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Abundância relativa e biometria da espécie *Bolivina ordinaria, Phleger &*
***Parker, 1952,* no talude continental norte da Bacia de Pelotas ao longo do**
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Dissertação submetida ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Santa Catarina como requisito parcial para a obtenção do título de Mestra em Oceanografia.

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O presente trabalho em nível de Mestrado foi avaliado e aprovado, em 18 de abril de 2024, pela banca examinadora composta pelos seguintes membros:

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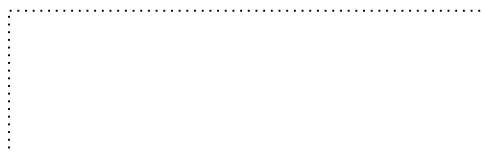Universidade Federal Espírito Santo

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RESUMO

O presente trabalho tem como objetivo avaliar as variações da abundância relativa, tamanho da testa e biomassa acumulada da espécie *Bolivina ordinaria* (Foraminifera) a fim de compreender as mudanças nas condições paleoceanográficas do talude continental norte da Bacia de Pelotas ao longo dos últimos 112 ka AP. As análises foram baseadas em 651 indivíduos de 42 amostras distribuídas ao longo dos testemunhos SIS-249 (Estágios Isótopos Marinhos 5 a 3) e SIS-188 (Estágios Isótopos Marinhos 3 a 1). As flutuações observadas na abundância relativa e na biomassa acumulada de *Bolivina ordinaria* são correspondentes com as oscilações no fluxo de carbono orgânico total e com as variações na produtividade primária entre os períodos interglaciais e glaciais. Os resultados sugerem que esta espécie da infauna é favorecida pelo fornecimento regular de matéria orgânica refratária durante os períodos mais quentes, mas enfrenta maior competição de espécies de infauna rasa e epifauna durante os períodos glaciais, quando o fluxo de matéria orgânica lábil aumenta. Com isso, vimos que o uso de medidas biométricas de foraminíferos bentônicos são descritores importantes para compreender a ecologia das espécies e a resposta destas em relação às mudanças ambientais ocorridas em determinada época.

Palavras-chave: Atlântico Sul; Foraminifera; Paleoecologia; Biometria.

ABSTRACT

The present work aims to evaluate the variations in the relative abundance, test size and accumulated biomass of the species *Bolivina ordinaria* (Foraminifera) in order to understand the changes in the paleoceanographic conditions of the northern continental slope of the Pelotas Basin during the last 112 ka BP. The analyses were based on 651 individuals from 42 samples distributed throughout cores SIS-249 (Marine Isotope Stages 5 to 3) and SIS-188 (Marine Isotope Stages 3 to 1). The observed fluctuations in the relative abundance and accumulated biomass of *Bolivina ordinaria* correspond with the oscillations in total organic carbon flux and with the variations in primary productivity between interglacial and glacial periods. The results suggest that this infaunal species is favored by the regular supply of refractory organic matter during warmer periods but faces greater competition from shallow infaunal and epifaunal species during glacial periods, when the flow of labile organic matter increases. With this, we saw that the use of biometric measurements of benthic foraminifera is an important tool for understanding the ecology of species and their response to environmental changes that occurred at a given time.

Keywords: South Atlantic; Foraminifera; Paleoecology; Biometry.

LISTA DE FIGURAS

SUMÁRIO

1 INTRODUÇÃO GERAL

Foraminíferos são protistas unicelulares que possuem uma carapaça de composição mineralógica variável, chamada de testa. Possuem ampla distribuição geográfica e são exclusivamente marinhos, com ocorrência desde zonas costeiras rasas até as áreas mais profundas. Podem ser planctônicos ou bentônicos, sendo que estes se dividem em epifaunais - habitam a porção mais superficial do sedimento (0-1 cm) ou infaunais – têm capacidade para viver dentro do sedimento (CORLISS & CHEN, 1988; CORLISS, 1991; RATHBURN & CORLISS, 1994).

Espécies e/ou associações de foraminíferos refletem condições ecológicas específicas; e devido a sua abundância e ao potencial de preservação das suas testas nos sedimentos marinhos, têm sido amplamente utilizados como *proxies* paleoambientais, bioestratigráficos e paleoceanográficos (BOLTOVSKOY, 1980; BÉ, 1977; HEMLEBEM, 1989; GOODAY, 2003; JORISSEN et. al., 2007).

O Quaternário é marcado por variações entre ciclos glaciais e interglaciais que refletem mudanças nas condições paleoceanográficas (ROBINSON et al., 1995; JIAN et al., 2000). As glaciações e interglaciações desse período são intervalos investigados com o objetivo de compreender o sistema climático atual e futuro. Intervalos glaciais (períodos frios) e interglaciais (períodos quentes) são identificados por meio da razão isotópica do oxigênio ($\delta^{18}O$) e representados pelos Estágios Isotópicos Marinhos (EIM). Os EIM's são nomeados por algarismos arábicos, onde os EIM's ímpares correspondem aos interglaciais e os pares aos glaciais, sendo o EIM 1 correspondente ao presente (Petro, 2018). Os EIM's nos permitem, entre outros, a elaboração de modelos de idade pela correlação de curvas de $\delta^{18}O$ locais com as curvas globais (Lisiecki & Stern, 2016).

Vários estudos utilizando foraminíferos para compreender as mudanças oceanográficas ocorridas ao longo do Quaternário já foram desenvolvidos na margem continental sul brasileira. Esse grupo taxonômico, individualmente ou associado a outros *proxies* (biológicos, sedimentológicos ou geoquímicos), tem permitido reconstruir a influência das mudanças climáticas (estágios glaciais e interglaciais): (1) nas flutuações do nível do mar, como nos trabalhos de Gonzales et al. (2017), Petró et al. (2021), Duque-Castaño et al. (2019), Santana et al. (2021); (2) nos deslocamentos dos limites latitudinais e batimétricos das massas d´água, tal qual Peterson & Lohmann (1982), Arz et al. (1999), Volbers & Henrich (2004),

Campos et al. (2017), Schmitt et al. (2019), de Gonçalves & Leonhardt (2021, 2022), Suárez-Ibarra et al. (2022); (3) na paleoprodutividade marinha e no aporte de carbono para os sistemas bentônicos, como apresentado nos estudos de Smart et al. (1994), Ferreira et al. (2014), Almeida et al. (2015), Petró et al. (2016); Rodrigues et al. (2018) e Portilho-Ramos et al. (2019).

O método mais comumente utilizado para aplicação de foraminíferos como *proxy* ambiental é pelo reconhecimento de variações nas abundâncias relativas das populações ao longo de testemunhos. No entanto, de acordo com Corliss & Chen (1988), Altenbach et al. (1999) e Altenbach & Struck, (2001), as relações entre a abundância de espécies de foraminíferos e suas respectivas biomassas também podem auxiliar na compreensão dos processos que governam o fluxo de carbono nos oceanos e assim possibilitarem uma avaliação complementar das flutuações ambientais ao longo do registro fóssil.

1.1 BIOMASSA E BIOMETRIA DE TESTAS DE FORAMINÍFEROS BENTÔNICOS

A biomassa pode ser expressa como quantidade de matéria orgânica, peso seco livre de cinzas, quantidade de carbono orgânico e ATP ou pelo volume da testa (Murray & Alve, 2000) que é geralmente calculado por meio do biovolume (ROWE et al. 2008).

O biovolume pode ser estimado entre outros pelo formato da carapaça, associado a formas geométricas e pela quantidade de material citoplasmático ocupada por ela (Murray, 2006; Movellan et al., 2012; Freitas et al. 2021) e é uma alternativa não destrutiva, acessível e relativamente de baixo custo.

A biomassa é um parâmetro importante porque está relacionada ao fluxo de nutrientes (Altenbach & Sarnthein, 1989) e os foraminíferos têm uma resposta muito rápida a essas mudanças. As relações entre associações de foraminíferos e suas respectivas biomassas também podem auxiliar na compreensão dos processos que governam o fluxo de carbono e assim permitir avaliar suas flutuações ao longo do registro fóssil (ALTENBACH et al., 1999; ALTENBACH & STRUCK, 2001; CORLISS & CHEN, 1988).

Dessa maneira, a análise biométrica das testas de foraminíferos bentônicos pode oferecer dados qualitativos e quantitativos sobre o passado do fundo marinho e suas mudanças paleoceanográficas, como nos trabalhos de Petersen et al. (2016),

Eder et al. (2017), Santana et al. (2021) e Tetard et al. (2021). Além disso, respostas biométricas de bolivinideos às mudanças ambientais já foram verificadas em trabalhos prévios. Um dos primeiros estudos envolvendo a família Bolivinitidae foi publicado por Smith (1963) sobre a fauna recente de El Salvador. O autor identificou variações de tamanho e forma em algumas espécies desta família de acordo com o gradiente de profundidade, sendo as formas maiores e mais abundantes encontradas a uma profundidade de cerca de 800-900 m. Brun et al. (1984) estudaram as alterações morfológicas da família Bolivinitidae ao longo do Paleógeno/Neógeno, associando-as a variações de salinidade, teor de oxigênio e paleobatimetria. Gary et al. (1989) relatam variações na forma das testas (triangularidade e lobacidade) de acordo com a profundidade e a sucessão das massas d'água, relacionando-as também com mudanças na temperatura e oxigênio dissolvido; Davis et al. (2016) aplicaram métricas derivadas do peso da testa para avaliar a resposta das espécies *Bolivina argentea*, *Bolivina interjuncta* e *Bolivina tumida* às flutuações de oxigênio e carbono ao longo do tempo na Bacia de Santa Bárbara, Califórnia; Keating-Bitonti & Payne (2017), em estudo realizado na Bacia de Santa Mônica, também na Califórnia, investigaram variações nas concentrações de oxigênio dissolvido ao longo dos últimos 15 ka e sua relação com o volume e biovolume das testas de *Bolivina spissa* e *Bolivina argentea*; Bayrón-Arcelay et al. (2020), estudando *Bolivina lowmani*, sugeriram que a composição do sedimento e o conteúdo de matéria orgânica (MO) podem impactar diretamente as taxas de crescimento dessa espécie. Belanger (2022) não encontrou relação estatisticamente significativa entre a relação área superficial:volume (SA/V) das testas de *B. argentea* e *B. seminuda* e a oxigenação de sedimentos marinhos durante um evento de deglaciação no Golfo do Alasca, sugerindo que outros fatores devem estar envolvidos nas variações morfológicas intraespecíficas.

Alguns estudos também investigaram a porosidade dos bolivinídeos, destacando seu papel como resposta biométrica aos processos ambientais, particularmente a relação entre densidade de poros e concentrações de oxigênio e nitrato dissolvidos (Glock et al., 2011; Kuhnt et al., 2013, e Govindankutty Menon et al., 2023).

A análise baseada na morfometria em foraminíferos tem se tornado cada vez mais comum como fonte para reconstruções paleoceanográficas, com o desenvolvimento de novas técnicas de aquisição de imagens e topografia de

superfície 3D (Giordano et al., 2019). No entanto, até o momento, não se conhece nenhum estudo que tenha investigado os descritores biométricos dos bolivinídeos e suas relações com variáveis oceanográficas no Atlântico Sul, apesar de sua abundância em testemunhos do final do Quaternário.

1.2 BOLIVINÍDEOS E *BOLIVINA ORDINARIA*

Associações dominadas por bolivinídeos são consideradas como indicadoras de fluxo elevado e contínuo de matéria orgânica, lábil ou refratária, para o fundo do mar, sendo comumente associadas à oxigenação reduzida das águas de fundo (GOODAY, 1994; MACKENSEN et al., 1995; SCHMIEDL et al., 1997; BERNHARD & GUPTA, 1999; ABU-ZIED et al., 2008).

O gênero *Bolivina* é considerado cosmopolita, sendo encontrado desde a plataforma continental até o talude, com hábito de vida infaunal, ou seja, vivem nos primeiros centímetros da coluna sedimentar e se alimentam de detritos (LOEBLICH & TAPPAN, 2015; MURRAY, 1991, MURRAY, 2006).

A espécie *Bolivina ordinaria* foraminífero bentônico pertencente à família Bolivinitidae, descrita por Phleger & Parker, (1952), foi identificada na literatura por várias nomenclaturas taxonômicas, incluindo *B. dilatata* (DUIJNSTEE et al., 2004; ERNST et al., 2005; MOJTAHID et al., 2009; DISARO 2014; DISARO et al., 2022); *Brizalina spathulata* (DIZ & FRANCES, 2008); *B. variabilis* (SCHIEBEL, 1992; DEBENAY et al., 2001; DUCHEMIN et al., 2005); e *Bolivina* ex. gr. *B. dilatata* (DUCHEMIN et al., 2007). Esses sinônimos se devem às semelhanças morfológicas entre esses organismos. Neste estudo, os principais critérios utilizados para distinguir *B. ordinaria* de outras espécies de bolivinídeos incluiram: formato levemente ovalado na extremidade apertural, suturas largas, opacas e levemente curvadas, com parede fina, exceto nas suturas onde é espessada e opaca, fazendo com que as suturas pareçam muito brancas em comparação com o resto do testa.

Segundo Mendes et al. (2012), esta espécie indica alta disponibilidade de matéria orgânica, muitas vezes em combinação com condições disóxicas. *Bolivina ordinaria* tem sido associada a ambientes lamosos e de baixa energia na plataforma continental (MARTINS et al., 2006, 2007; ANBUSELVAN, 2019). Também vale a pena mencionar que esta espécie ainda é relativamente pouco estudada, com dados

limitados sobre as suas preferências ecológicas provavelmente devido a conflitos na identificação das espécies e/ou documentação taxonômica insuficiente.

1.3 APRESENTAÇÃO

Esta dissertação foi dividida nas seções: resultados, discussões e conclusões em forma de artigo, intitulado "Relative abundance and biometry of *Bolivina ordinaria* on the Northern continental slope of the Pelotas Basin during the late Quaternary" publicado na revista *Marine Micropaleontology* (Elsevier, Qualis A2). Previamente apresenta-se a introdução, os objetivos, a área de estudo e a metodologia. Ao final, são apresentadas as considerações finais, as referências bibliográficas e os apêndices. Por esse motivo algumas informações podem se repetir.

2 OBJETIVOS

2.1 OBJETIVO GERAL

Avaliar a aplicabilidade dos descritores abundância relativa, comprimento da testa e biomassa da espécie de foraminífero bentônico *Bolivina ordinaria* em relação aos períodos de flutuações na produtividade primária e mudanças na circulação oceânica que ocorreram no talude norte da Bacia de Pelotas ao longo dos ciclos glacias e integlaciais do Quaternário tardio.

