 2024). Therefore, the increasing dominance of cyanobacteria will likely pose a greater threat to PUFA production by phytoplankton and, consequently, to consumer production (Strandberg et al., 2022).

These impacts on the trophic chain have been evaluated mainly using planktonic microorganisms (e.g., larvae and adult stages of chironomids), bivalves, and fungal parasites (Hardenbicker et al., 2015; Tseng et al., 2021; Strandberg et al., 2022; Abonyi et al., 2023). Despite the relevance of studies on lipids, it is important that future research also considers other metabolites (e.g., proteins, carbohydrates,

and vitamins), not only because of the ecological consequences these changes may bring, but also to better understand the main metabolic pathways affected by global warming and the associated defense mechanisms.

Another interesting point is that, in general, the experiments considered treatments with static temperatures. Only Akter et al. (2024) evaluated the effects of heatwaves and nitrate enrichment (multi-stressor experiment) on freshwater communities. Heatwaves are defined as increases in the intensity, frequency, and duration of extreme heat events that threaten aquatic biota and occur as a consequence of global warming. According to the authors, the synergistic effects of heatwaves and nitrate enrichment varied. In a scenario defined as “moderate and short” heatwave, phytoplankton growth was stimulated. In contrast, in a “long and intense” scenario, oxidative stress and massive phytoplankton mortality were observed. The authors suggest that future studies should focus on how aquatic consumers respond to changes in algal food quality (in terms of sugar, protein, and antioxidant content) under scenarios of eutrophication and heatwaves (Akter et al., 2024).

4. Conclusion

Our scientometric and systematic review reveals a recent increase (2023–2024) in studies examining the effects of climate change on algal metabolite production, while also exposing significant gaps in the current literature. Marine aquatic environments and organisms predominate when compared to other ecosystems, with a noticeable underrepresentation of freshwater and transitional environments—despite their ecological relevance, as they influence the maintenance of ecosystem services, primary production, and biodiversity.

Studies have been conducted under controlled laboratory conditions using isolated algal strains, however there is a pressing need for studies involving *in situ* communities or those that consider community-level interactions, especially in freshwater environments. Although pH plays a crucial role in shaping aquatic communities, it has received less attention compared to temperature. Studies on metabolite production have mainly focused on lipids, but carbohydrates, proteins, and vitamins are also important indicators of adaptation processes to environmental conditions and the quality of biomass produced and need further investigation.

Identifying these research gaps is essential to guide future studies toward a more comprehensive understanding of algal responses to environmental change.

Declarations

The authors declare no conflicts of interest

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Data Availability Statement

Data will be made available on request.

Authors' Contributions

Manuela Passos Tourinho: Conceptualization, literature search and data analysis, writing – original draft, review and editing. **Fabiana Schneck**: Conceptualization, supervision, writing – review and editing. **Muryllo Santos Castro**: Conceptualization, supervision, writing – review and editing. **Pablo Santos Guimarães**: Conceptualization, supervision, writing – review and editing. **Danilo Giroldo**: Conceptualization, supervision, writing – review and editing.

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CAPÍTULO 2

Artigo submetido para a Hydrobiologia

Chronic warming and heat waves reshape phytoplankton–bacterioplankton dynamics and dissolved carbohydrate composition in a subtropical coastal lagoon

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ABSTRACT

This study aimed to investigate how chronic warming and heat-wave exposure affect phytoplankton–bacterioplankton dynamics and dissolved carbohydrate dynamics in a shallow subtropical aquatic ecosystem. Community exposure experiments were conducted under projected future temperature conditions based on scenarios predicted by the Intergovernmental Panel on Climate Change (IPCC). The control (CTRL) was maintained at 24 °C, while Chronic Warming (CW) was maintained at 29 °C and Heat Wave (HW) consisted of three 29 °C heat-wave events interspersed with periods at 24 °C. Nitrate, phytoplankton and bacterioplankton communities, and dissolved carbohydrates were analyzed throughout the experiment. Warming altered

phytoplankton community dynamics, primarily by accelerating community senescence and reducing phytoplankton taxonomic richness, with HW producing responses comparable to those observed under CW. Warming also altered dissolved carbohydrate dynamics, reducing their final concentration and changing the temporal composition of individual carbohydrates, particularly mannose, rhamnose, glucose, and glucosamine. Bacterioplankton abundance showed tendency toward higher values at the end of the experiment under CTRL, whereas both warming treatments showed declining bacterial abundance. Overall, our results indicate that CW and HW can reshape phytoplankton–bacterioplankton dynamics and the temporal availability and composition of phytoplankton-derived dissolved carbohydrates, potentially altering carbon processing in shallow subtropical aquatic ecosystems.

KEY-WORDS: Climate change; carbon cycling; phytoplankton senescence; extracellular polymeric substances; microbial interactions.

Introduction

Considering one of the major drivers of change in continental aquatic ecosystems, global warming results in shifts in thermal regimes and pH, as well as alterations in biodiversity (Dudgeon, 2019; IPCC, 2023). Thermal changes have been projected based on scenarios developed by the IPCC, which are associated with different levels of greenhouse gas emissions into the atmosphere and encompass a high risk of extreme climatic events, fluctuations in hydrological regimes, and thermal alterations such as chronic warming and heatwaves (IPCC, 2023). Chronic warming (CW) is characterized by a long-term increase in mean temperature, whereas heatwaves (HW) are characterized by an abrupt increase of 5°C above the average temperature for at least three consecutive days (Fischer and Schär, 2010). These impacts can

affect all trophic levels, from microorganisms to large predators, and are of particular concern given their increasing magnitude and frequency (Benitez et al., 2023).

Temperature fluctuations and nutrient availability are among the potentially important factors determining phytoplankton community composition, as metabolic responses exhibit species-specific and individualized characteristics (Anderson et al., 2026). Furthermore, the carbohydrates produced by these organisms may undergo changes in both production and release, thereby influencing their degradation and consumption by the heterotrophic bacterial community (Baines & Pace, 1991; Guimarães et al., 2013). Such changes may modify nutrient availability and metabolic pathways within aquatic environments (Wagner, 2016), with potential implications for the functioning of the microbial loop. Moreover, the utilization of these compounds may depend on the metabolic capabilities of the bacterial community, as certain carbohydrates require specific enzymes for their degradation. Consequently, shifts in bacterial community composition may determine which fractions of dissolved organic matter (DOM) are effectively hydrolyzed and made available for microbial metabolism (Krull et al. 2026).

This study aimed to investigate how chronic warming and heat-wave exposure affect phytoplankton–bacterioplankton dynamics and dissolved carbohydrate production in a shallow subtropical aquatic ecosystem. The specific objectives were: (i) to assess changes in phytoplankton richness, abundance, and temporal dynamics under chronic warming and heat-waves conditions; (ii) To assess the influence of thermal changes on bacterioplankton abundance; (iii) to evaluate changes in the concentration and composition of dissolved carbohydrates and their temporal association with phytoplankton dynamics; and (iv) to examine the relationships among phytoplankton, bacterioplankton, dissolved carbohydrates, and nutrient availability under different temperature regimes.

Methodology

The methodology consisted of conducting community exposure experiments based on projected future temperature increases under scenarios predicted by the Intergovernmental Panel on Climate Change (IPCC, 2023), as detailed below.

Sampling

The sample was collected in March 2025 at a sampling site located 1,000 m from the eastern shore of Mirim Lagoon (32°52′44″S, 52°46′04″W). The site was selected based on previous studies on phytoplankton diversity at the same location (Crossetti et al., 2013; Guimarães et al., 2013), providing prior knowledge of the organisms investigated in this study.

The limnological variables pH (8.23), electrical conductivity (0.100 mS cm^{-1}), dissolved oxygen (10.24 mg L^{-1}), and surface temperature (24 °C) were measured at the time of sampling using a Horiba U-53 multiparameter probe. For the experiment, 10 L of subsurface water (30 cm depth) were collected. The water was aseptically filtered through a 68 µm mesh to remove zooplankton and stored in a sterile carboy. Sampling was performed 8 hours before the beginning of the experiment.

Microcosm Experiment

The experiment consisted of a control group and two treatments (Fig. 1) representing two distinct temperature conditions based on IPCC projections indicating that temperatures may increase by more than 5 °C by 2100. For the control (CTRL), a temperature of 24 °C was used, corresponding to the subsurface temperature observed in Mirim Lagoon at the time of sampling. The first treatment, referred to as Chronic Warming (CW), consisted of a constant elevated temperature of 29 °C (5 °C above the control), according to the pessimistic IPCC scenario (SSP5-8.5). For the second treatment, referred to as Heat Wave (HW), a temperature variation profile was established to simulate three heat waves at 29 °C, each lasting 4 h, over three consecutive days, interspersed with periods at 24 °C. The experiments lasted 7 days; in the HW treatment, temperature fluctuated between days 2 and 4, whereas temperature was maintained at 24 °C on the remaining days.