2.2 ESPECÍFICOS

a) Analisar os valores da abundância relativa, comprimento das testas, biomassa média individual e acumulada da espécie *Bolivina ordinaria* em relação aos Estágios Isotópico Marinhos (EIMs).

b) Avaliar a capacidade da abundância relativa e das medidas biométricas da espécie *Bolivina ordinaria* em discriminar zonas paleoecológicas marinhas e avaliar seu poder discriminatório.

c) Determinar e avaliar as relações lineares entre abundância relativa, comprimento das testas, biomassa média individual e acumulada de *Bolivina ordinaria* no intervalo estudado.

d) Avaliar as relações entre fluxo de carbono orgânico total (COT, razão isotópica de carbono estável ($\delta^{13}C$), abundância relativa de *B. ordinaria* e de uvigerinídeos, biomassa média individual de *B. ordinaria* e de uvigerinídeos e biomassa acumulada de *B. ordinaria* e de uvigerinídeos.

e) Analisar a relação entre abundância relativa de *B. ordinaria* e de uvigerinídeos, biomassa média individual de *B. ordinaria* e de uvigerinídeos e biomassa acumulada de *B. ordinaria* e de uvigerinídeos obtidas das mesmas amostras dos testemunhos SIS-188 e SIS-249.

3 ÁREA DE ESTUDO

Os testemunhos estudados foram coletados no talude norte da Bacia de Pelotas, nas profundidades 1514 m (SIS-188) e 2091 m (SIS-249) entre as coordenadas geográficas 29°13'16,266"S / 47°17'1,761"O; 30°5'6,389"S / 47°5'35,628"O, respectivamente (Figura 1). No momento presente, a região de estudo, está sob influência da Corrente do Brasil (CB), que se caracteriza por transportar no sentido N-S, águas quentes, oligotróficas e mais salinas (Água Tropical - AT) (Figura 1).

Figura 1: Mapa da localização dos testemunhos SIS-188 e SIS-249 e representação esquemática das correntes do Brasil e das Malvinas. *CBM: Confluência Brasil-Malvinas.
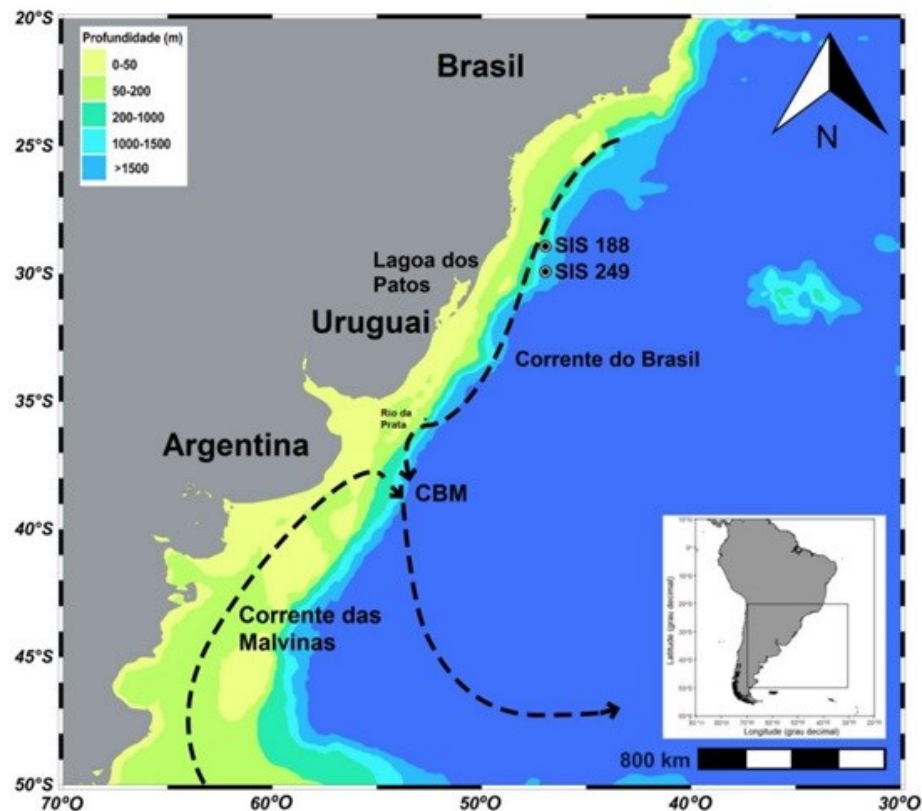
Fonte: Modificado de Santana et al. (2021).

Além da AT (superfície), a CB transporta, na camada da picnoclina, a Água Central do Atlântico Sul (ACAS), mais fria e rica em nutrientes e que flui para sul (Figura 2). Em níveis intermediários, essa camada é constituída também pela Água

Intermediária Antártica (AIA) que é transportada para sul e pela Água Circumpolar Superior (ACS) (abaixo da AIA). A Água Profunda do Atlântico Norte (APAN), formada em altas latitudes no Atlântico Norte é transportada para o sul pelas correntes de contorno oeste. A Água de Fundo Antártica (AFA), formada no Oceano Austral é observada apenas a profundidade maiores que 3000 m (CAMPOS et al., 1995; SILVEIRA et al., 2000).

A AMOC (Atlantic Meridional Overturning Circulation - Célula de Revolvimento Meridional do Atlântico) é uma das principais componentes do sistema climático global. Nas condições atuais, essa circulação de larga escala, transporta quantidades importantes de calor (JOHNS et al., 2011) do Atlântico Sul em direção a altas e médias latitudes do Hemisfério Norte. Além disso, essa circulação também é responsável por armazenar CO_2 oceânico (BOHM et al., 2015) e por causar alterações na produtividade marinha (PEREIRA et al., 2018).

Figura 2: Distribuição atual das massas d´água ao longo da margem oeste do Oceano Atlântico Sul (perfil A17 do eWOCE, SCHLITZER, 2000), baseado nos valores de oxigênio dissolvido (µmol/kg), indicando as posições dos testemunhos SIS-188 e SIS-249. (ACAS: Água Central do Atlântico Sul; ACS: Água Circumpolar Superior; AIA – Água Intermediária Antártica Água Circumpolar Superior; AFA: Água de Fundo Antártica; APAN: Água Profunda do Atlântico Norte).
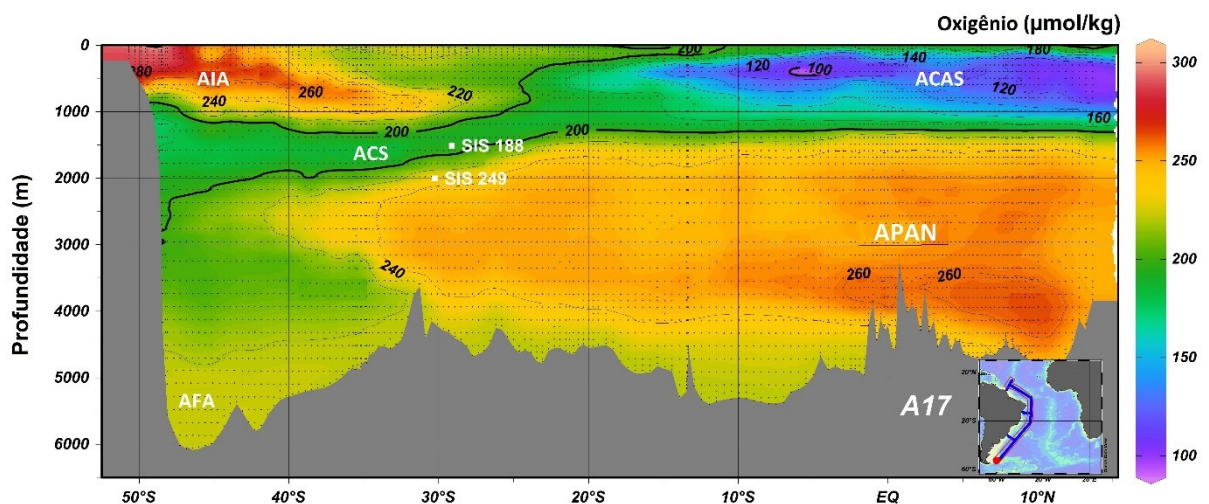
Fonte: Modificado de Santana et al., (2021) e Schlitzer, (2000).

4 MATERIAIS E MÉTODOS

4.1 AQUISIÇÃO DE DADOS

Para a elaboração do presente trabalho foram utilizados os testemunhos, SIS-188 e SIS-249, coletados em dezembro de 2007 pela Fugro Brasil–Serviços Submarinos e Levantamentos Ltda., contratada pela agência Nacional do Petróleo (ANP). Estes foram descritos previamente quanto a sua composição sedimentar por Petró et al. (2021), Lopes et al. (2021) e de Gonçalves & Leonhardt et al. (2021, 2022). Os testemunhos SIS-188 e SIS-249 são constituídos predominantemente por lamas ricas em carbonato com uma fácies lamo-arenosa, cada um deles, e algumas lâminas de sedimentos organicamente enriquecidas. No topo do testemunho SIS-249 ocorre uma fácies arenosa (siliciclástica).

Os modelos de idade adotados para os testemunhos SIS-188 e SIS-249 também foram anteriormente caracterizados por Petró et al. (2021), Rodrigues et al. (2018), Duque-Castaño et al. (2019) e de Gonçalves & Leonhardt et al. (2021, 2022). Eles foram baseados na correlação entre a razão isotópica de oxigênio das testas de foraminíferos bentônicos e a referência proposta pela curva de Lisiecki & Stern (2016), adotando a datação por radiocarbono por espectrometria de massa com aceleradores (AMS), sendo quatro pontos de controle para o testemunho SIS-188 e apenas um para o testemunho SIS-249 (devido à falta de amostras suficientes para análise). As datações AMS foram realizadas no Laboratório de Radiocarbono do Instituto de Física da Universidade Federal Fluminense (LACUFF), em amostras monoespecíficas do foraminífero planctônico *Globigerinoides ruber* (todos os morfotipos). As datações por radiocarbono foram corrigidas em idades calibradas usando a curva Marine13 (Reimer et al., 2013) e considerando um ΔR de - 59 com base no Banco de Dados de Correção de Reservatórios Marítimos. O testemunho SIS-249 variou do MIS 5 (~ 112 ka) a MIS 3 (~ 30 ka), enquanto o testemunho SIS-188 variou de MIS 3 (~ 41 ka) a MIS 1 (~ 7 ka). Para idades dos MIS consideramos Railsback et al. (2015).

No total 42 amostras foram analisadas: 26 do testemunho SIS-188 e 16 do testemunho SIS-249. O intervalo amostral ao longo dos testemunhos foi de aproximadamente 10 cm. Uma alíquota de cada amostra, após este pré-

processamento, foi enviada ao Laboratório de Oceanografia Costeira da UFSC (LOC) para a análise das comunidades de foraminíferos bentônicos. No LOC, as amostras foram pesadas novamente para o controle da densidade populacional. Depois elas foram separadas nas frações >500 μm, 500-125 μm e 125-63 μm, quarteadas e triadas. Foram recolhidos em lâminas micropaleontológicas cerca de 300 indivíduos de cada amostra. Este número foi definido com base no estudo de Patterson & Fishbein (1989), sobre a curva de rarefação de espécies de microfósseis.

Também foram realizadas pela equipe do LOC as identificações das espécies, tanto em nível específico quanto genérico com o auxílio de guias taxonômicos, tais como Loeblich & Tappan (2015) e Debenay (2012), "World Register of Marine Species" – WORMS (consultado em 2018), entre outros. Estes resultados encontram-se detalhados em Schmitt et al. (2019). Essa mesma equipe elaborou planilhas de identificação das espécies encontradas nos testemunhos.

A partir das planilhas de identificação de Schmitt et al. (2019), selecionamos a espécie da infauna *B. ordinaria*, por ter boa representatividade (alta abundância relativa >1%) nos testemunhos, ampla distribuição geográfica na margem continental brasileira, e por pertencer a um grupo taxonômico (bolivinídeos) associado a orgânicos insumos e períodos de flutuações na produtividade primária.Também vale ressaltar que esta espécie ainda é relativamente pouco estudada, com dados limitados sobre as suas preferências ecológicas.

4.2 ANÁLISE BIOMÉTRICA E DETERMINAÇÃO DA BIOMASSA

No total 651 testas de *B. ordinaria* foram analisadas nesta pesquisa. Para a elaboração e interpretação dos resultados foram calculadas as abundâncias relativas da espécie ao longo dos EIMs e obtidas às medidas morfométricas (comprimento, largura e espessura) de 355 testas, a partir de fotomicrografias obtidas em um estereomicroscópio *AxioZoomV16* e importadas pelo pacote *ForImage* disponível no *software R-Studio* (FREITAS et al., 2021) para obtenção dos valores de volumes. Nas 296 testas restantes foi medido apenas o comprimento com um estereomicroscópio da marca Carl Zeiss, com aumento de 160x e uma lâmina micrométrica com 0,01 mm de resolução. Para essas testas, o volume foi inferido a partir de um modelo de regressão linear usando o comprimento como variável

preditora (n=509 testas) e após a análise dos resíduos foram descartadas as testas fora do intervalo entre 100 e 270 µm (compreendendo duas testas menores que 100 µm e 29 maiores que 270 µm).

Para avaliar as diferenças entre os valores de volumes gerados no *ForImage* e os valores de volumes obtidos por meio da equação de regressão foram usados o o Teste de *Bland-Altman* (teste que compara medidas obtidas por dois métodos diferentes) e o valor da Raiz do Erro Quadrático Médio. Com as medidas de volume das 620 testas foram estimados o biovolume, a biomassa individual, a biomassa média e a biomassa acumulada (somatório da biomassa de todas as testas medidas em uma amostra).

O biovolume foi calculado a partir da aproximação do formato da testa ao modelo geométrico de um *gomphonemoide* (Figura 3) assumindo-se um volume médio de ocupação celular de 71,6% (FREITAS et al., 2021).

Figura 3: Modelo geométrico *gomphonemoid* usado para estimar volume da testa de *B. ordinaria*. Legenda: h = espessura/altura; d1= comprimento d2=largura
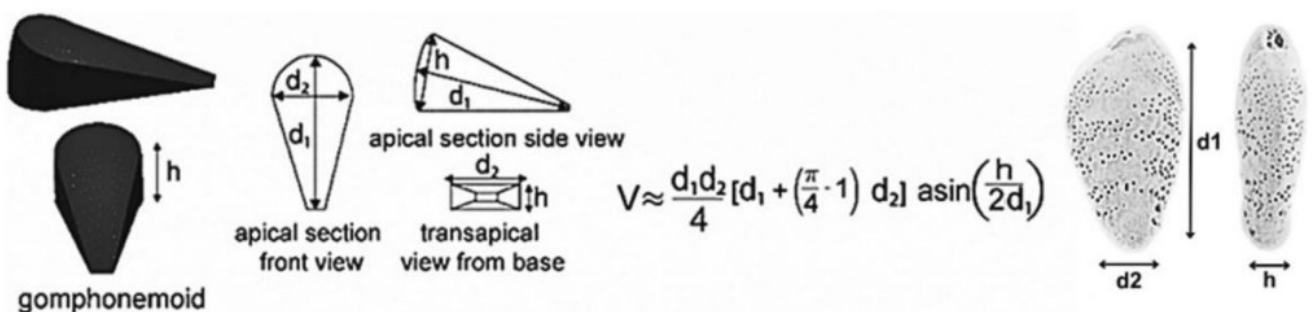
Fonte: adaptado de Freitas et al. (2021).

Na conversão de biovolume para biomassa adotou-se densidade celular de 0,089 pgCorg.µm-3, conforme proposto por Michaels et al. (1995). Essa metodologia (pacote *ForImage)* está detalhada em Freitas et al. (2021) e Santana et al. (2021).

4.3 ANÁLISES ESTATÍSTICAS

O ajuste dos dados à distribuição Normal foi avaliado com o teste de normalidade de Shapiro-Wilk (valores de W e de p). Como a maioria das variáveis não se apresentou normalmente distribuída optou-se por utilizar estatísticas não-

paramétricas. Assim, as medidas de tendência e de dispersão foram descritas pela mediana e a amplitude interquartil, respectivamente. Foram usados também o teste de *Mann-Kendall, Kruskal-Wallis* e *Dunn*.

Mann-Kendall é um teste utilizado para determinar se uma série de dados apresenta uma tendência temporal estatisticamente significativa. Um valor de S próximo à zero indica um número quase igual de diferenças positivas e negativas (ausência de tendência), enquanto o valor de S negativo indica tendência de diminuição e o valor de S positivo indica uma tendência de aumento.

A sucessão das zonas ecológicas a partir da análise das associações de espécies, conforme proposto por Schmitt et al. (2019), foi utilizada como base para a definição de quatro zonas paleoecológicas no testemunho SIS-188 e três zonas paleoecológicas no testemunho SIS-249 (Figura 4).

Essas zonas paleoecológicas foram consideradas representativas de períodos com diferentes condições ambientais para a fauna bentônica, sendo utilizadas como variável categórica para comparar mudanças nas métricas das populações de *B. ordinaria* (abundância relativa e biometria). A análise estatística das diferenças entre estas zonas paleoecológicas (Z1 a Z7) foi realizada através da aplicação do teste de comparação de medianas de *Kruskal-Wallis* e do teste *post-hoc* de *Dunn* (sempre que a hipótese estatística de igualdade H0 foi rejeitada).

Todos os processamentos foram obtidos com apoio do programa *Paleontological Statistics (PAST),* do *software* livre R-Studio e do *software* Excel.
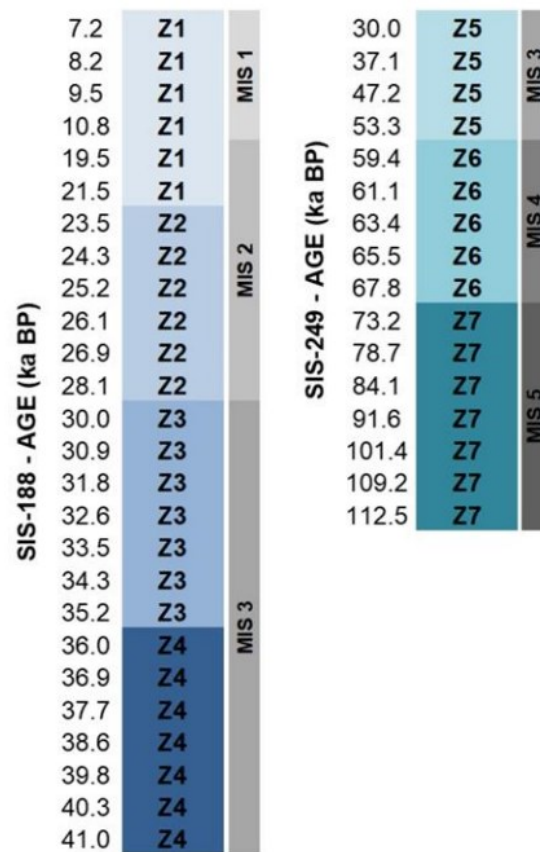
Figura 4: Zonas paleoecológicas (Z) dos testemunhos SIS-188 e SIS-249 ao longo do EIMs 5 a 1 (SCHMITT et al., 2019). As barras em tons de cinza representam os EIMs e os números à esquerda correspondem à idade estimada de cada amostra.

5 RELATIVE ABUNDANCE AND BIOMETRY OF *BOLIVINA ORDINARIA* ON THE NORTHERN CONTINENTAL SLOPE OF THE PELOTAS BASIN DURING THE LATE QUATERNARY

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RELATIVE ABUNDANCE AND BIOMETRY OF *BOLIVINA ORDINARIA* ON THE NORTHERN CONTINENTAL SLOPE OF THE PELOTAS BASIN DURING THE LATE QUATERNARY

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HIGHLIGHTS

- The high relative abundance of bolivinids is associated with the dominance of meso-eutrophic conditions throughout the late Quaternary on the northern slope of the Pelotas Basin.

- The biometrics of *Bolivina ordinaria*, including test length and biomass, provide insights into paleoceanographic processes associated with glacial and interglacial cycles

- *B. ordinaria* appears to thrive in response to the regular contribution of refractory organic matter during warmer periods, but experiences increased competition from shallow infaunal taxa, such as *Uvigerina*, when the flow of labile organic matter to the benthic compartment increases during glacial periods.

ABSTRACT – This study examines the variations in relative abundance, test size, and biomass of the species *Bolivina ordinaria* (Foraminifera) over the last 112 ka BP on the northern slope of the Pelotas Basin, Southern Brazil. The analyses were based on 651 individuals from 42 samples distributed along the cores SIS-249 (Marine Isotope Stage 5 to 3) and SIS-188 (Marine Isotope Stage 3 to 1). *Bolivina ordinaria* was the most abundant species of the Bolivinitidae family in these cores, particularly during warmer periods (MIS 1 and 5). Nine other species of this family were identified: *B. compacta, B. doniezi, B. lowmani, Bolivina* sp., *B.striatula, Brizalina* sp., *Brizalina spinescens, Brizalina subaenariensis,* and *Brizalina subspinescens.* Larger test lengths were observed during MIS 3 in the both cores. The summed biomass was higher during MIS 5 in the SIS-249 core and lower during MIS 3 in the SIS-188 core. The fluctuations observed in the relative abundance and summed biomass of *B. ordinaria* are consistent with the oscillations in total organic carbon flow, and the variations in primary productivity between the interglacial and glacial periods. The results suggest that this infaunal species is favored by the regular supply of refractory organic matter during warmer periods but faces increased competition from shallow infaunal and epifaunal species during glacial periods, when the flow of labile organic matter increases.

INTRODUCTION

Species or associations of benthic foraminifera reflect specific ecological conditions and have been widely used as paleoenvironmental, biostratigraphic, and paleoceanographic proxies due to their high abundance and the potential to have their tests preserved in marine sediments (Jorissen et al., 2007). In the western South Atlantic Ocean, the relative abundance of benthic foraminifera has been used to characterize water depth and mass-transport movement (Almeida et al., 2022; 2023), oceanic circulation and water mass properties (Peterson and Lohmann, 1982; Saupe et al., 2022), and determine carbon flux and paleoproductivity (Nagai et al., 2010; Ferreira et al., 2014; Almeida et al., 2015; Rodrigues et al., 2018), among other factors.

Species associations dominated by taxa tolerant to reduced oxygenation of bottom waters, such as bolivinids, are considered indicators of high and continuous organic matter flux to the seafloor (Gooday, 1994; Mackensen et al., 1995; Schmiedl et al., 1997; Bernhard and Gupta 1999; Abu-Zied et al., 2008). Saupe et al., (2022) observed an increase in the relative abundance of *Bolivina variabilis* and *Bolivina subreticulata* in areas of the Brazilian continental margin (11° – 22°S) with nutrient-enriched waters, and *Bolivina subreticulata* and *Bolivina variabilis* in more clayey sediments and with higher values of total organic carbon (TOC).

One of the first studies about Bolivinitidae family was published by Smith (1963) on the recent fauna of El Salvador. The author identified variations in size and shape in some species of this family according to the depth gradient, with the largest and most abundant forms being found at a depth of about 800-900 meters. Brun et al. (1984) studied the morphological changes of the Bolivinitidae family throughout the Paleogene/Neogene, associating them with variations in salinity, oxygen content, and paleobathymetry. Gary et al. (1989) report variations in the shape of the tests (triangularity and lobacy) according to the

depth and succession of the water masses when studying *Bolivina albatrossi* in the Gulf of Mexico, also relating them to changes in temperature and dissolved oxygen. Davis et al. (2016) applied metrics derived from test weight to evaluate the response of species *Bolivina argentea, Bolivina interjuncta,* and *Bolivina tumida* to fluctuations in oxygen and carbon over time in the Santa Barbara Basin. Keating-Bitonti and Payne (2017), in study conducted at the Santa Monica Basin, California, investigated variations in dissolved oxygen concentrations over the last 15 ka and their relationship with the volume and biovolume of *Bolivina spissa* and *Bolivina argentea* tests. Bayrón-Arcelay et al. (2020) suggest that sediment composition and organic matter (OM) content may directly impact the growth rates of *Bolivina lowmani*. Belanger (2022) found no statistically significant relationship between the surface area:volume ratio (SA/V) of the tests of *B. argentea* and *B. seminuda* and the oxygenation of marine sediments during a deglaciation event in the Gulf of Alaska, suggesting that other factors must be involved in the intraspecific morphological variations. Some studies have also investigated the porosity of bolivinids, highlighting its role as a biometric response to environmental processes, particularly the relationship between pores densities and oxygen and nitrate concentrations (Glock et al. (2010; Kuhnt et al., 2013, and Govindankutty Menon et al., 2023).

As examples of biometric studies applied in the Brazilian margin, Duque-Castaño et al. (2019) focused on planktonic tests, while Freitas et al. (2021) and Santana et al. (2021) studied benthic tests. The morphometrics-based analysis in foraminifera has become increasingly common as a source for paleoceanographic reconstructions, with the development of new techniques of image acquisition and 3D surface topography (Giordano et al., 2019). Nevertheless, to date, no studies are known to have investigated the biometric descriptors of bolivinids and their relationships with oceanographic variables in the South Atlantic, despite their importance in late Quaternary cores.

We investigated the behavior of relative abundance and biometric responses (test length and biomass) of the species *Bolivina ordinaria* Phleger and Parker, 1952 concerning the periods of fluctuations in primary productivity and changes in ocean circulation that

occurred on the northern continental slope of the Pelotas Basin in the last 112 ka BP. The objective was to evaluate the applicability of these intraspecific descriptors in the face of paleoceanographic oscillations, comparing the results obtained with evidence of oceanographic changes corroborated by other proxies in previous works.

Bolivina ordinaria was chosen for having good representativeness (high relative abundance) in the analyzed cores, having a wide geographical distribution in the Brazilian continental margin, and belonging to a taxonomic group (bolivinids) associated with organic input and periods of fluctuations in primary productivity. According to Mendes et al. (2012), this species indicates high availability of organic matter, often in combination with dysoxic conditions. *B. ordinaria* has been associated with muddy and low-energy environments on the continental shelf (Martins et al., 2006; 2007; Anbuselvan, 2019). It is also worth mentioning that this species is still relatively understudied, with limited data on its ecological preferences. Knowledge of its ecology may be limited by conflicts in species identification and/or insufficient taxonomic documentation.

STUDY AREA

The cores studied, SIS-188 and SIS-249, were collected on the northern slope of the Pelotas Basin, between 28ºS and 34ºS, at depths of 1514 m and 2091 m, respectively (Figure 1). The study region is under the influence of the Brazil Current (BC) which flows in the N-S direction, and transports warm, oligotrophic, and more saline waters (Tropical Water - TW) at the surface. In the pycnocline layer, the BC carries the cooler, nutrient-rich South Atlantic Central Water (SACW). At intermediate levels, the Antarctic Intermediate Water (AAIW), and the Upper Circumpolar Deep Water (UCDW) (below the AAIW) occur. In greater depths, the North Atlantic Deep Water (NADW), which is formed at high latitudes in the North Atlantic, is transported southward by the deep western boundary current. Antarctic Bottom Water (AABW), formed in the Southern Ocean, is observed only at depths greater than 3000 m (Campos et al., 1995; Silveira et al., 2000).
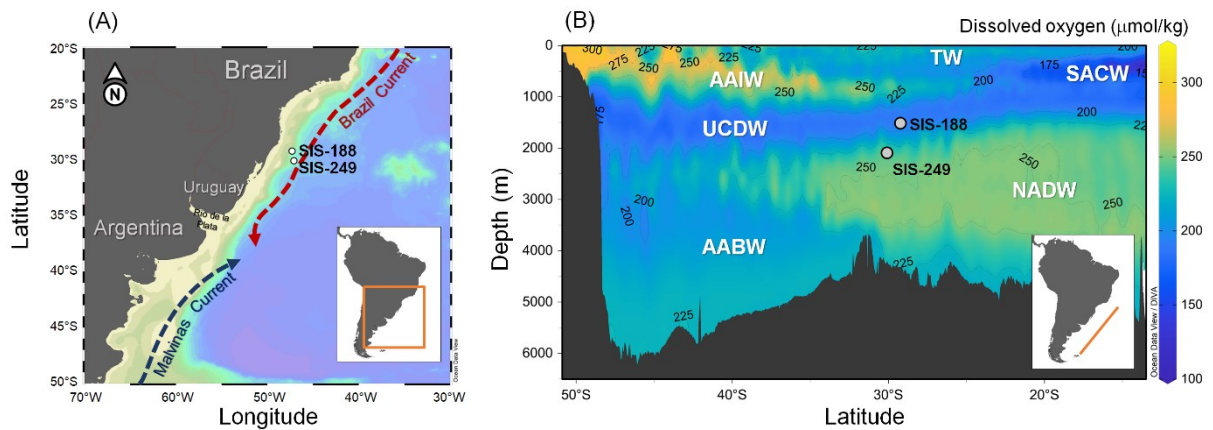
Figure 1: A) Map of the location of core sites SIS-188 and SIS-249 (29°13'16,266"S, 47°17'1,761"W and 30°5'6,389"S, 47°5'35,628"W, respectively), and schematic representation of the surface currents, Brazil Current and Malvinas Current. B) Current distribution of water masses along the South Atlantic Ocean based on dissolved oxygen values (µmol/kg) according to the A17 profile of the *eWOCE* (Schlitzer, 2000). The dots in white indicate the location of SIS-188 and SIS-249 cores (coordinates in (A) and the latitude and depth in (B).