The experiment was conducted in microcosms in an incubation room under a 12:12 h light/dark photoperiod, a light intensity of 55.00 µmol m^{-2} s^{-1} (measured using a Light Meter LI-250A, LI-COR), and a constant temperature of 24 °C. Temperature variation among treatments was achieved using water-bath systems equipped with FullGauge MT-512E2HP/13 temperature controllers and aquarium heaters. The systems consisted of water-filled containers in which the replicate flasks were partially submerged. Each treatment block consisted of three 500 mL Erlenmeyer flasks (replicates) and one Erlenmeyer flask containing water and a thermostat for temperature control. Each treatment was maintained in a separate water-bath system, with independent temperature controllers and heaters.

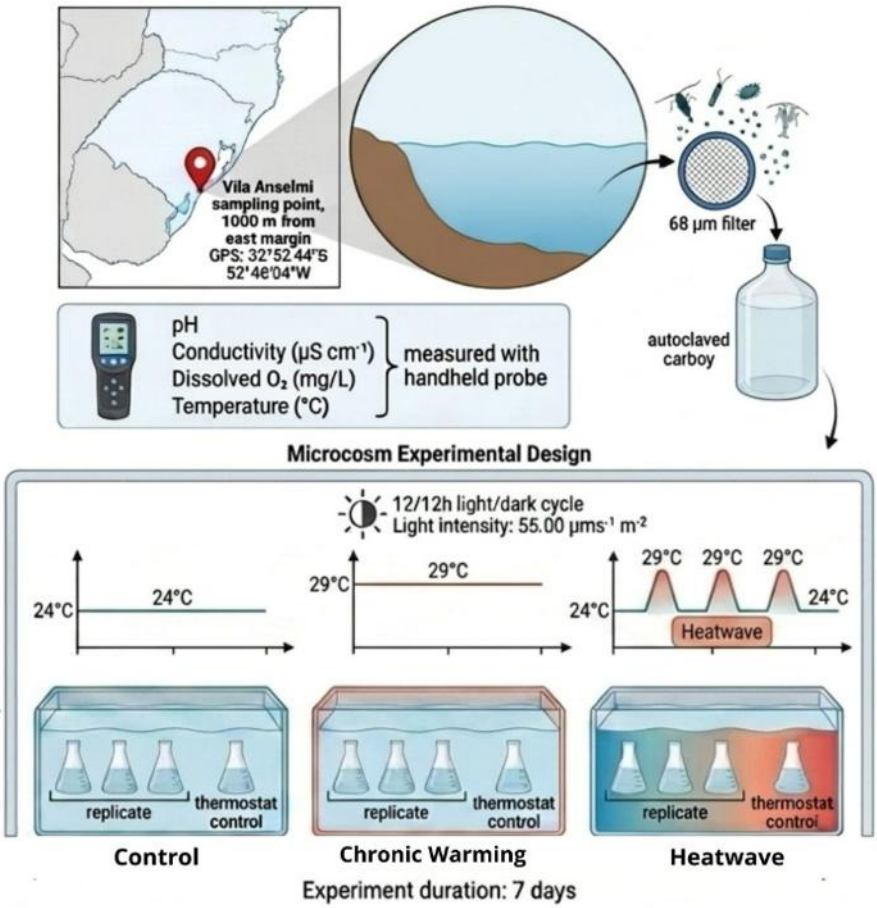


Figure 1. Schematic diagram of the microcosm experiment designed to assess the effects of global warming (chronic warming according to SSP5-8.5 and heat waves) on phytoplankton and bacterioplankton communities from a sampling site in Mirim lagoon (RS, Brazil) and on carbohydrate production.

Samples for nitrate concentration analysis and phytoplankton quantification were collected daily from day 0 to day 4 and on day 7. For analyses of dissolved carbohydrate concentrations, bacterioplankton quantification, and chlorophyll and carotenoid content, samples were collected on days 0, 2, 4, and 7.

Phytoplankton Analysis

For the analysis of phytoplankton diversity and abundance, 10 mL samples were collected from each replicate and fixed with a 0.5% Lugol's solution. Community quantification was performed using a 2 mL Utermöhl sedimentation chamber (Edler & Elbrächter, 2010). For cell counting, the results were expressed as an abundance of individuals (solitary cells, colonies, coenobia, and filaments) per mL. Taxonomic identification was performed to the lowest possible taxonomic level, generally genus or species, using specialized literature such as Barber

& Haworth (1981), Round, Crawford & Mann (1990), Wehr & Sheath (2002), and Bicudo & Menezes (2006).

Heterotrophic Bacterial Community Analysis

The collected samples were fixed with 4% formaldehyde and filtered through quantitative filter paper (95% cellulose; 2.0–4.0 μm mean retention; Macherey-Nagel). For slide preparation, the samples were filtered using a filtration apparatus (Kitasato flask) with the aid of a vacuum pump through a 0.2 μm Nuclepore membrane previously stained with Irgalan Black. After filtration, 1 mL of 1% acridine orange fluorochrome solution was added to the filter and incubated for 5 min. The excess solution was filtered off, and the filter was rinsed with sterile distilled water. The filters were then dried for 15 min in an oven at 35 °C. Subsequently, semi-permanent slides were prepared using mineral oil.

The slides were examined under an Olympus® BX53 upright microscope equipped with epifluorescence and a 12.5-megapixel DP72 camera. A total of 30 images per filter were captured, and 10 randomly selected images were processed (Massana et al., 1997). After image processing, the images were binarized, and CMEIAS/Image Tool software (v. 1.28) was used for cell counting, measurement of cell dimensions, and classification into morphotypes (Liu et al., 2001). Bacterial density was determined from the mean number of cells using the equation described by Kepner Jr. & Pratt (1994).

Qualitative Analysis of Dissolved Carbohydrates

Samples of 10 mL were collected and filtered through GF/3 glass-fiber filters with a pore size of 0.45 μm (Macherey-Nagel, Düren, Germany), and the filtrate was frozen and stored at −4 °C. For each sample, a 1 mL aliquot was hydrolyzed with HCl (0.64 M final concentration) at 100 °C for 12 h and subsequently evaporated to dryness under reduced pressure (Gremm & Kaplan, 1997), in triplicate. Carbohydrates were analyzed by high-performance ion chromatography (HPLC) with pulsed amperometric detection (PAD) for the analysis of total dissolved carbohydrates, including mono-, di-, oligo-, and polysaccharides.

Nitrate Analysis

For the analysis of dissolved nitrate (NO_3^--N, mg L^{-1}), 10 mL samples were collected for spectrophotometric determination following the protocol described by García-Robledo et al. (2014). Nitrate concentrations were monitored throughout the experiment and used to determine its duration based on nitrate availability to the microbial community.

Chlorophyll (a and b) and Carotenoid Analyses

Samples of 10 mL were collected for pigment determination following the method described by Wellburn (1994), using DMSO neutralized with 5% $CaCO_3$. The samples were

incubated in a water bath at 60 °C for 60 min and subsequently centrifuged for 20 min at 4,000 rpm. Absorbance readings were performed using the supernatant in a spectrophotometer at wavelengths of 665 and 649 nm.

Statistical Analyses

Data normality was assessed using the Shapiro–Wilk test, and homogeneity of variances was assessed using Levene's test. For each treatment, temporal differences in nitrate, chlorophyll a, carotenoid concentrations, and the chlorophyll-to-carotenoid ratio were assessed using one-way analysis of variance (one-way ANOVA), with time as a fixed factor. When significant differences were detected ($p < 0.05$), means were compared using Tukey's test. All analyses were performed using PAST software, version 2.17b, with a significance level of 5%.

Homogeneity of variances was confirmed for all variables evaluated (Levene's test, $p > 0.05$). One-way ANOVA indicated significant temporal differences in nitrate, chlorophyll a, carotenoid concentrations, and the chlorophyll-to-carotenoid ratio for all treatments ($p < 0.05$). Multiple comparisons using Tukey's test identified significant differences between specific time points ($p < 0.05$), indicating significant nitrate consumption accompanied by increases in chlorophyll a and carotenoid contents. The growth rate was calculated based on the interval between day zero of the experiment and the day on which phytoplankton reached its highest absolute abundance. (Andersen, 2005)

Relationships among chemical and biological parameters were analyzed using Principal Component Analysis (PCA) in PAST software (Hammer et al., 2001), after standardizing the data using z-scores (Bini, 2007; Mann, 2003).

Schematical Diagram Preparation

The schematical diagram was prepared using https://www.figurelabs.ai/ to generate conceptual illustrations of the experiment. Canva was subsequently used for graphic design, layout, and final assembly of the figure. All visual elements were reviewed, edited, and validated by the authors.

Results

For nitrate (NO_3^-), a consistent pattern was observed across all treatments, with a significant decline in nutrient concentrations ($p < 0.05$) over the experimental period until the fourth day. On the seventh day, an increase in nitrate concentrations was observed, suggesting a pattern consistent with remineralization (Fig 2a).

Despite the thermal changes tested, photosynthetic pigments exhibited similar patterns among treatments, suggesting the maintenance of the community's photosynthetic capacity. Up

to the fourth day of the experiment, a temporary increase in total chlorophyll and carotenoid concentrations was observed, followed by a decreasing trend in pigment contents. Although no significant differences were detected, the chlorophyll-to-carotenoid ratio tended to show higher values in the control treatment than in the warming treatments (Fig 2).

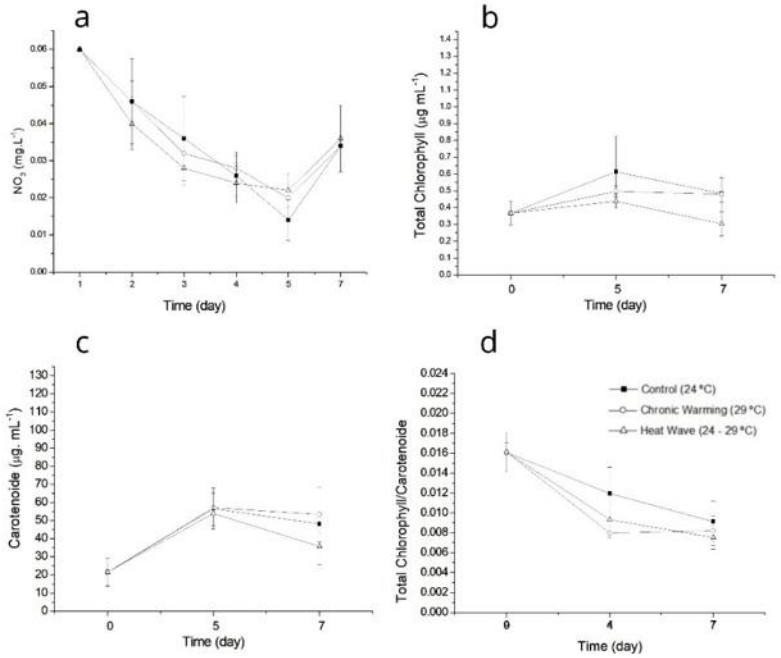


Figure 2. Nitrate (NO_3^-), total chlorophyll, carotenoids, and total chlorophyll-to-carotenoid ratio throughout the microcosm experiment.

Phytoplankton species richness was higher in the control treatment, with the highest values recorded on days 2 and 4, with 29 and 30 species, respectively. The CW and HW treatments showed their highest species richness on day 3, with 23 and 26 species, respectively (Fig. 3). In both the control and HW treatments, species richness began to decline from the fourth day of the experiment, whereas in the CW treatment, a decline in species richness was already observed from the third day onward. Despite this decline, during the loss of species richness in the final days of the experiment, two taxonomic groups emerged that had not previously been observed in the control treatment: Euglenophyceae and Trebouxyophyceae. However, Euglenophyceae was observed only in the CW treatment from the fourth day of exposure onward, whereas Trebouxyophyceae was observed only in the HW treatment between the second and fourth days of the experiment, coinciding with the peak of growth.

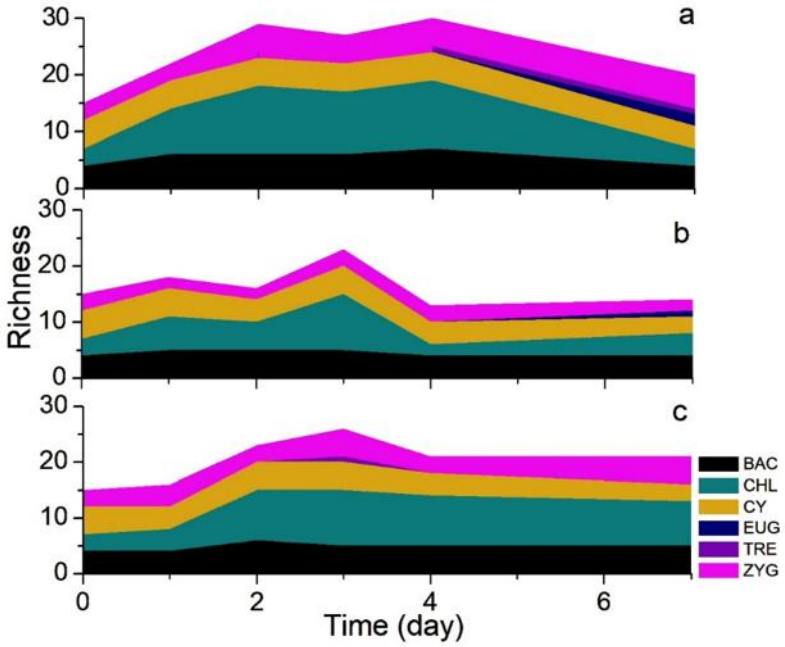


Figure 3. Phytoplankton species richness under the following conditions: control at a constant 24 °C (a), chronic warming at 29 °C (b), and heat-wave scenario (c). Bacillariophyceae (BAC); Chlorophyceae (CHL); Cyanophyceae (CY); Euglenophyceae (EUG); Trebouxiophyceae (TRE); and Zygnematophyceae (ZYG).

When absolute phytoplankton abundance was evaluated, a clear trend was observed in the control treatment, with progressive and continuous growth until the third day of the experiment (growth rate 0,93), when the highest values were recorded, reaching nearly 8×10^3 cells mL^{-1}. After the fourth day, a marked and continuous decrease was observed until the end of the experiment. Cyanophyceae showed the highest absolute abundance among the taxa, whereas Zygnematophyceae, Bacillariophyceae, and Chlorophyceae maintained relatively low and stable densities throughout the experiment, with growth peaks between the second and fourth days. Their abundances subsequently continued to decline throughout the experimental period (Fig. 4a).

Two growth peaks were observed in the CW treatment, on days 2 (growth rate 0,88) and 4, reaching approximately 4×10^3 and 5×10^3 cells mL^{-1}, respectively. These growth peaks were accompanied by increases in the densities of Cyanophyceae and Bacillariophyceae, with Cyanophyceae showing the greater contribution to the observed increase in phytoplankton abundance.

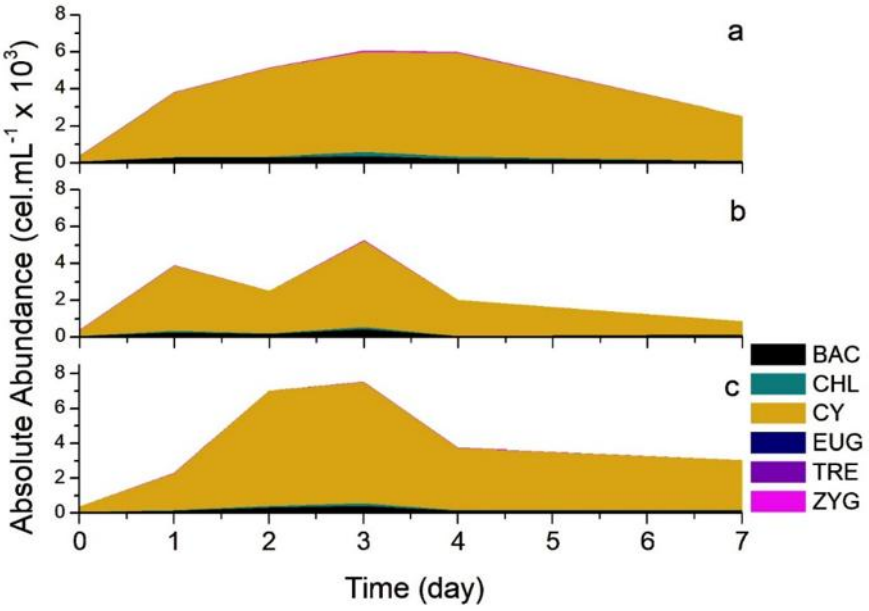


Figure 4. Absolute abundance of the phytoplankton community under the following conditions: control at a constant 24 °C (a), chronic warming at 29 °C (b), and heat-wave scenario (c). Bacillariophyceae (BAC); Chlorophyceae (CHL); Cyanophyceae (CY); Euglenophyceae (EUG); Trebouxiophyceae (TRE); and Zygnematophyceae (ZYG).