The NADW and AABW are respectively the southward and northward deep branches of the AMOC (Atlantic Meridional Overturning Circulation), which is one of the primary components of the global thermohaline circulation. Under current conditions, this large-scale circulation transports significant amounts of heat (Johns et al., 2011) from the South Atlantic towards the high and mid-latitudes of the Northern Hemisphere. This circulation is also responsible for regulating the storage of oceanic CO_2 (Böhm et al., 2015) and causing changes in marine productivity (Pereira et al., 2018). Today, core SIS-249 is bathed by NADW and core SIS-188 by UCDW (Fig. 1 B). However, due to past changes in water mass geometry and AMOC configuration, the water masses to which both sites were exposed very likely changed through time, with a shallower North Atlantic Deep Water (Glacial North Atlantic Intermediate Water) and increased influence from southern-sourced deep waters during glacial times (e.g. Curry and Oppo 2005; Marchitto and Broecker 2006; Howe et al., 2015).

In terms of paleoproductivity, reconstructions based on planktonic foraminifera for this region (Pereira et al., 2018; Portilho-Ramos et al., 2019; Frozza et al., 2020; Suárez-Ibarra et al., 2022, 2023) suggest it was higher during glacial times and lower during interglacials. On the other hand, higher total organic carbon values were obtained by Rodrigues et al. (2018) for MIS 5 (Marine Isotope Stage 5) in core SIS-249 and by Gonçalves and Leonhardt (2022) for MIS1 in core SIS-188. Also, the coccolithophore record (Gonçalves and Leonhardt, 2022) suggests increased productivity during the Early Holocene. This apparent contradiction is likely the response to contrasting modes of fertilization with higher productivity during glacial periods related to phytoplankton blooms and more labile organic matter available to benthos, while interglacials are characterized by more refractory organic matter. The proposed mechanisms behind the high glacial productivity include enhanced summer upwelling and more frequent intrusions of the Plata Plume during prolonged winter conditions (Portilho-Ramos et al., 2018) as well as iron fertilization through increased supply of eolian dust (Lopes et al., 2021). The supply of labile organic matter to the seafloor during glacial times resulted in increased remineralization, thus lowered pH more corrosive conditions for calcium carbonate (Suárez-Ibarra et al., 2022). Dissolution may have also been amplified by changes in water mass geometry with more corrosive southern component waters during glacial times (Suárez-Ibarra et al., 2023).

MATERIAL AND METHODS

Data collection

Two cores were used for this study, SIS-188 and SIS-249, collected in 2007 by *Fugro Brasil–Serviços Submarinos e Levantamentos Ltda*., contracted by the Brazilian National Agency of Petroleum, Natural Gas and Biofuels (ANP - *Agência Nacional do Petróleo, Gás Natural e Biocombustíveis*). These were previously described as to their sedimentary composition by Duque-Castaño et al. (2019), Petró et al. (2021), Lopes et al. (2021), and Gonçalves and Leonhardt (2021, 2022).

The age models adopted for SIS-188 and SIS-249 cores were those previously characterized by Petró et al. (2021) and Rodrigues et al. (2018). They were based on the correlation between the oxygen isotope ratio of benthic foraminifera tests and the reference curve proposed by Lisiecki and Stern (2016), also adopting five Accelerator Mass Spectrometry (AMS) radiocarbon datings as control points, being four in core SIS-188 and only one in core SIS-249 due to the lack of enough specimens for analysis. The AMS datings were performed at the Radiocarbon Laboratory of the Physics Institute of the Universidade Federal Fluminense (LACUFF), on monospecific samples of the planktonic foraminifer *Globigerinoides ruber* (all morphotypes). Conventional radiocarbon dates were converted to calibrated ages using the Marine13 curve (Reimer et al., 2013) and considering a ΔR of − 59 based on the Marine Reservoir Correction Database. SIS-249 core ranges from MIS 5 (~ 112 ka) to MIS 3 (~ 30 ka), while SIS-188 core ranges from MIS 3 (~ 41 ka) to MIS 1 (~ 7 ka). For MIS ages we followed Railsback et al. (2015). Although the two cores succeed each other regarding the recorded interval, with a slight temporal overlap in MIS 3, they cannot be considered a single and continuous record since they were collected in close locations but at different depths, where they were exposed to different bottom water masses (Figure 1).

To investigate benthic foraminiferal assemblages, 42 sediment samples (26 from SIS-188, 16 from SIS-249) were collected at approximately 10 cm intervals along the cores. At least 300 individuals per sample were randomly picked from the >63 μm fraction and mounted in micropaleontological slides. The taxonomic composition and relative species abundance were determined previously by Schmitt et al. (2019). Species identification followed established and regional references, including Boltovskoy et al. (1980), Holbourn et al. (2013), Sen Gupta et al. (2009), Sousa et al. (2012), Debenay (2012), Disaró et al. (2022), and the WoRMS (World Register of Marine Species), accessed in 2023.

In the present study, all specimens of *B. ordinaria* found among the approximately 300 individuals per sample were used for biometric analysis. Its relative abundance was calculated as the percentage of *B. ordinaria* individuals relative to the total number of

individuals of all species counted in each sample. While both microspheric and megalospheric individuals were observed in the samples, the proportion of these morphologic variants of *B. ordinaria* was not quantified. The biometric analyses were based on randomly picked tests, assuming that this procedure reflets the original proportion and variability of these forms through the cores. Thus, the biometric results might also be influenced by changes in reproductive strategies. However, careful consideration should be given to the potential limitations imposed by this assumption when drawing conclusions from the biometric data.

Biometric analysis and biomass determination

In addition to its high relative abundance in the analyzed cores, *B. ordinaria* was chosen for its appropriate morphological characteristics that allow for biomass estimation using volume determination techniques based on approximations to a geometric shape. The elongated shape of the test facilitates the recognition of its longest axis, allowing for the arrangement of all individuals consistently during microscope image acquisition. This simplifies and streamlines the process of acquiring multi-focal images (Z-stacking) for accurate determination of test thickness (Plate 1, Appendix A2).

In total, 651 *B. ordinaria* tests were analyzed. The morphometric measurements (length, width, and thickness) of 355 tests were extracted from photomicrographs obtained using an *AxioZoom*V16 stereomicroscope and imported by the *ForImage* package available in the *R-Studio software* (Freitas et al., 2021). These metrics were used to calculate the volume of each test, assuming the approximation of the test shape to the geometric model of a gomphonemoid (Figure 2).
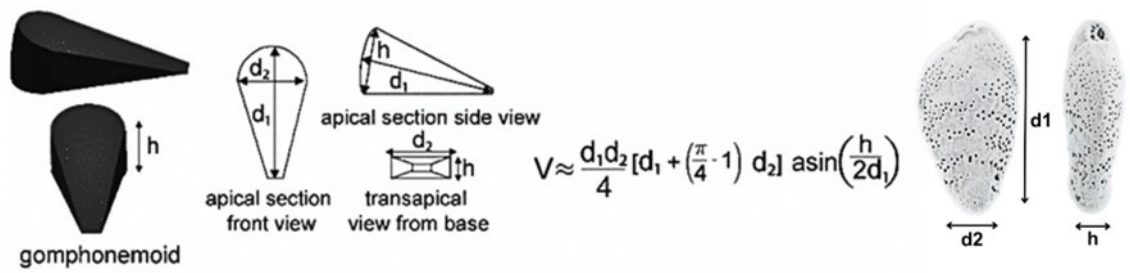
Figure 2: *Gomphonemoid* geometric model used to estimate *B. ordinaria* test volume. Caption: H = thickness/height; d1 = length and d2 = width. Adapted from Freitas et al. (2021).

It was not possible to obtain 3D images for all the tests; therefore, a portion of them (n = 296) had only their lengths measured, using a *Carl Zeiss* stereomicroscope with 160x magnification and an ocular micrometer with 0.01 mm resolution. The Bland-Altman test, applied to compare measurements obtained by digital processing and manually measured, suggests equivalence between these values, considering a bias of -5.0 ± 8.5 μm.

The analysis of linear correlation between test length and volume showed that these variables are strongly correlated (n = 509 individuals; r = 0.88; p < 0.000), indicating that a linear regression analysis could be applied in order to obtain an equation for the conversion of length (independent variable) into volume (dependent variable) for those tests manually measured. The developed model (Figure 3) was statistically significant (F=1.67E+03, p=3.26E-50). Length measurements explain 74% of the volume variance (R^2), with a RMSE of 4.83E+04 μm^3. The residuals were larger in tests outside the range of 100 to 270 μm, so the model was adjusted to its interval, which encompasses 95% of the total tests analyzed. It is important to note that the tests not used in the conversion model (two tests smaller than 100 μm and 29 larger than 270 μm) were retained for all other biometric analyses. In SIS-188, 174 tests were measured using the regression model (54% of the total tests analyzed in this core), while in SIS-249 there were 122 tests (37% of the total tests)
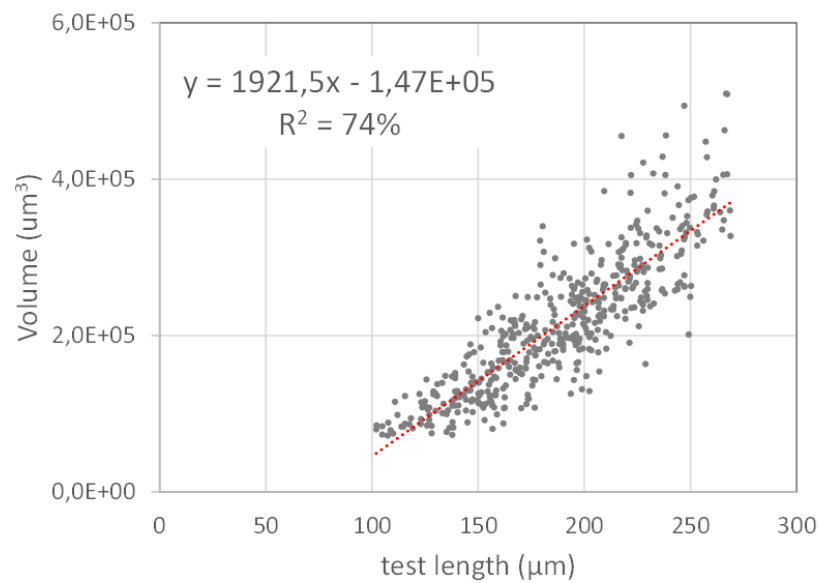
FIGURE 3: SCATTER PLOT WITH LINEAR REGRESSION MODEL FOR TEST VOLUME (Y) BASED ON TEST LENGTH (X).

Test volume was converted to biovolume using an average cell occupancy of 71.6% (Freitas et al., 2021) and then to biomass using a cell density of 0.089 pgCorg.µm-3 (Michaels et al., 1995). This methodology is detailed in Freitas et al. (2021) and Santana et al. (2021). Two distinct metrics were employed to investigate biomass variability along the cores: mean individual biomass and summed biomass. Mean individual biomass refers to the sum of individual biomasses of *B. ordinaria* specimens divided by the number of tests (n) of this species identified in each sample. For core SIS-188, this "n" ranged from 4 to 44 specimens per sample, while in core SIS-249, it ranged from 5 to 51 specimens per sample. Summed biomass, on the other hand, represents the sum of individual biomass of all *B. ordinaria* specimens within a sample, reflecting the combined influence of both individual size and relative abundance of *B. ordinaria*.

It's crucial to emphasize that the biomass measurements derived from this study did not consider the absolute abundance of *B. ordinaria* individuals in the samples nor were they standardized by sediment accumulation rates. Given that they rely on the relative abundance of this species, they provide a standardized comparison across samples that is more easily

acquired than the "true" biomass. However, their values should be interpreted strictly as comparative measures within the analyzed cores or among studies using similar methodologies (e.g., Santana et al., 2021).

Statistical analysis

Descriptive statistics based on the median and quartiles, as well as non-parametric tests (Mann-Kendall, Kruskal-Wallis and Dunn tests), were employed in this research due to the non-normal distribution of the analyzed variables, as verified by the Shapiro-Wilk normality test (Appendix A3).

Mann-Kendall is used to determine whether a data series has a statistically significant monotonic time tendency. An S value close to zero indicates an almost equal number of positive and negative differences (no tendency). In contrast, a negative S value indicates a decreasing tendency, and a positive S value indicates an increasing tendency.

The succession of species associations of benthic foraminifera through the cores, as proposed by Schmitt et al. (2019), was used to define four paleoecological zones in SIS-188 core and three paleoecological zones in SIS-249 core (Figure 4). These paleoecological zones were considered representative of periods with different environmental conditions for benthic fauna, being used as categorical variable to compare changes in the metrics of the *B. ordinaria* populations (relative abundance and biometry). The statistical analysis of the differences between these paleoecological zones (Z1 to Z7) was performed by applying the Kruskal-Wallis median comparison test and the Dunn *post-hoc* test (whenever the statistical hypothesis of equality H_0 was rejected).

Data processing was carried out with the support of the *Paleontological Statistics (PAST)* program, the *R-Studio* free software and the *Excel software.*
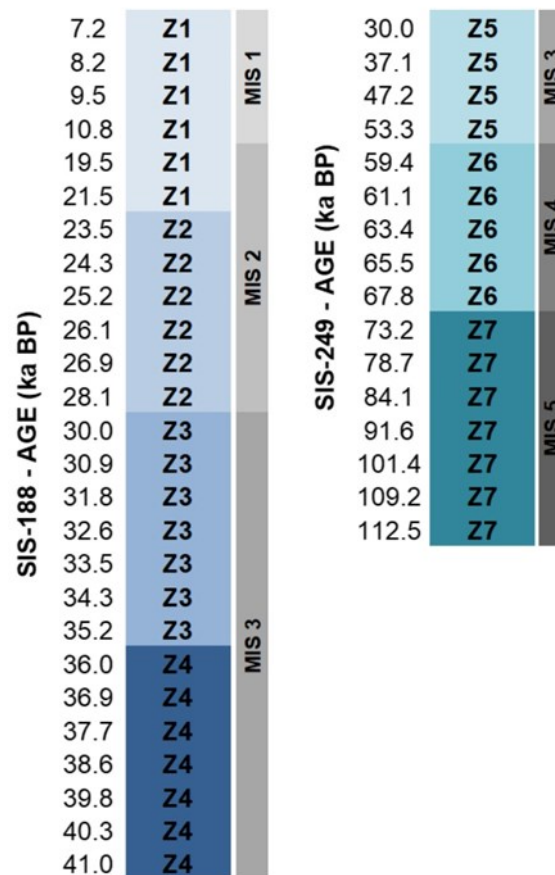
Figure 4: Paleoecological zones (Z) of SIS-188 and SIS-249 cores throughout MIS 5 to 1 (Schmitt et al., 2019). The grayscale bars represent the MIS and the numbers on the left correspond to the estimated age of each sample.