In the HW treatment, abundances increased progressively throughout the experiment, particularly during the heat-wave exposure period, reaching a peak on the third day (growth rate 1,00). After this period, a more pronounced decrease occurred until the fourth day, followed by a more gradual decline until the seventh day, particularly for Cyanophyceae. In contrast, Bacillariophyceae and Chlorophyceae showed a decrease in abundance from the third to the fourth day, followed by stabilization of their values.

The absolute concentrations of dissolved carbohydratess howed distinct patterns among treatments (Fig. 5). Absolute concentrations and relative proportions were similar among all treatments until the second day of the experiment. The fourth day in the control treatment was characterized by a peak in mannose concentration and the onset of a gradual increase in glucosamine. Rhamnose appeared only on the final part of the experiment, concomitantly with the disappearance of mannose. Overall, the treatments followed a similar pattern, with low initial carbohydrate concentrations, mainly mannose, rhamnose, glucosamine, and fucose, followed by a period of carbohydrate accumulation around the fourth day and a predominance of glucosamine and rhamnose on the final part. However, in both treatments (CW and HW), rhamnose appeared earlier, on the fourth day, while mannose showed a lower relative

contribution after the second day. Both the control and CW treatments showed increasing carbohydrate concentrations toward the end of the experiment, reaching final values of 5.11 and 2.39 mg L^{-1}, respectively. In contrast, HW was the only treatment to show a decrease in total carbohydrate concentration at the end of the experiment, reaching 0.71 mg L^{-1} (Fig. 5).

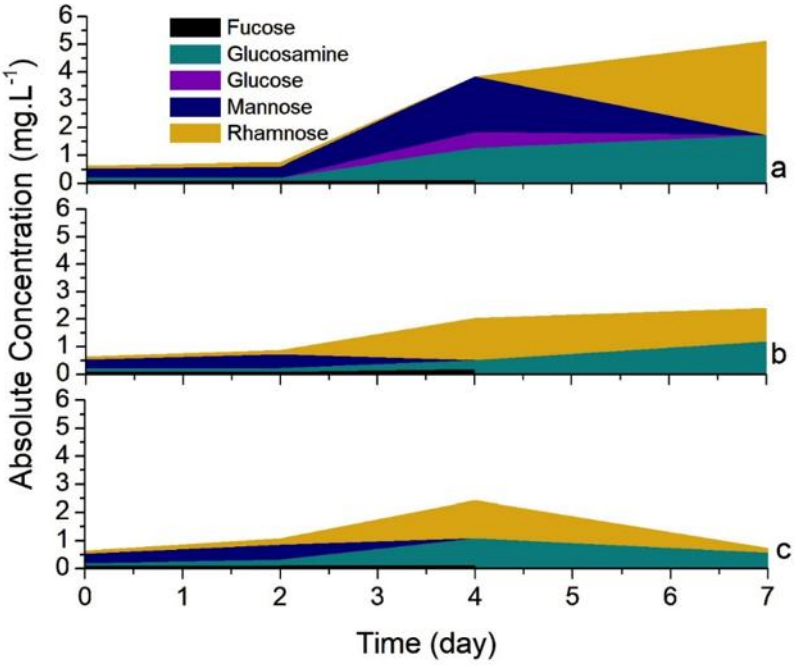


Figure 5. Absolute concentration of dissolved carbohydrates throughout the microcosm experiment under the following conditions: control at a constant 24 °C (a), chronic warming at 29 °C (b), and heat-wave scenario (c).

The relative concentrations of carbohydrates differed among treatments (Fig. 6). At the beginning of the experiment (day 0), the three treatments showed similar carbohydrate compositions, with mannose representing approximately 53% of the dissolved carbohydrates, followed by rhamnose (18%), glucosamine (17%), and fucose (10%), while glucose was absent. In the control treatment, higher relative proportions of mannose, glucosamine, rhamnose, and fucose were observed until the second day (Fig. 6a). From the second day onward, glucose appeared, accounting for 14% of the dissolved carbohydrates, while glucosamine increased to 30%. In contrast, the relative proportion of fucose progressively decreased until the end of the experiment in all treatments.

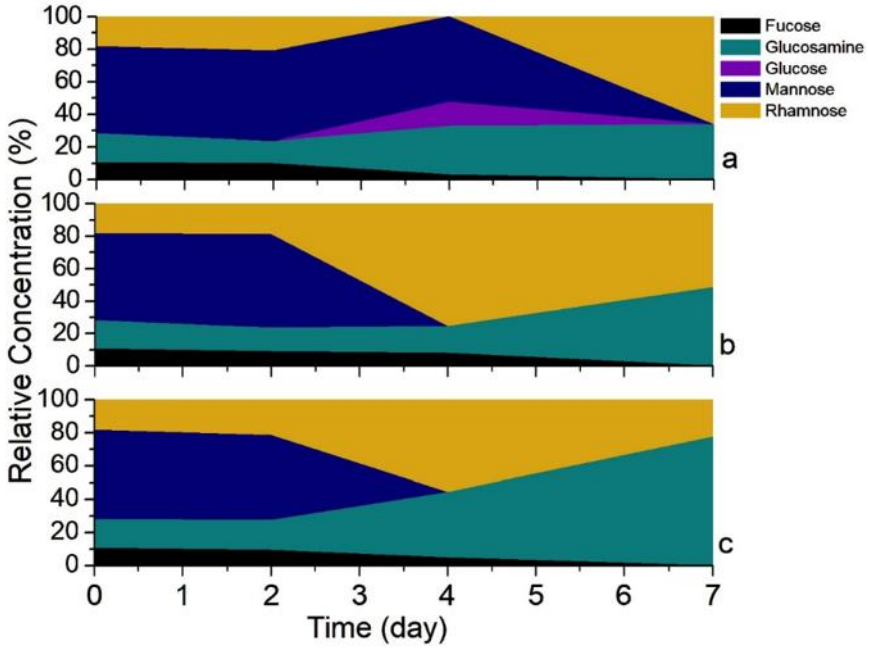


Figure 6. Relative concentration of dissolved carbohydrates throughout the microcosm experiment under the following conditions: control at a constant 24 °C (a), chronic warming at 29 °C (b), and heat-wave scenario (c).

The highest proportion and persistence of mannose were detected in the control treatment, whereas in the CW and HW treatments, the fourth day was characterized by the early disappearance of mannose, accompanied by an increase in the relative proportions of rhamnose and glucosamine, as well as a decrease in the relative contribution of fucose. When comparing the treatments, the control was characterized by the final predominance of rhamnose, whereas CW showed a relatively balanced composition of rhamnose and glucosamine on the final day. In contrast, HW promoted a more pronounced shift in the composition of dissolved carbohydrates, favoring the predominance of glucosamine, which accounted for approximately three-quarters of the relative composition at the end of the experiment.

The most abundant bacterial morphotypes were Coccus, Regular Rod, Curve Rod, and Shaped Rod, whereas the less abundant morphotypes were grouped into a category designated as "Others." Regarding absolute bacterioplankton abundance, the control treatment showed fluctuations throughout the experiment, ranging from 2.5 to 3.4 × 10^6 ind. mL^{-1}. The CW and HW treatments also showed fluctuations until the fourth day. The HW treatment reached its highest values on the fourth day, ranging from 2.4 to 3.25 × 10^6 ind. mL^{-1}, whereas CW showed its highest density at the beginning of the experiment, ranging from 2.1 to 2.4 × 10^6 ind. mL^{-1}. However, both warming treatments showed a decreasing trend toward the end of the

experiment, reaching their lowest values on day 7. In contrast, the control treatment showed a tendency toward bacterial growth over the same period (Fig. 7).

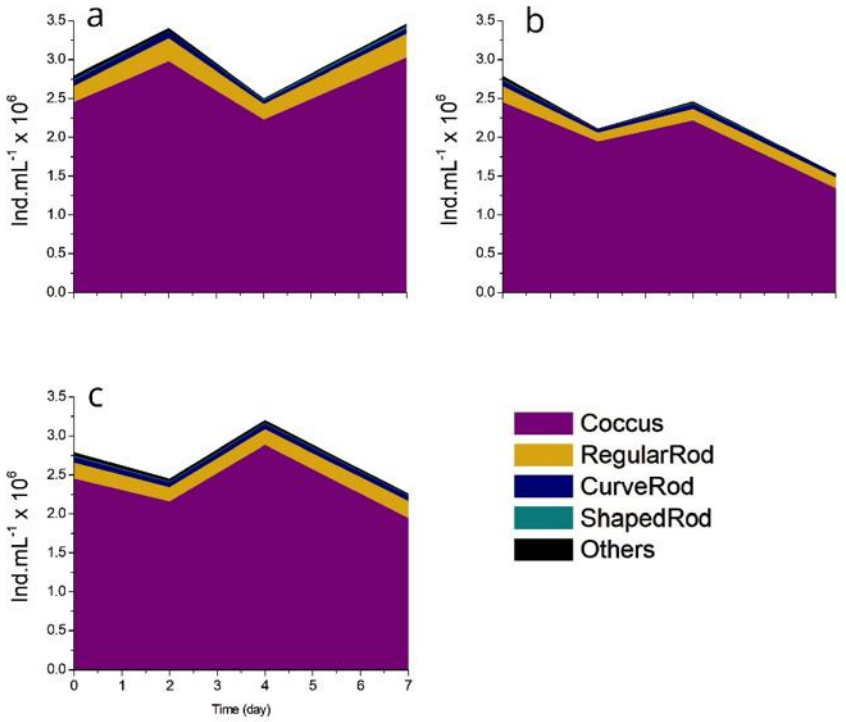


Figure 7. Bacterioplankton community abundance throughout the microcosm experiment using samples from a sampling site in Mirim Lagoon (RS, Brazil) under the following conditions: control at a constant 24 °C (A), chronic warming at 29 °C (B), and heat-wave scenario (C).

When comparing the patterns of planktonic communities and carbohydrates throughout the experiment (Fig. 8), a relationship between the increase in dissolved carbohydrates and phytoplankton growth was observed until the fourth day across all treatments. In the control and chronic warming treatments, the relationship between carbohydrates and phytoplankton changed on the seventh day, with phytoplankton community senescence accompanied by an increase in total carbohydrate concentrations. Only in the HW treatment did the two variables continue to show the same pattern on the final day, with phytoplankton community senescence accompanied by a decrease in dissolved carbohydrate concentrations. Although bacterioplankton data showed a more variable pattern, only the control treatment exhibited a tendency toward bacterial growth on the final day, coinciding with the pattern observed for carbohydrates. In contrast, the CW and HW treatments showed a decreasing trend in bacterial abundance, associated with the lower total dissolved carbohydrate concentrations.

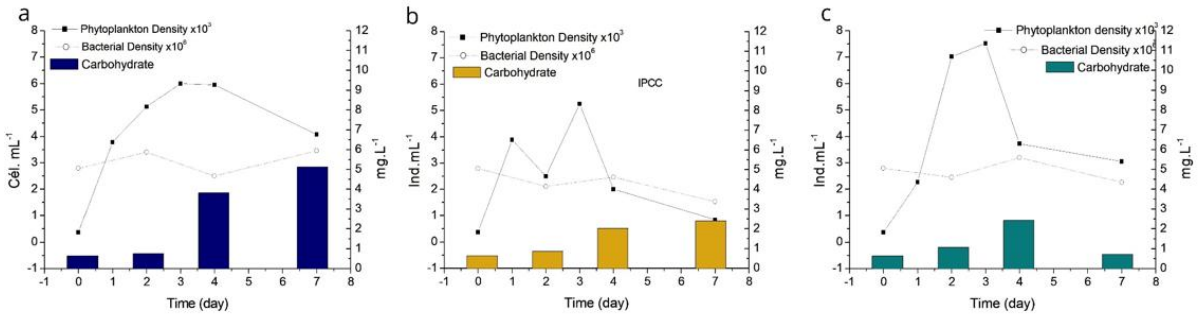


Figure 8. Absolute abundance of phytoplankton and bacterioplankton communities and total carbohydrate concentration throughout the microcosm experiment using samples from a sampling site in Mirim Lagoon (RS, Brazil) under the following conditions: control at a constant 24 °C (a), chronic warming at 29 °C (b), and heat-wave scenario (c).

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The PCA (Fig 9) showed that the first two principal components explained 51.32% of the total variability in the data. Principal Component 1 explained the largest proportion of the variance (31.20%), whereas Principal Component 2 explained 20.12%. Component 1, which best explained the distribution of the data, showed positive correlations with carbohydrates that exhibited higher concentrations at the end of the experiment (glucosamine and rhamnose), which were similarly associated with total phytoplankton and bacterioplankton abundance. In contrast, carbohydrates whose relative concentrations decreased throughout the experiment were negatively correlated with Component 1 (mannose and fucose). The samples were also associated with Component 1, showing a distribution more strongly related to experimental time than to treatment, as indicated by the colors of the points. Initial samples were negatively

correlated with Component 1, whereas final samples showed positive correlations. In contrast, glucosamine and rhamnose were more strongly associated with phytoplankton community senescence, showing correlations with Component 2 similar to those observed for nitrate, whose concentrations decreased throughout the experiment, followed by a subsequent increase in availability at the end of the experiment.

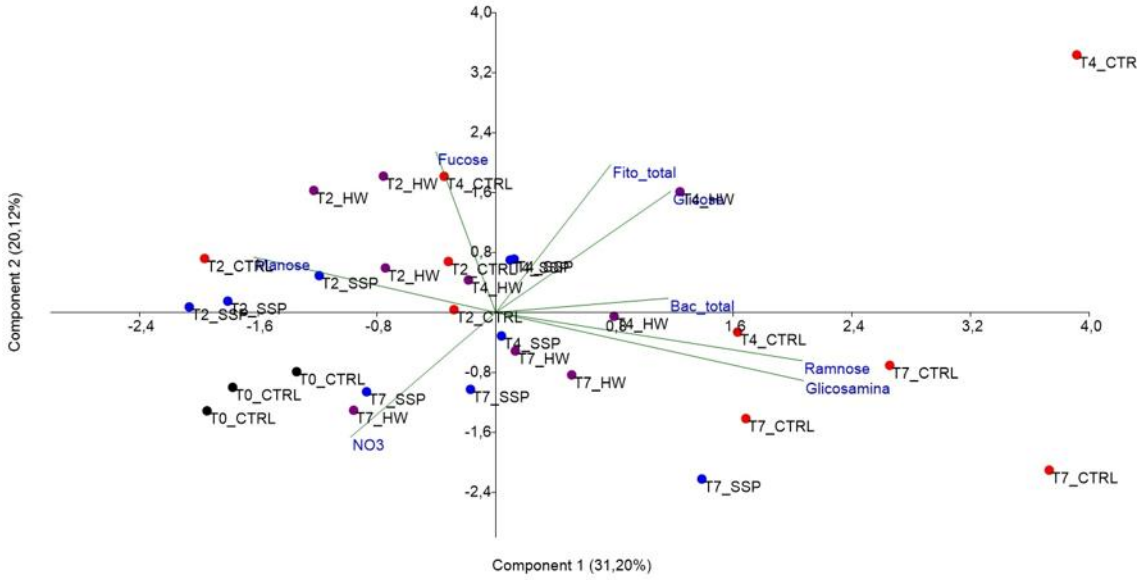


Figure 9. Principal Component Analysis (PCA) of the microcosm experiment assessing the effects of temperature on phytoplankton and bacterioplankton community dynamics and dissolved carbohydrate production at a sampling site in Mirin lagoon (RS, Brazil) under the following conditions: control at a constant 24 °C (A), chronic warming at 29 °C (B), and heat-wave scenario (C). Point colors indicate treatments: black, CTRL; blue, CW; and purple, HW. Sample codes indicate the sampling day (T0, T2, T4, and T7), followed by the treatment designation (CTRL, CW, or HW). T0 represents the initial sample collected before the experimental treatments.

Discussion

To our knowledge, this is the first experimental study investigating the influence of global warming on carbohydrate production and phytoplankton–bacterioplankton interactions in Lagoa Mirim. Although conducted under controlled and semi-natural conditions, this study provides insights into how global warming may affect the complex dynamics of shallow lakes and phytoplankton–bacterioplankton interactions.

The gradual decrease in nitrate concentrations during the first days of the experiment indicates nitrate assimilation by the phytoplankton community, which was undergoing exponential growth. In the final days of exposure, however, an increase in nitrate concentrations was observed, consistent with processes of organic matter remineralization, potentially involving nitrification. A similar pattern was observed by Listmann et al. (2026), who evaluated $NO_2^- + NO_3^-$, SiO_3, and PO_4 fluxes and observed a similar mineralization process involving nitrogen sources. Although no significant differences were detected among treatments, the observed variations suggest that active ecosystem processes, such as nutrient cycling, occurred within the experimental system, as nutrient regeneration can make previously assimilated nutrients available again to the microbial communities. Melo et al. (2025) demonstrated synergistic effects of temperature with different nutrient limitations and light availability in freshwater microalgal cultures, showing that light limitation was among the main factors reducing growth rates under increased temperatures, followed primarily by nitrogen limitation. Therefore, the low nitrogen availability, together with other nutrients that were not analyzed at the end of the experiment, may have contributed to phytoplankton community senescence and increased stress under elevated temperatures.