RESULTS

Relative abundance, test length, and biomass of _B. ordinaria_

The most abundant species of the Bolivinitidae family in both cores was _B. ordinaria_, However, nine other species represented this family in the study area: _Bolivina compacta, Bolivina doniezi, Bolivina lowmani, Bolivina_ sp_., Bolivina striatula, Brizalina_ sp_., Brizalina spinescens, Brizalina subaenariensis,_ and _Brizalina subspinescens_ (Appendix 1).

The lowest value of relative abundance of Bolivinitidade was found in the sample 30.9 ka (SIS-188), while the highest value was in the 101.4 ka (SIS-249). In this last sample, after _B. ordinaria_, the second most abundant species was _Brizalina subaenariensis_.

The relative abundance of *B. ordinaria* ranged from 0% (sample 30.9 ka from SIS-188) to 13.0% (61.1 ka and 65.5 ka from SIS-249). Higher values were observed during interglacials, i.e., MIS 1 of SIS-188 and MIS 5 of SIS-249 core, while the lower values occurred during MIS 2 in the SIS-188 and MIS 3 in the SIS-249 core (Figure 5A and 5B). The Mann-Kendall values suggest no significant tendency of increase or decrease in relative abundance from the base to the top of the cores (SIS-188: S=17, p= 0.72; SIS-249: S=24, p= 0.30).
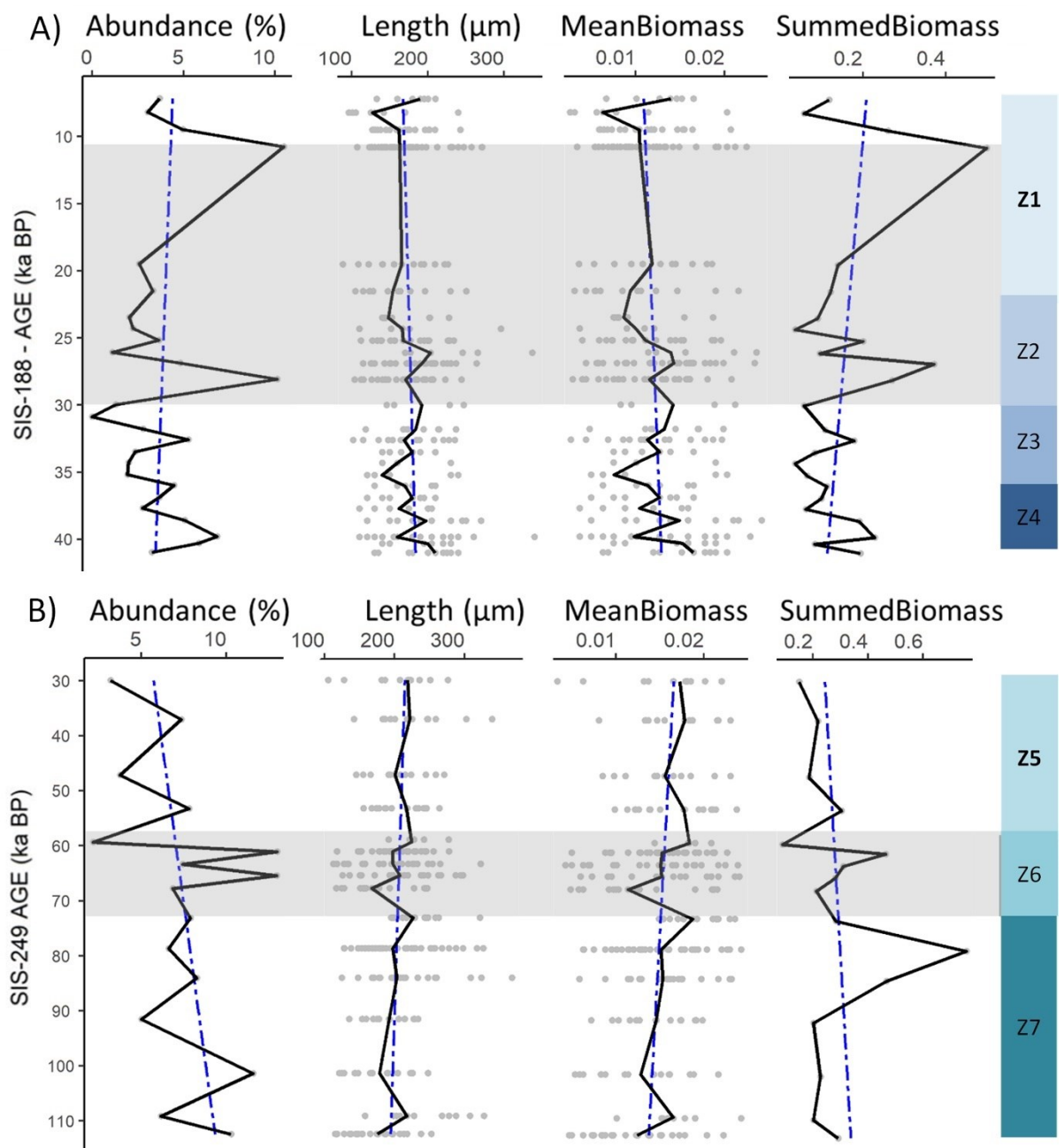
Figure 5. Relative abundance, test length, mean individual biomass and summed biomass of *B. ordinaria* in the SIS-188 (A) and SIS-249 (B). The dots represent individual values; black lines represent the median values (except for the relative abundance plots) and blue lines represent the *Mann Kendall* trends. The gray bands represent the Marine Isotope Stage - MIS 1 to SIS-188 and MIS 4 to SIS-249. The color bar on the right indicates the paleoecological zones (Z1 to Z7) defined by Schmitt et al. (2019).

Variations in the size of the tests of *Bolivina ordinaria*

Figure 5 (C and D) shows the variations of the test length over time. The smallest test size was 88.09 µm (SIS-188, 19.5 ka BP), and the largest was 370.00 µm (SIS-249, 84.1 ka BP). Considering both cores, the median length was 190 µm (IQR = 65 µm). The Mann-Kendall test results suggest no significant changes in the size of the tests from the base to the top in SIS-188 core (S=78, p= 0.07), while the tendency is for an increase in size in SIS-249 core (S=-45, p=0.04).

Variations in individual and cumulative biomass of *Bolivina ordinaria*

The distribution of individual biomass values indicated that MIS 3 of SIS-188 core has the highest value of this descriptor and MIS 1 has the lowest (Figure 5E). MIS 3 revealed the highest values, and MIS 5 was the lowest in SIS-249 core (Figure 5F). The Mann-Kendall test values suggest no significant change in the individual biomass of the tests from the base to the top in SIS-188 core (S=76, p= 0.07), while the tendency is for an increase in the individual biomass in SIS-249 core (S=-47, p=0.03).

The distribution of the summed biomass values (sum of the individual biomasses of each sample) showed that the highest summed biomass value in SIS-188 core was in MIS 1 and the lowest in MIS 3 (Figure 5G). The highest value for SIS-249 core was in MIS 5 and the lowest in MIS 3 (Figure 5H). The p-values associated with S for the summed biomass were greater than 0.05, (S=18, p= 0.70 for SIS-188; S=21, p=0.36 for SIS-249),

demonstrating no statistically significant monotonic tendency in the behavior of the summed biomass over time.

Relative abundance and biometry of *Bolivina ordinaria* as discriminators of paleoecological zones

Figure 6 represents the relative abundances, length, mean individual biomass, and summed biomass of the species *B. ordinaria* for each paleoecological zone previously identified in cores SIS-188 (Z1 to Z4) and SIS-249 (Z5 to Z7).

The paleoecological zones Z6 and Z7 have the highest values (median), and Z3 has the lowest relative abundance values (Figure 6A). However, it is worth mentioning that both Z1 and Z2 have maximum values well above the median (strong positive asymmetry). The Kruskal-Wallis test result (KW=17.7; p = 0.007) indicated a significant statistical difference in relative abundances between paleoecological zones. The differences' level of significance between each two zones, as determined by the post hoc Dunn's multiple comparisons test, are presented in Figure 6.
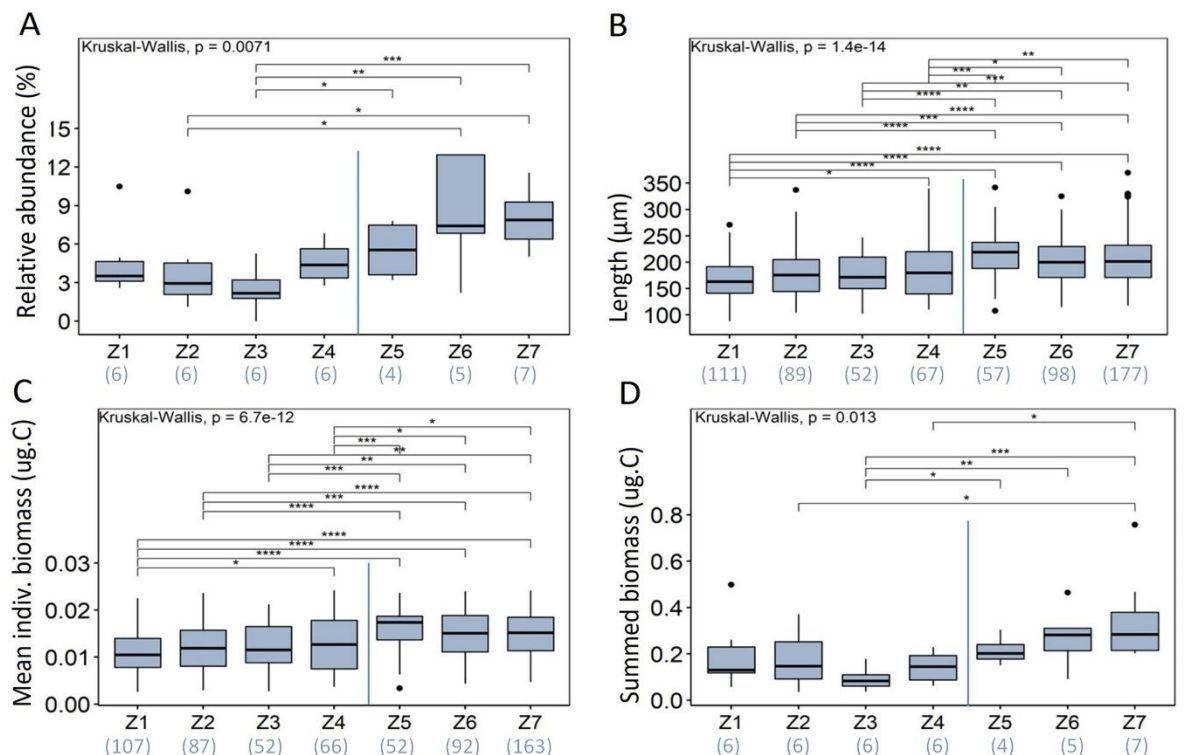
Figure 6. Boxplots comparing paleoecological zones (Z1 to Z7) regarding the (A) relative abundance of B. ordinaria, (B) test length (µm), (C) mean individual biomass, and (D) summed biomass. In the x-axis, below the zones names is indicated the number of the samples in each group (n). Z1 to Z4 correspond the samples from SIS-188 and Z5 to Z7 from the SIS-249. Whiskers: 1.5 * interquartile range (IQR); bar: median; box: IQR. Brackets indicate statistically different comparison pairs, and the number of points corresponds to the level of statistical significance. Only statistically significant differences are shown. Level of statistical significance: * p ≤ 0.05; ** p ≤ 0.01; *** p ≤ 0.001; **** p ≤ 0.0001

Figure 6B shows that Z5 has the highest median value for test length (219.30 µm), while Z1 has the lowest value (163.00 µm). Test sizes generally varied little but still present significant differences between some paleoecological zones (KW=77.1, p < 0.001). Mean Individual biomass (Figure 6C) had a similar behavior as the test length, also presenting the highest median (0.0175 µCorg) in Z5 (MIS 3 in SIS-249) and the lowest (0.0105 µCorg) in Z1 (MIS 1 in SIS-188). The Dunn test differentiated the same paleoecological zones discriminated by the length of the tests. The values of the summed biomass (Figure 6D) revealed that Z6 and Z7 have the highest values of this descriptor (0.2815 µCorg, 0.2840 µCorg, respectively), while Z3 demonstrated the lowest value (0.0832 µCorg). The Kruskal-Wallis test result (KW=16.1, p=0.013) and the Dunn test values also indicated significant differences in the medians of individual biomass. The results of Dunn test are available as supplementary material (Appendix A4).

Relationship between relative abundance, length, and biomass

Figure 7 shows the linear relationships between the abundance, length, mean individual biomass, and summed biomass. We found a strong and statistically significant Spearman correlation (r_s= 0.84; p= < 0.001) between relative abundance of *B. ordinaria* and summed biomass (Figure 7C), and between length *versus* summed biomass (Figure 7D; r_s= 0.37; p= 0.018). On the other hand, the correlations between relative abundance *versus*