Although no significant differences were observed among treatments, the pattern observed in chlorophyll and carotenoid concentrations, with increases up to the fourth day followed by decreases on the seventh day, was consistent with the nutrient patterns observed. This suggests an initial phase of nutrient uptake accompanied by increased phytoplankton growth, followed by phytoplankton community senescence coinciding with nitrate remineralization. However, the control treatment showed a slight tendency toward higher total chlorophyll-to-carotenoid ratios, which may indicate a response to temperature stress in the warming treatments. Experiments with microalgal cultures have shown that increased carotenoid production may be associated with protection against oxidative stress induced by elevated temperatures (Huang et al. 2017). Similarly, a pigment-monitoring study in a Mediterranean coastal lagoon found a relationship between increased carotenoid concentrations relative to chlorophyll and higher mean temperatures (Molner et al. 2024).

The species richness recorded in the control treatment indicates that milder and more stable thermal conditions favored the coexistence of different taxonomic groups throughout the experiment. In addition, the community included all six of the most abundant classes, with the highest species richness recorded on the second and fourth days. In the chronic warming and heat-wave treatments, the peak in species richness occurred earlier and reached lower values than in the control, suggesting that warming accelerated phytoplankton community dynamics

and, even under fluctuations in environmental conditions, may promote a decline in species richness.

Exposure to extreme temperature events may accelerate ecological succession, altering community composition and increasing the relative importance of thermotolerant species at the expense of temperature-sensitive taxa. Despite the higher species richness observed in the control treatment, our study did not show significant changes in the composition of the most abundant taxa throughout the experiment. This may be related to the timing of sample collection and its initial community composition. Because sampling was conducted during the warmer months, when surface water temperature was approximately 24 °C, the phytoplankton community may have already been subjected to selective pressure from environmental temperature. This hypothesis is supported by the initial composition of the phytoplankton community, which showed a strong dominance of Cyanophyceae, including *Planktolyngbya contorta* and *Planktolyngbya limnetica*. Tourinho et al. (2025), in a scientometric analysis, identified a recurrent association in the literature between global warming scenarios and shifts in the relative importance of Cyanophyceae and Bacillariophyceae. In the same lake where the samples for our experiment were collected, an increase in the absolute abundance of Cyanophyceae and diatoms during the warmer months of the year has previously been observed (Guimarães et al., 2013).

Regarding phytoplankton absolute abundance, the control treatment maintained high density values for a longer period than the warming treatments, whereas HW showed a lower initial growth rate and both warming treatments exhibited earlier phytoplankton community senescence compared with the control. Although it is difficult to disentangle the effects of temperature from those of other limiting factors in the environment, increased temperature is known to enhance metabolic demand when light and nutrient availability are not limiting, thereby altering the optimal growth range, particularly in experimental systems such as ours, in which nutrients are not replenished in mesocosms (Grimaud et al. 2017; Heinrichs et al. 2025).

Our experiment further showed that the effects of heat waves were similar to those observed under the warming treatment representing the projected conditions for 2100 under the IPCC SSP5-8.5 scenario. This suggests that warming-related effects may rapidly alter the metabolic state of the phytoplankton community. Akter et al. (2024) emphasized that, although heat waves are distinct from sustained increases in mean temperature, their metabolic effects on phytoplankton communities may persist even after mean temperatures decline. The authors further highlighted that the recent thermal history of a community can modulate its responses

to future temperature changes and accelerate ecological succession, leading to a shift toward communities dominated by thermotolerant species.

According to Hall and Cotner (2007), bacterioplankton community dynamics result from the stoichiometric balance between carbon and nutrient availability. Since the carbon source available to bacterioplankton in our experimental system was derived from phytoplankton-released saccharides, bacterioplankton growth would be expected to exhibit a temporal lag relative to phytoplankton growth and the associated release of EPS. The absence of a clear growth curve for bacterioplankton, unlike that observed for phytoplankton, may be explained by shifts in the limiting factors affecting this community throughout the experiment. Initially, bacterioplankton may have been primarily limited by the availability of organic carbon, whereas toward the end of the experiment, nutrient availability may have become a more important limiting factor. Moreover, not all carbon released by phytoplankton is rapidly assimilated by bacterioplankton (Peierls & Paerl, 2010). Therefore, the different types of carbohydrates released by phytoplankton throughout the experiment may have influenced bacterioplankton community dynamics. Another possibility, also described by Hall and Cotner (2007), is that bacterial abundance does not necessarily reflect bacterial activity. Thus, even though relatively little variation was observed in bacterial abundance, bacterial activity may nevertheless have responded to the dynamics of the experimental system.

The treatments showed different absolute carbohydrate concentrations over the course of the experiment. However, the beginning of the experiment was characterized by the absence of marked differences in total carbohydrate concentrations or in the presence of the main monosaccharides. This suggests that thermal changes did not immediately alter the absolute concentrations of dissolved carbohydrates, as different components of the planktonic community may respond at different temporal scales. It may also indicate that production and consumption processes were still relatively balanced at this stage (Jørgensen et al., 2014).

From the fourth day onward, differences in carbohydrate concentrations became more evident among treatments. In the control treatment, a peak in mannose concentration and a gradual increase in glucosamine were observed. At this stage, rhamnose was detected only in the CW and HW treatments, whereas its detection in the control occurred later. This suggests that thermal exposure accelerated temporal changes in dissolved carbohydrate dynamics, particularly under the HW treatment. This pattern is consistent with results from a marine mesocosm experiment, in which the authors observed an increase in dissolved carbohydrate concentrations, particularly under elevated temperature conditions (Engel et al., 2010). They also reported that future increases in temperature in cold marine environments may affect the

release of metabolites by phytoplankton and, consequently, influence the microbial loop (Engel et al., 2010).

By the end of the experiment, the differences among treatments became even more evident. The control treatment was characterized by a peak in mannose concentration, a gradual increase in glucosamine, and the appearance of rhamnose on the final day. In contrast, the HW and CW treatments showed only two types of carbohydrates from the fourth day until the end of the experiment, namely rhamnose and glucosamine, indicating an early simplification of the carbohydrate composition.

The thermal treatments promoted distinct responses; however, both had the potential to advance the appearance of some carbohydrate types and alter the composition of phytoplankton-derived carbohydrates. Total carbohydrate concentrations also differed among treatments. The control reached 5.11 mg L^{-1}, whereas CW reached 2.39 mg L^{-1}. The higher dissolved carbohydrate concentrations observed in the control than in the CW and HW treatments may indicate a greater accumulation of phytoplankton-derived carbohydrates under lower temperatures, potentially reflecting a more pronounced carbon overflow mechanism (Smith & Underwood, 2000; Perkins et al., 2001). However, HW showed a more pronounced shift in carbohydrate dynamics, characterized by an earlier peak in carbohydrate concentration followed by a decrease in carbohydrate proportions over time.

Phytoplankton EPS release is stimulated by environmental conditions such as nutrient deficiency (Vieira & Myklestad, 1986; Giroldo & Vieira, 2002). Thus, nutrient-limited phytoplankton may increase the supply of carbon to heterotrophic bacteria, which are potential competitors for limiting nutrients (Bratbak & Thingstad, 1985). However, phytoplankton–bacterioplankton interactions extend far beyond competition. These communities engage in a variety of metabolic interactions, including the exchange of cofactors, nutrients, and signaling molecules, resulting in consortia of high ecological complexity (Muñoz & Guieysse, 2006; Ramanan et al., 2016).

According to Bittar & Vieira (2010), the release of soluble exopolysaccharides (EPS) by a Cyanophyceae species may follow two distinct patterns depending on the growth phase. During the growth phase, soluble saccharides are released through fragmentation of the extracellular capsule, whereas during senescence, release is associated with structural and intracellular compounds derived from cell lysis. This dynamic may help explain the changes in carbohydrate composition observed throughout the experiment, particularly the predominance of mannose during the growth phase and of rhamnose and glucosamine during phytoplankton community senescence.

It is important to emphasize that the EPS present in the water column result from the dynamic interaction between compounds produced by phytoplankton and those consumed, transformed, and released by bacterioplankton. The nutrient regeneration observed at the end of the experiment may be associated with bacterial growth fueled by excess photoassimilated carbon released through overflow (Fogg, 1983; Wood & Van Valen, 1990). Thus, two non-mutually exclusive hypotheses may explain the lower carbohydrate concentrations observed in the CW and HW treatments: (1) reduced carbon overflow due to greater carbon consumption associated with acclimation and nutrient regeneration processes (Grimaud et al. 2017; Akter et al. 2024; Heinrichs et al. 2025); and (2) increased bacterial activity and remineralization throughout the experiment (Hall & Cotner, 2007).