length and *versus* mean individual biomass and (Figure 7A and 7B, respectively) are weak and lack statistically significant support at the 5% level. It is also noticeable that some samples exhibited a significantly distinct pattern of behavior from the others. For instance, at 78.7 ka BP (SIS-249), the highest summed biomass value (0.76 µCorg) corresponds to a relative abundance of *B. ordinaria* of only 6.6%. In addition to the sample at 78.7 ka, others (such as 10.8, 26.9, and 84.1 ka) also exhibit biomass values higher than those expected based on the linear trend defined by the regression model using relative abundance as the predictor variable.
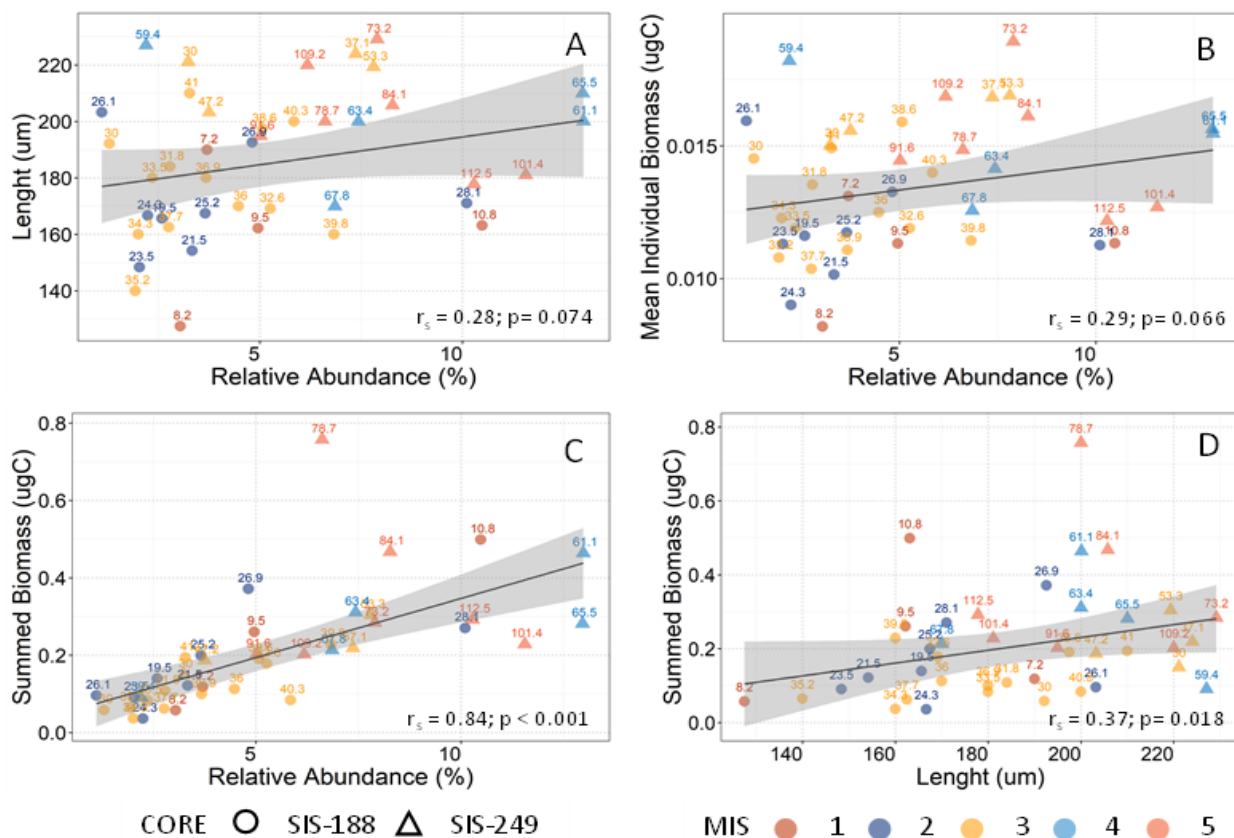
Figure 7. Linear relationships between *Bolivina ordinaria* metrics: A) Relative abundance versus length; B) Relative abundance versus mean individual biomass; C) Relative abundance versus summed biomass; D) Length versus summed biomass. The intensity of the correlations is expressed by the Spearman´s rank coefficient (rs) and its statistical significance is indicated by the p-value (p).

The relationship between bolivinids and uvigerinids was analyzed to determine whether there exists a discernible pattern of association between these taxa. This statistical analysis was made possible by utilizing uvigerinids data obtained from the same samples of the SIS-188 and SIS-249 cores and employing the same biometric determination methodology (data published in Santana et al., 2021). A weak negative correlation was observed between the relative abundance of bolivinids and uvigerinids (rs= -0.14; p= 0.4). However, a statistically significant negative correlation emerged when analyzing the relationship between the mean individual biomass of *B. ordinaria* and the mean individual biomass of uvigerinds (rs= -0.56; p= < 0.001).

The relationship between *Bolivina ordinaria*-based metrics, uvigerinids, and organic carbon flux was evaluated by integrating these variables into a Principal Components Analysis (Figure 8). According to these results, higher total organic carbon (TOC) values are associated with MIS 2 and MIS 1 and correlate with higher values of uvigerinids biomass (both mean and summed biomass). Intermediate values of TOC and δ13C are associated with higher values of *B. ordinaria* relative abundance and summed biomass, especially in MIS 5. Lower values of TOC were observed in MIS 3, together with lower values of mean individual biomass of *B. ordinaria*.
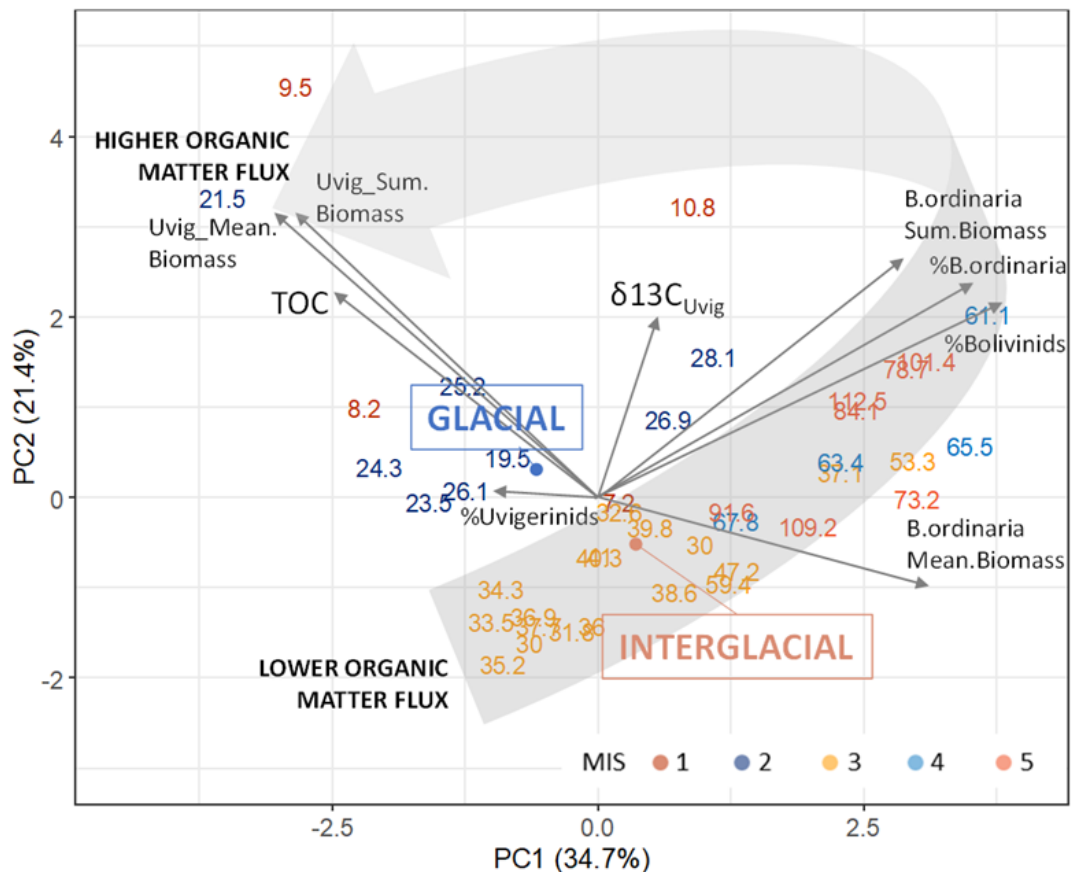
Figure 8: PCA biplots showing the relationships between total organic carbon (TOC), stable carbon isotope ratio (δ13C), relative abundance of *Bolivina ordinaria* (%Bordinaria) and of uvigerinids (%Uvigerinids), mean individual biomass of *B. ordinaria* and of uvigerinids (B.ordinaria_Mean.Biomass and Uvig_MeanBiomass, respectively), and summed biomass of *B. ordinaria* and of uvigerinids (B.ordinaria_Sum.Biomass and Uvig_Sum.Biomass, respectively). The cases (SIS-188 and SIS-249 core samples named by age – ka) are color-coded according to their respective Marine Isotope Stages (MIS). The percentages presented in the axis titles correspond to the variance explained by each principal component (PC).

DISCUSSION

Deep-sea benthic foraminifera are strongly influenced by a variety of factors related to their environment. One of the primary factors is the quantity, periodicity, and quality of the organic input to the ocean floor. The availability of organic matter, often originating from

surface primary productivity, significantly impacts the benthic foraminiferal community structure, as these organisms rely on organic material as a food source. Additionally, temperature, salinity, turbidity, oxygen levels, substrate type, and competition also play critical roles in shaping their distribution and abundance (Thomas et al., 1995; Jorissen et al., 2007; Gooday, 2003; Diz and Barker, 2015).

The Bolivinitidae family has an infaunal life habit and is commonly found in areas with high organic matter input, often associated with reduced oxygen levels in the bottom waters (Gooday, 1994; Mackensen et al., 1995; Schmiedl et al., 1997; Bernhard and Gupta 1999; Abu-Zied et al., 2008). *Bolivina ordinaria*, in particular, has been considered an indicator of a high carbon influx, often in combination with dysoxic conditions by Mendes et al. (2012) and Martins et al. (2006) and upwelling areas by Disaró (2014).

In this sense, the dominance of meso-eutrophic conditions in the northern slope of the Pelotas Basin during the late Quaternary, as previously discussed by Rodrigues et al. (2018), Schmitt et al. (2019), and Santana et al. (2021), can be the main explanation for the high relative abundance of *B. ordinaria*, as this area provides environmental conditions suitable for this species (Gooday 1994; Mackensen et al., 1995; Schmiedl et al., 1997; Bernhard and Gupta 1999; Abu-Zied et al., 2008). In addition, the highest relative abundances of this species in MIS 1 of SIS-188 core and MIS 5 of SIS-249 core coincide with the highest levels of TOC reported by Rodrigues et al. (2018) for SIS-249 core and by Gonçalves and Leonhardt (2021) for SIS-188 core.

Gonçalves and Leonhardt (2021) also found larger amounts of coccoliths and higher values of the N ratio at the top of SIS-188, suggesting a period of high surface primary productivity in the Holocene. The coccolithophore-based proxy "N ratio" of Flores et al. (2000) is used to infer paleoproductivity and monitor the nutricline depth. It is based on the relative abundances of opportunistic species, which benefit when nutrients increase in the upper photic zone (*Gephyrocapsa* spp. and *Emiliania huxleyi*), and the lower-photic zone dwelling *Florisphaera profunda*, which increases its relative abundance under deep-nutricline conditions. The high surface primary productivity may has influenced the increase in the

relative abundance of benthic r-strategist species, since the reproduction of some opportunistic species, such as some species of uvigerinids and bolivinids (possibly *B. ordinaria*), is controlled by rapid increments in the flow of OM (Duchemin et al., 2007).

Rodrigues et al. (2018) found negative values of *OrgInd*, which is a biotic index based on the ratio between infaunal and epifaunal species indicators of organic contribution, during the MIS 5, suggesting higher concentrations of TOC related to the contribution of refractory OM and increased bacterial density, which may have led to a low dissolved oxygen content in the interstitial water. On the other hand, during the MIS 3, the authors found positive values of this index due to the increase in the relative abundance of epifauna, which coincided with the lower relative abundances of *B. ordinaria*.

According to Hottinger (2000), the morphological characteristics of an organism represent important instruments of interaction with the environment around it. Thus, besides the species abundance discussed above, the morphometric analysis of the tests of benthic foraminifera may offer qualitative and quantitative information about paleoceanographic changes, as demonstrated in the works carried out by Petersen et al. (2016), Eder et al. (2017), Santana et al. (2021), and Tetard et al. (2021). In particular, the morphometric responses of bolivinids to environmental changes have already been studied by Brun et al. (1984), Gary et al. (1989), Glock et al. (2010), Kuhnt et al. (2013), Davis et al. (2016), Keating-Bitonti and Payne (2017), Bayrón-Arcelay et al. (2020), Belanger (2022), and Govindankutty Menon et al. (2023). These authors report different behaviors between species, with no common response of this group to changes in water mass properties such as dissolved-oxygen and temperature. Even within the same species, responses to variations in water chemistry can differ according to life strategies, as reported by Douglas and Staines-Urias (2007). The authors examined both live and dead specimens of dimorphic generations (microspheric and megalospheric), along with morphovariants of three *Bolivina* species found in the Oxygen Minimum Zone in the Gulf of California. From a depth of 500 m, as the flux of phytodetritus to the seafloor becomes less important, a *B. subadvena* population composed predominantly of small, live megalospheric forms and fewer large,

dead microspheric tests was observed. These authors also noticed that distinct morphovariants develop as benthic oxygen concentrations decrease. For instance, the tests of *B. subadvena*, especially the microspheric forms, become larger and more compressed when bottom-water oxygen concentrations drop below 0.2 ml/l.

In our study, general trends of decreasing test size and mean biomass of *B. ordinaria* were observed towards the top of the SIS-188 (corresponding to MIS 1) and towards the base of the SIS-249 (corresponding to MIS 5), while the summed biomass tended to be lower in MIS 2 and 3. Although MIS 3 is considered a relatively mild interglacial compared to full interglacials MIS 1 and 5, there has been some controversy regarding its true nature. The marine oxygen isotope record suggests relatively large continental ice volumes, contradicting recent relative sea-level reconstructions (e.g., Dalton et al., 2022; Dillenburg et al., 2019). In any case, our results suggest that conditions during MIS 3 were different from those that occurred during full interglacials.

Despite the hypothesis that the size variations are related to intra-specific variations linked to the alternation between generations cannot be ruled out, the results may also be partially interpreted based on the TROX-2 model proposed by Van Der Zwaan et al. (1999). According to the authors, competition for food and space is the third element structuring microhabitats, next to organic flux and redox-gradients. In this sense, it is likely that the increased competition between species for labile organic matter is a controlling factor of biomass. Comparing the mean biomass values obtained for *B. ordinaria* with the results presented by Santana et al. (2021) for uvigerinids from the same samples, it is noted that these taxa do not always respond simultaneously to the increase in the organic matter flow. The highest value of uvigerinids mean individual biomass occurred during the Last Glacial Maximum, with a secondary peak in the Holocene, also during an event of high marine productivity, according to Gonçalves and Leonhardt (2021), while mean individual biomass peaks of *B. ordinaria* occurred when the flux of organic detritus from the sea surface to the bottom was not as high. Additionally, attention is drawn to the increase in the representation of uvigerinids (relative abundance and summed biomass) from MIS 3 to MIS 1 (SIS-188), a

behavior different to that of bolivinids, which increased during MIS 5 (SIS-249). Although the intermittent flow of OM to the ocean floor favors opportunistic species of both groups (Koho et al., 2008; Schmiedl et al., 2010; Enge et al., 2014), the observations above lead to the hypothesis that uvigerinids and bolivinids (*B. ordinaria*) may compete for food, with uvigerinids having probably a greater ability to exploit labile organic matter. Nevertheless, further studies are necessary to thoroughly evaluate this hypothesis. For instance, understanding whether uvigerinids and *B. ordinaria* in this region live at the same depth in the sediments and/or have their vertical distribution driven by organic matter availability and quality could be crucial. Additionally, investigating potential variations in their ability to access different fractions of organic carbon (labile and refractory) could deepen our understanding of their temporal distribution patterns.
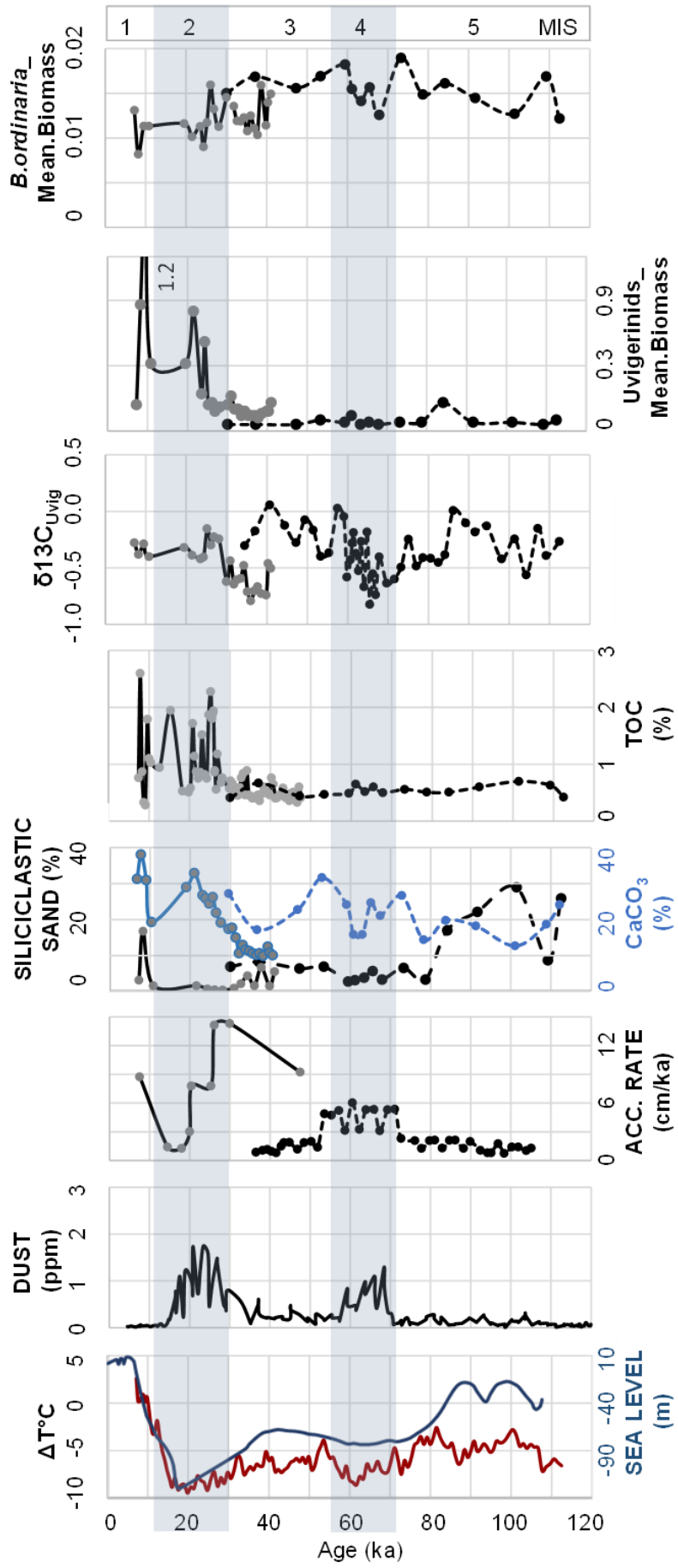
Figure 9: Environmental, geochemistry and benthic foraminiferal proxies along the cores SIS-188 and SIS-249. (A) Temperature change reconstruction from oxigen and hydrogen isotopes ratios (Vostok ice core, Petit et al., 2001) and sea-level curve (Rohling et al., 1998). (B) Dust flux in Antarctica (Vostok ice core, Petit et al., 2001). (C) Rates of sediment accumulation (cm/ka) (Lopes et al., 2021 for SIS-249 and Bottezini et al., 2021 for SIS-188. (D) Siliciclastic sand (%) and carbonate content (%) (Lopes et al., 2021 for SIS-249, and Gonçalves & Leonhardt, 2021 for SIS-188. (E) Total Organic Carbon (%) (Rodrigues et al., 2018 and Bottezini et al., 2022). (F) δ13C from *Uvigerina peregrina* (Rodrigues et al., 2018). (G) Summed Biomass of uvigerinids (µg C) (Santana et al., 2021). (H) Summed Biomass of *Bolivina ordinaria* (µgC) (from this study). MIS boundaries according to the LR04 stack of Lisiecki and Raymo (2005) and Railsback et al. (2015).

In summary, the results obtained suggest that test size and biomass-based metrics of *Bolivina ordinaria* are linked to the input of organic matter to the continental slope. In turn, this flow is determined by a set of climatic-oceanographic factors, which alternate on the southern Brazilian continental margin throughout the interglacial and glacial periods of the Quaternary (Figure 9). Among them are the upwelling of nutrient-rich waters (SACW), the continental outflow from the Lagoa dos Patos and Rio de la Plata, the increased input of terrigenous sediments during periods of lower sea level, and fertilization by iron-rich wind dust associated with the strengthening of south-southwest winds. These factors contribute to increased surface marine productivity which, in turn, increases the OM flow to the sea floor and reduces the oxygen concentration in the sediments (Soares and Möller 2001; Mahiques et al., 2007; Möller et al., 2008; Nagai et al., 2010; Leonhardt et al., 2013; Lopes et al., 2021).

The descriptors of *B. ordinaria* (relative abundance, test length, and biomass) did not exhibit the same discriminatory power for biozones as those obtained using similarity matrices (Bray-Curtis) based on relative species abundance of all taxa identified in the samples. While Schmitt et al. (2019) managed to define the succession of four

paleoecological zones along SIS-188 and three along SIS-249 using Bray–Curtis similarity matrices (Q-mode), the bolivinids-based metrics proved to be valuable indicators for tracking only two broader environmental shifts over time, likely associated with glacial and interglacial periods. The temporal resolution of results based on *B. ordinaria* appears to be primarily associated with large changes in primary productivity. Thus, higher relative abundance and summed biomass were observed during interglacial periods, and lower relative abundance and summed biomass were observed during glacial periods.

The linear relationships between relative abundance, test length, and biomass (individual mean and summed biomass) indicated that the samples with higher percentages of *B. ordinaria* in the benthic foraminifera assemblage composition are generally those with greater summed biomass. However, this relationship is not necessarily a rule among foraminifera populations. Vincent et al. (2021) observed no general pattern between biomass and density of living individuals in the Campos Basin, SE Brazil, and that species with similar densities presented biomasses ranging from 0.10 to 10,000.00 $mgC.m^{-2}$. Keating-Bitonti and Payne (2017) verified in their study in the Santa Monica Basin, California, that the test volume of the *Bolivina spissa* does not respond to the decrease in dissolved oxygen concentrations, while the biovolume of *Bolivina argentea* decreases but in the test volume:surface ratio does not show a decrease with decreasing oxygen concentrations, as expected from physiological predictions. Therefore, as previously discussed by Belanger (2022), although foraminifera are expected to decrease in size as a reproductive strategy to exploit episodic food inputs or to reduce metabolic demand in environments with restrictive ecological conditions, not all species respond with similar morphological patterns.

Difficulties related to the taxonomic classification of the species

Mendes et al. (2012) noted that the species *B. ordinaria* has been identified in the literature by various taxonomic nomenclatures, including *B. dilatata* (Duijnstee et al., 2004; Ernst et al., 2005; Mojtahid et al., 2009, Disaró et al., 2022); *Brizalina spathulata* (Diz and

France 2008); *B. variabilis* (Schiebel 1992; Debenay et al., 2001; Duchemin et al., 2005); and *Bolivina* ex. gr. *B. dilatata* (Duchemin et al., 2007). These synonyms are due to the morphological similarities between these organisms. In this study, the primary criterion used to distinguish *B. ordinaria* from other bolivinids species included: a shape slightly ovate at the apertural end, broad, opaque, and slightly curved sutures, with a thin wall except at sutures where it is thickened and opaque, causing sutures to appear very white compared to the rest of the test. These test features could be clearly visualized in the images presented in Plate 1 (Appendix A2).

The different classifications of *B. ordinaria*, a problem also common to several other species of foraminifera, may be one of the reasons for the limited availability of references on their specific ecological preferences. One of the primary challenges of taxonomy based on morphological criteria is that the same species can show variations in its tests depending on the ontogenetic stage and the conditions of its microhabitat. Thus, the constant taxonomic revision and the search for complementary taxonomic classification methods (morphological and genetic) are fundamental for better understanding species diversity, geographical distribution, phylogenetic affinities, and ecological requirements or tolerances.

CONCLUSION

The dominance of meso-eutrophic conditions throughout the late Quaternary contributes to explain the high relative abundance of bolivinids in the cores collected on the northern slope of the Pelotas Basin, since it is assumed that conditions of organic enrichment are favorable to the development of this taxon. However, it is necessary to consider the interaction among multiple environmental and biotic factors to understand the smaller fluctuations in the relative abundance, size, and biomass of *B. ordinaria* in the last 112 ka BP, highlighting the complexity of its ecological niche.

Bolivina ordinaria had lower relative abundance and summed biomass during MIS 1 and MIS 2, which coincide with periods of higher surface primary productivity and supply of labile organic matter to the seafloor. This behavior may be explained, among other reasons,

by the fact that this species is likely favored by the regular contribution of refractory organic matter during warmer periods due to its infaunal habit. However, during glacial stages, when the flow of labile organic matter to the benthic compartment increases, *B. ordinaria* likely loses competition with other species of shallow infauna and epifauna.

CREDIT AUTHORSHIP CONTRIBUTION STATEMENT

Patricia T. Kother: Conceptualization, Formal analysis, Investigation, Data curation, Visualization, Writing – original draft, Writing – review & editing. Maria Alejandra G. Pivel: Conceptualization, Resources, Writing – review & editing, Supervision, Project administration. Kalina M. Brauko: Conceptualization, Writing – review & editing. Carla Bonetti: Conceptualization, Methodology, Writing – review & editing, Resources, Supervision, Project administration, Funding acquisition.

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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6 AVALIAÇÃO DA EXPERIÊNCIADE MESTRADO

A proposta inicial do projeto de pesquisa era explorar os dados e avaliar as relações de dependência do comportamento da abundância, do comprimento das testas e da biomassa de *Bolivina ordinaria*, desenvolvidos por Kother (2021) com os descritores sedimentológicos (granulometria e grau de seleção) e geoquímicos (carbono orgânico total, teor de carbonato de cálcio, razões de isótopos estáveis de carbono e de oxigênio) nos testemunhos SIS-188 e SIS-249 coletados na Bacia de Pelotas. A partir disso, buscou se comparar as inferências paleoceanográficas obtidas a partir dos *proxies* derivados do estudo de *Bolivina ordinaria* com resultados obtidos a partir de outros taxa (outras espécies de foraminíferos bentônicos, foraminíferos planctônicos e nanofósseis) para os mesmos testemunhos.

Então iniciei com uma análise exploratória de dados que envolviam os testemunhos SIS-188 e SIS-249 e compilei os resultados bióticos e abióticos com seus respectivos "n" amostrais e suas representatividades temporais (EIMs). Depois dessa etapa partimos para a análise estatística que envolveu entre outros transformação de dados, testes de normalidade, testes não-paramétricos, teste de comparação de medianas, análise de componentes principais, MDS, NMDS, entre outros.

Após vários testes e análises o conjunto de variáveis relacionadas a foraminíferos bentônicos (abundância e biometria) e *proxies* geoquímicos permitiu chegar a resultados que atingiram os objetivos gerais da proposta inicial do projeto de pesquisa. Esses resultados foram consolidados no formato de um artigo científico publicado na revista *Marine Micropaleontology* (Elsevier, Qualis A2) apresentado nessa dissertação (Kother et al., 2024).

Embora a elaboração de um segundo artigo fosse prevista, não foi possível concluí-lo devido ao final do prazo regular para entrega da dissertação e também devido às dificuldades em relação à compilação de mais dados para subsidiar os resultados. No entanto, parte dos objetivos desse segundo artigo foi incorporada ao primeiro artigo e outra parte foi publicada no formato de resumo apresentado no V Simpósio Brasileiro de Geologia e Geofísica Marinha (SBGGM) em 2023. Neste último, foram exploradas as relações entre abundâncias de foraminíferos bentônicos e índices bióticos de dissolução do carbonato (foraminíferos planctônicos) em

profundidades acima da lisoclina, o que nos permitiu identificar *proxies* bentônicos de variações do pH nos sedimentos de fundo.

Além do desenvolvimento da dissertação, ao longo da pesquisa cursei as disciplinas obrigatórias e participei de dois eventos: XVIII Congresso Brasileiro de Estudos do Quaternário, 2022, Porto Seguro e V SBGGM, 2023, USP/UNESP e conclui o estágio (não obrigatório) de docência na disciplina de Paleoceanografia.

O desenvolvimento da pesquisa com certeza foi uma parte importante na formação do meu mestrado, porém considero que as experiências adquiridas como professora no estágio de docência, bem como as decorrentes da submissão e revisão do artigo foram essenciais nessa formação. Organizar um conteúdo e ministrar uma aula perante uma turma é uma vivência imprescindível para um mestre. A humildade que devemos ter é o grande aprendizado dessa vivência. Ademais, ter a oportunidade de receber correções de especialistas na área com certeza enriqueceu muito a minha forma de escrever e fez entender sobre dar "boas explicações".

Por fim, acredito que cumpri meu trabalho com louvor, apesar dos percalços que muitas vezes são necessários para que possamos crescer.