Cyanophyceae was the dominant taxonomic group in this study, accounting for more than 90% of the community in most samples throughout the experiment and was therefore likely responsible for a substantial proportion of the EPS released. Gaignard et al. (2019) conducted an extensive survey of EPS produced by Cyanophyceae and eukaryotic microalgae and performed a phylogenetic analysis of the main monosaccharides produced by different taxa. They highlighted the importance of glucose, xylose—which can often be difficult to distinguish analytically from mannose—and glucosamine production, supporting the predominance of these carbohydrates among the main saccharides observed throughout our experiment.

Polysaccharides containing mannose play an important role as carbon sources (Krull et al. 2026), and their recurrent occurrence in aquatic ecosystems and cultures suggests that they are widely distributed and functionally important components (Bertocchi, 1990). Mannose was the dominant carbohydrate in all treatments during phytoplankton growth. It showed a pronounced peak in the control treatment, whereas its relative contribution decreased rapidly in the HW and CW treatments. Mannose-containing polysaccharides are among the exudates produced by diatoms (Giroldo et al. 2002; Guimarães et al. 2013), are components of the cell walls of several cyanobacterial genera (Bertocchi, 1990; Bertolin et al.), and are also present in marine species belonging to groups such as Charophyta, Chlorophyta, and Rhodophyta (Gaignard et al., 2019).

Mannose is an important carbohydrate that may regulate phytoplankton–bacterioplankton interactions by favoring the selection of bacteria with specialized enzymes for mannose hydrolysis. Once hydrolyzed, mannose is no longer detected among the dissolved EPS carbohydrates, representing an important mechanism for nutrient cycling within aquatic ecosystems and highlighting phytoplankton–bacterioplankton interactions (Krull et al. 2026). This dynamic may have restricted the occurrence of mannose among the dissolved

carbohydrates to the phytoplankton growth phase, with mannose potentially being rapidly consumed by bacterioplankton.

As mannose concentrations decreased, a continuous increase in glucosamine (N-acetylglucosamine) was observed until the end of the experiment. N-acetylglucosamine monomers form chitin, a polysaccharide composed of linear units that occurs in some pennate and centric diatoms (Hackman & Goldberg, 1965; Tiwari et al., 2025). These units are extruded through fultoportulae, structures involved in regulating buoyancy and reinforcing frustule rigidity (Tiwari et al., 2025). In addition, glucosamine is a component of extracellular polymeric substances (EPS) produced by cyanobacterial species (Gaignard et al., 2019).

The most pronounced increase in glucosamine concentrations occurred shortly after the onset of phytoplankton community senescence, suggesting an increase in intracellular material released during cell lysis and the decomposition of cellular structures. Because chitin is a relatively refractory molecule, its degradation depends on chitinases, enzymes produced by specialized bacteria that release N-acetylglucosamine during the degradation process. Thus, the increase in carbohydrate concentrations observed throughout the experiment may indicate enhanced degradation of chitin-rich polymers and greater availability of these compounds to the bacterial community (Donderski, 1998). However, the accumulation of glucosamine until the end of the experiment suggests that this monosaccharide may not be as readily processed by bacterioplankton as mannose.

In contrast to the other carbohydrates, glucose showed a distinct pattern and was detected only on the fourth day in the control treatment. However, the predominance of this compound might be expected, as glucose is one of the main constituents of EPS produced by cyanobacteria and some groups of microalgae (Gaignard et al. 2019), particularly under conditions of reduced phytoplankton growth (Myklestad 2021). Glucose was also identified as the predominant component in the profiles analyzed by Gaignard et al. (2019), being present in 65% of the cyanobacterial taxa evaluated. Nevertheless, its low relative contribution in our study suggests that its dynamics were strongly influenced by transformation processes, since glucose is highly bioavailable and its rapid consumption may have prevented its accumulation in the dissolved pool (Kennedy, 2002). Thus, even if glucose production was substantial, given the high abundance of cyanobacteria, rapid uptake by heterotrophic bacteria may have limited its persistence and accumulation. This process may have been particularly pronounced in the HW and CW treatments, where increased microbial activity could have accelerated glucose utilization. Therefore, the occurrence of glucose in the dissolved carbohydrate pool likely

reflected not only the taxonomic composition of the community but also the recycling and transformation of organic matter throughout the experiment.

Fucose showed a low relative abundance throughout the experiment, with a progressive decreasing trend in all treatments. This monosaccharide is frequently associated with mucilage formation and EPS production involved in cell adhesion and biofilm formation, potentially contributing to organic matter aggregation and carbon retention in aquatic environments (Tiwari et al., 2025). However, in the HW and CW treatments, this decrease occurred earlier and coincided with an increase in the relative contribution of rhamnose and glucosamine, suggesting that increased temperature may have accelerated changes in dissolved carbohydrate composition.

Rhamnose is a monosaccharide frequently found in EPS produced by microalgae and cyanobacteria. It may also contribute to the formation of mucilaginous matrices, particularly under stress conditions, altering interactions between cells and their surrounding environment (Tiwari et al., 2025), and may contribute to more hydrophobic properties of extracellular material (Giroldo et al. 2003). In our experiment, the increase in rhamnose may be associated with nutrient stress in the control treatment, as its increase was particularly pronounced on the final day of the experiment. However, thermal stress appears to have advanced the occurrence of this monosaccharide to the fourth day, followed by a decline by the seventh day, potentially reflecting bacterial degradation or transformation. This process may modify the physicochemical properties of EPS, particularly by increasing its hydrophobicity and adhesive capacity, thereby favoring EPS formation and modification and the development of aggregates (Giroldo et al., 2003; Vieira et al., 2006). Thus, EPS reorganization and increased cell aggregation may promote the formation of larger particles and their subsequent sedimentation, potentially transferring organic matter from the water column to the sediment and linking phytoplankton production, bacterial activity, and organic matter cycling in aquatic ecosystems.

Therefore, our results indicate that warming affected not only the persistence and structure of the phytoplankton community, but also the temporal dynamics and composition of dissolved carbohydrates, potentially altering the availability of phytoplankton-derived carbon. Both CW and HW exposure accelerated community senescence and reduced taxonomic richness, with HW producing responses comparable to those observed under CW. These changes were accompanied by an earlier shift in dissolved carbohydrate composition, characterized by the disappearance of mannose and the earlier occurrence of rhamnose and glucosamine, suggesting a reorganization of phytoplankton-derived EPS during community senescence. The lower accumulation of dissolved carbohydrates under warming conditions may

have resulted from reduced carbon overflow, increased bacterial processing, or a combination of both, indicating that warming may alter not only the amount of available carbon but also the temporal availability and composition of substrates for bacterioplankton. The carbohydrate profile, primarily dominated by mannose, rhamnose, and glucosamine, was strongly influenced by the contribution of cyanobacteria, while the temporal dynamics of these compounds were consistent with differential bacterial processing of individual carbohydrates. Thus, warming may shift the balance from phytoplankton carbon production and accumulation toward more rapid transformation and recycling, potentially modifying the physicochemical properties and fate of organic matter and reshaping the link between phytoplankton dynamics, bacterial activity, and carbon cycling in shallow aquatic ecosystems.

COMPETING INTERESTS

The authors declare that they have no financial or non-financial competing interests that could have influenced the work reported in this manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Suplementar Material

Table 1. List of phytoplankton taxa by treatment in the microcosm experiment assessing the effects of temperature on phytoplankton and bacterioplankton community dynamics and dissolved carbohydrate production at a sampling site in Lagoa Mirim (RS, Brazil), under the following conditions: control at a constant 24 °C (CTRL), chronic warming at 29 °C (CW), and heat-wave scenario (HW).

Taxa	Inicial	CTRL	CW	HW
BACILLARIOPHYCEAE				
Aulacosera sp.	x	x	x	x
Craticula cuspidata (Kützing) D.G.Mann	x	x		
Stephanocyclus meneghinianus (Kützing) Kulikovskiy	x	x	x	x
Fragilaria sp.		x		
Hydrosera sp.		x	x	x
Melosira sp.	x	x	x	x
Navicula sp.		x	x	x
Staurosira longirostris (Frenguelli) Metzeltin, Lange-Bertalot & García-Rodíguez		x	x	x
CHLOROPHYCEAE				
Acutodesmus sp.		x		
Ankistrodesmus fusiformis Corda				x
Closteriopsis		x		
Coelastrum sphaericum Nägeli	x	x		x
Coelastrum microporum Nägeli			x	
Coelastrum pulchrum Schmidle		x	x	
Crucigeniella sp.		x		x
Desmodesmus communis (E.Hegewald) E.Hegewald	x	x	x	x
Golenkinia sp.		x		
Lobocystis fottiana A.Comas, M.C.Pérez, & Novello		x	x	x
Monoraphidium sp.	x	x	x	x
Pediastrum duplex Meyen		x	x	x
Tetradesmus lagerheimii M.J.Wynne & Guiry		x	x	x
Desmodesmus denticulatus (Lagerheim) S.S.An, T.Friedl & E.Hegewald		x		x
Selenastrum sp.		x		
Tetrastrum sp. 1		x	x	x
Tetrastrum sp. 2			x	
CYANOPHYCEAE				
Aphanocapsa sp.	x	x		
Dolichospermum sp.		x	x	x
Gloeothece sp.			x	x
Oscillatoria sp.		x		

Planktolyngbya contorta (Lemmermann) Anagnostidis & Komárek	x	x	x	x
Planktolyngbya limnetica (Lemmermann) Komárková-Legnerová & Cronberg	x	x	x	x
Pseudanabaena cf. *limnetica* (Lemmermann) Komárek	x	x	x	x
EUGLENOPHYCEAE				
Trachelomonas armata (Ehrenberg) F.Stein		x	x	
Trachelomonas sp.		x		x
TREBOUXYOPHYCEAE				
Lagerheimia genevensis (Chodat) Chodat		x		
Quadricocos sp.		x		
ZYGNEMATOPHYCEAE				
Closterium aciculare T.West		x		
Closterium acutum Brébisson	x	x	x	x
Closterium sp.1	x			
Closterium kuetzingii Brébisson		x	x	x
Closterium parvulum Nägeli		x	x	x
Closterium sp.2		x	x	x
Closterium setaceum Ehrenberg ex Ralfs	x	x	x	x
Closterium sp.3		x	x	x
Euastrum sp.		x		
Staurastrum cf. *sebaldi* Reinsch	x	x	x	x
Staurodesmus sp.				x

CONSIDERAÇÕES FINAIS E PERSPECTIVAS

A tese apresenta uma abordagem integrada sobre os impactos das mudanças climáticas na microbiota, sua atividade metabólica e interações. Esta estrutura permitiu entender o que se sabe sobre o tema até o presente momento e as principais lacunas, para então elaborar o segundo capítulo da tese.

Nossa revisão cienciométrica e sistemática revela um aumento recente (2023–2024) no número de estudos que investigam os efeitos das mudanças climáticas sobre a produção de metabólitos por algas, ao mesmo tempo em que evidencia lacunas significativas na literatura atual. Apesar da importância da microbiota nos processos ecológicos, o crescimento e consolidação desta temática surge de forma tardia se comparado a outras áreas associadas a mudanças climáticas, que tiveram início por volta de 2007 (Machado *et al.* 2023; Castro *et al*. 2025).

Os ambientes aquáticos marinhos e os organismos marinhos predominam como foco dos estudos em comparação com outros ecossistemas, enquanto ambientes de água doce e de transição são consideravelmente sub-representados, apesar de sua relevância ecológica, uma vez que contribuem para a manutenção dos serviços ecossistêmicos, da produção primária e da biodiversidade.

Entre as principais lacunas e tendências observadas, podemos observar que: (1) Estudos têm sido conduzidos sob condições laboratoriais controladas, utilizando linhagens algais isoladas, refletindo a necessidade de estudos envolvendo comunidades *in situ* ou que considerem interações em nível de comunidade, especialmente em ambientes de água doce; (2) Embora o pH desempenhe um papel fundamental na estruturação das comunidades aquáticas, esse fator tem recebido menos atenção em comparação com a temperatura e isto pode estar relacionado aos desafios metodológicos no estudo de variações do pH se comparado com a logística necessária para estudos com temperatura; (3) Os estudos sobre produção de metabólitos têm se concentrado principalmente nos lipídios, mas carboidratos, proteínas e vitaminas também são importantes indicadores dos processos de adaptação às condições ambientais e da qualidade da biomassa produzida, sendo necessários estudos adicionais sobre esses compostos.

A identificação dessas lacunas possibilitou desenvolver o segundo capítulo com foco nas lacunas destacadas, em especial acerca de estudos que envolvam dinâmicas de comunidades microbianas, suas interações e produção/consumo de carboidratos.

As flutuações de temperatura e a disponibilidade de nutrientes estão entre os fatores potencialmente importantes na determinação da composição da comunidade fitoplanctônica (Anderson et al., 2026). Além disso, os carboidratos produzidos por esses organismos podem sofrer alterações tanto em sua produção quanto em sua liberação, influenciando, consequentemente, sua degradação e consumo pela comunidade bacteriana heterotrófica (Baines & Pace, 1991; Guimarães et al., 2013). Essas alterações podem modificar a disponibilidade de nutrientes e as vias metabólicas nos ambientes aquáticos (Wagner, 2016), com potenciais implicações para o funcionamento da alça microbiana. Além disso, alterações na composição da comunidade bacteriana podem determinar quais frações da matéria orgânica dissolvida (MOD) são efetivamente hidrolisadas e disponibilizadas para o metabolismo microbiano (Krull et al., 2026).

Nossos resultados indicam que o aquecimento afetou não apenas a persistência e a estrutura da comunidade fitoplanctônica, mas também a dinâmica temporal e a composição dos carboidratos dissolvidos, potencialmente alterando a disponibilidade de carbono derivado do fitoplâncton. Tanto a exposição ao aquecimento crônico (CW) quanto às ondas de calor (HW) acelerou a senescência da comunidade e reduziu a riqueza taxonômica, sendo que as HW produziram respostas comparáveis às observadas sob CW. Akter et al. (2024) destacaram que, embora as ondas de calor sejam distintas de aumentos sustentados da temperatura média, seus efeitos metabólicos sobre as comunidades fitoplanctônicas podem persistir mesmo após a redução das temperaturas médias.

As mudanças na dinâmica da comunidade fitoplanctônica foram acompanhadas por uma mudança mais precoce na composição dos carboidratos dissolvidos, caracterizada pelo desaparecimento da manose e pela ocorrência antecipada de ramnose e glucosamina, sugerindo uma reorganização dos EPS derivados do fitoplâncton durante a senescência da comunidade. Embora a composição de espécies ao longo do experimento não tenha mudado muito, e dada a importância que espécies de cianobactéria tiveram para este estudo, é de se esperar que estas tenham grande contribuição para a os EPS disponíveis. Segundo Bittar & Vieira (2010), a liberação de EPS por uma espécie de cianobactéria pode seguir dois padrões distintos, dependendo da fase de crescimento. Durante a fase de crescimento, os sacarídeos solúveis são liberados por meio da fragmentação da cápsula extracelular, enquanto, durante a senescência, a liberação está associada a compostos estruturais

e intracelulares provenientes da lise celular. Este padrão pode explicar parte da variação temporal na composição de EPS.

Além disso, a composição de EPS presentes na coluna d'água resultam da interação dinâmica entre os compostos produzidos pelo fitoplâncton e aqueles consumidos, transformados e liberados pelo bacterioplâncton. Duas hipóteses não mutuamente excludentes podem explicar as menores concentrações de carboidratos observadas nos tratamentos CW e HW em comparação com CTRL: (1) redução do *carbon overflow* devido ao maior consumo de carbono associado aos processos de aclimatação e regeneração de nutrientes (Grimaud et al., 2017; Akter et al., 2024; Heinrichs et al., 2025); e (2) aumento da atividade bacteriana e da remineralização ao longo do experimento (Hall & Cotner, 2007). Assim, o aquecimento pode deslocar o equilíbrio da produção e do acúmulo de carbono pelo fitoplâncton para uma transformação e reciclagem mais rápidas, potencialmente modificando as propriedades físico-químicas e o destino da matéria orgânica e remodelando a conexão entre a dinâmica do fitoplâncton, a atividade bacteriana e o ciclo do carbono em ecossistemas aquáticos rasos.

Juntos, os resultados da tese demonstraram que os efeitos das mudanças climáticas nos ecossistemas aquáticos não estão restritos a mudança na estrutura e dinâmica de comunidades algais, mas também se estendem a produção e transformação dos compostos orgânicos, resultantes da interação entre fito e bacterioplâncton. A integração do capítulo de cienciometria com o experimento em microcosmos destacam a importância em investigar estas respostas da perspectiva de comunidade, particularmente em ambientes de água doce e sob condições de diferentes temperaturas. Ainda que seja necessário entender melhor os mecanismos que definem as mudanças observadas na composição de carboidratos, os resultados sugerem que o aquecimento global pode alterar o fluxo de carbono de origem fitoplanctônica e sua disponibilidade para microbiota. Desta forma, entender como o aquecimento crônico e os eventos extremos, como ondas de calor, simultaneamente afetam a produção e consumo de compostos chave na interação entre microrganismos é essencial para entender as consequências das mudanças climáticas no funcionamento de ecossistemas aquáticos.

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