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APÊNDICE A

Appendix A1 –

**Table A1: Relative abundance (%) of Bolivinitidae species in the cores SIS-188 and SIS249.**

CORE	MIS	Age (ka)	Bolivina compacta	Bolivina doniezi	Bolivina lowmani	Bolivina ordinaria	Bolivina sp.	Bolivina striatula	Brizalina spinescens	Brizalina subaenariensis	Brizalina subspinescens	Brizalina sp.	Bolivinitidae (total)
SIS-188	1	7,2	0,4	1,2	2,1	3,7	0,4	2,1	0,0	0,8	1,6	0,0	**12,3**
		8,2	1,4	0,0	0,7	3,0	1,0	1,4	0,0	0,0	0,0	0,0	**7,4**
		9,5	0,2	0,0	0,4	5,0	2,2	1,1	0,4	0,4	0,0	0,0	**9,7**
		10,8	2,0	0,0	0,0	10,5	0,0	0,8	0,8	0,4	0,2	0,0	**14,7**
	2	19,5	0,0	0,2	4,7	2,6	0,2	0,2	0,0	0,7	1,0	0,0	**9,5**
		21,5	0,0	0,2	2,1	3,3	0,0	0,6	0,0	0,2	0,0	0,0	**6,5**
		23,5	1,0	0,8	0,0	2,0	0,0	1,0	0,5	0,0	0,0	0,0	**5,3**
		24,3	0,4	0,0	0,9	2,2	0,0	1,3	0,0	0,9	0,9	0,0	**6,7**
		25,2	0,4	0,0	0,2	3,7	0,0	1,4	0,2	0,0	0,0	0,0	**5,9**
		26,1	0,5	0,9	0,8	1,1	0,3	0,0	0,6	0,0	0,0	0,0	**4,3**
		26,9	0,7	0,3	0,4	4,8	0,4	0,9	0,4	0,7	0,0	0,0	**8,8**
		28,1	0,8	0,0	0,3	10,1	0,0	1,1	0,0	0,3	0,5	0,0	**13,0**
	3	30,0	1,0	0,0	0,0	1,3	0,0	0,6	0,0	1,6	0,0	0,0	**4,5**
		30,9	0,0	0,3	0,3	0,0	0,5	0,0	0,8	0,8	0,0	0,0	**2,7**
		31,8	0,3	0,6	0,0	2,8	0,0	0,6	0,6	0,0	0,0	0,0	**5,0**
		32,6	1,0	0,7	1,6	5,3	0,0	1,0	0,0	1,0	0,3	0,0	**10,9**
		33,5	0,7	0,0	0,0	2,4	0,0	0,0	0,0	0,0	0,3	0,0	**3,4**
		34,3	2,7	0,0	1,0	2,0	0,3	0,0	0,3	0,0	0,0	0,0	**6,4**
		35,2	0,3	0,3	0,6	1,9	0,6	0,3	0,3	0,0	0,0	0,0	**4,5**
		36,0	0,0	0,0	0,5	4,5	0,0	0,5	0,0	1,5	1,0	0,0	**8,0**
		36,9	0,4	0,7	0,4	3,7	0,0	1,1	0,0	0,0	0,4	0,0	**6,6**
		37,7	0,7	0,0	1,4	2,8	1,7	0,0	1,4	0,0	0,0	0,0	**7,9**
		38,6	0,3	0,0	0,6	5,1	0,3	0,6	0,8	0,6	0,0	0,0	**8,2**
		39,8	0,3	0,5	0,8	6,8	0,5	0,8	0,0	0,0	0,3	0,0	**10,1**
		40,3	0,6	0,0	0,0	5,8	0,0	0,0	0,6	0,0	0,0	0,0	**7,1**
		41,0	0,3	0,3	0,5	3,3	0,3	0,0	1,0	0,3	0,0	0,0	**5,8**
SIS-249		30,0	0,9	1,5	0,6	3,2	0,0	0,9	0,3	0,3	0,0	0,0	**7,6**
		37,1	1,9	0,0	0,0	7,4	0,0	1,9	0,8	1,2	0,0	0,8	**14,0**
		47,2	0,8	0,0	0,3	3,8	1,8	1,3	0,8	1,0	0,0	0,0	**9,5**
		53,3	2,6	0,0	0,4	7,8	0,0	4,1	0,7	2,2	0,0	0,4	**18,2**
	4	59,4	0,3	2,8	0,6	2,2	1,9	1,3	0,0	0,3	0,0	0,0	**9,4**
		61,1	0,4	0,0	0,0	13,0	0,0	3,2	1,1	1,4	0,0	0,7	**19,6**
		63,4	1,2	0,6	0,0	7,4	1,9	1,5	0,9	0,6	0,0	0,0	**14,2**
		65,5	1,4	0,0	0,5	13,0	0,5	0,5	0,5	3,7	0,0	0,9	**20,8**
		67,8	0,9	0,0	0,3	6,9	0,6	0,6	0,3	0,9	0,0	0,0	**10,6**
	5	73,2	1,8	0,9	0,4	7,9	0,0	0,9	0,4	3,1	0,0	0,4	**15,8**
		78,7	3,3	0,0	0,5	6,6	1,0	1,1	1,0	0,2	0,0	0,0	**13,8**
		84,1	3,3	0,0	0,0	8,3	0,0	1,0	0,3	0,5	0,0	0,3	**13,5**
		91,6	1,6	0,3	0,3	5,0	0,9	1,3	0,9	0,3	0,0	0,0	**10,7**
		101,4	1,0	6,0	0,0	11,6	0,0	2,5	1,0	1,0	0,0	0,0	**23,1**
		109,2	1,2	0,3	0,3	6,2	2,8	1,5	0,0	0,6	0,0	0,3	**13,3**
		112,5	0,4	0,0	0,4	10,3	0,0	0,4	0,7	5,0	0,0	0,4	**17,4**

Appendix A2 –
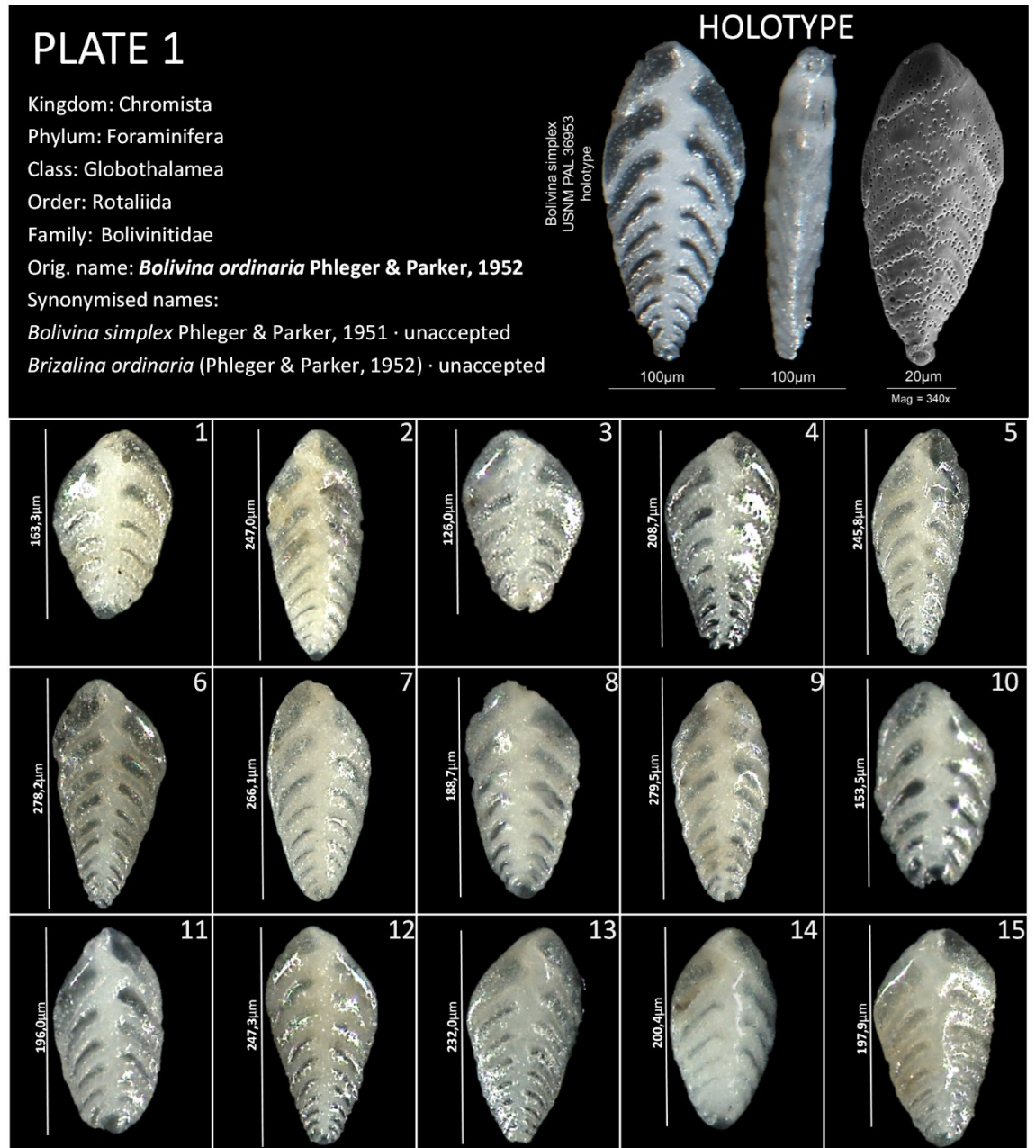
Plate 1. *Bolivina ordinaria* from the SIS-188 and SIS-249 cores. 1-2: SIS-188, MIS 1; 3–5: SIS-188, MIS 2; 6-8: SIS-249, MIS 3; 9-11: SIS-249, MIS 4; 12-15: SIS-249, MIS 5. Vertical lines indicate the length (µm). Taxonomic citation: Hayward et al. (2024). Holotype: *Bolivina simplex* USNM PAL 369353 Smithsonian National Museum of Natural History. EZID:http://n2t.net/ark:/65665/3aa6e46ce-bbff-4074-a48a-b9c0d639384e.

Appendix A3 – Frequency distribution for biometric descriptors of *Bolivina ordinaria*
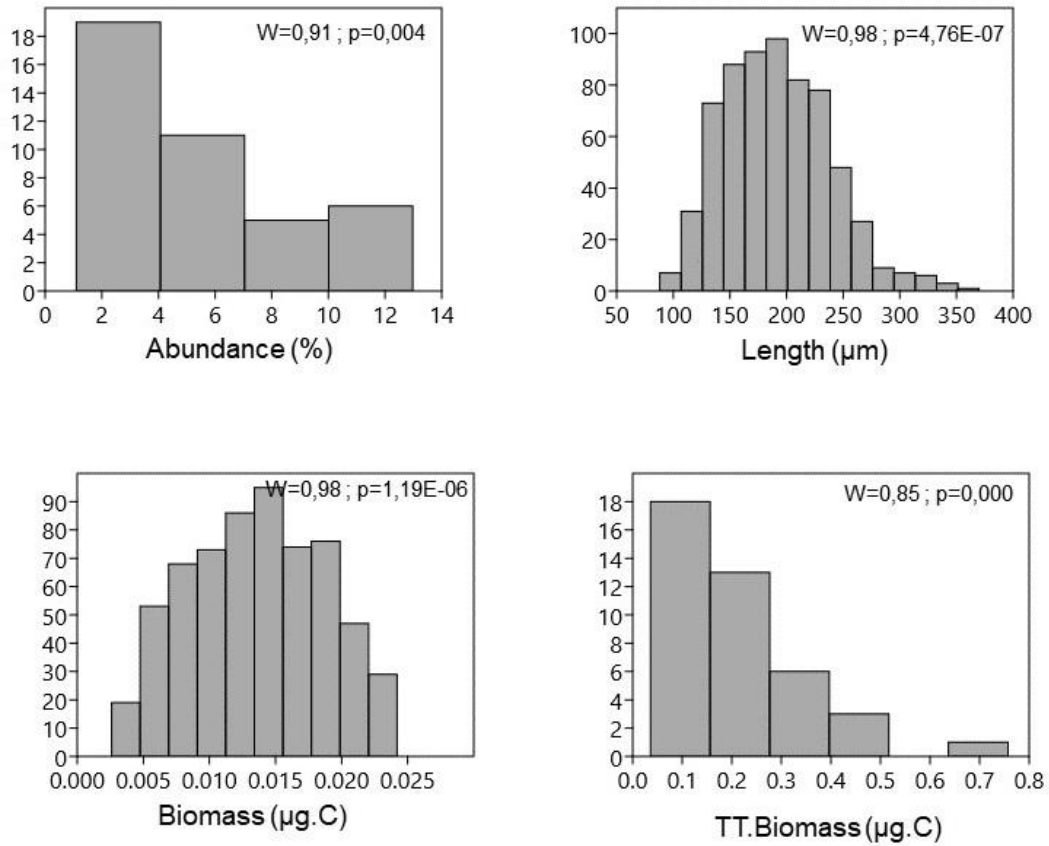
Figure A3 - Histograms depicting relative abundance, test length, mean individual and summed biomass for *Bolivina ordinaria*, accompanied by the respective results of Shapiro-Wilk normality tests (W).

Appendix A4 – Post hoc Dunn's multiple comparisons test

Table A4 - Results of post hoc Dunn's multiple comparisons test applied to compare palaeoecological zones regarding the relative abundance (A), test length (B), mean individual biomass (C), and summed biomass (D) of *B. ordinaria* from SIS - 188 (GR1 to GR4) and SIS-249 (GR5 to GR7) cores. Highlighted cells indicate groups with statistically different medians ($p < 0.05$)

A – RELATIVE ABUNDANCE

	GR1	GR2	GR3	GR4	GR5	GR6	GR7
GR1		0,5100	0,1361	0,8877	0,5278	0,1460	0,0596
GR2	0,5100		0,4318	0,4237	0,2222	0,0373	0,0102
GR3	0,1361	0,4318		0,1007	0,0477	0,0031	0,0003
GR4	0,8877	0,4237	0,1007		0,6135	0,1871	0,0823
GR5	0,5278	0,2222	0,0477	0,6135		0,4809	0,3069
GR6	0,1460	0,0373	0,0031	0,1871	0,4809		0,7746
GR7	0,0596	0,0102	0,0003	0,0823	0,3069	0,7746	

B – TEST LENGTH

	GR1	GR2	GR3	GR4	GR5	GR6	GR7
GR1		0,1067	0,1979	0,0197	0,0000	0,0000	0,0000
GR2	0,1067		0,9400	0,4166	0,0000	0,0004	0,0000
GR3	0,1979	0,9400		0,4343	0,0000	0,0018	0,0002
GR4	0,0197	0,4166	0,4343		0,0003	0,0136	0,0023
GR5	0,0000	0,0000	0,0000	0,0003		0,1082	0,1470
GR6	0,0000	0,0004	0,0018	0,0136	0,1082		0,7105
GR7	0,0000	0,0000	0,0002	0,0023	0,1470	0,7105	

C – MEAN INDIVIDUAL BIOMASS

	GR1	GR2	GR3	GR4	GR5	GR6	GR7
GR1		0,1442	0,1492	0,0192	0,0000	0,0000	0,0000
GR2	0,1442		0,8506	0,3406	0,0000	0,0008	0,0001
GR3	0,1492	0,8506		0,5087	0,0001	0,0070	0,0022
GR4	0,0192	0,3406	0,5087		0,0006	0,0323	0,0123
GR5	0,0000	0,0000	0,0001	0,0006		0,0933	0,0885
GR6	0,0000	0,0008	0,0070	0,0323	0,0933		0,8779
GR7	0,0000	0,0001	0,0022	0,0123	0,0885	0,8779	

D - SUMMED BIOMASS

	GR1	GR2	GR3	GR4	GR5	GR6	GR7
GR1		0,8283	0,1025	0,5630	0,5319	0,2563	0,0758
GR2	0,8283		0,1592	0,7177	0,4127	0,1796	0,0454
GR3	0,1025	0,1592		0,3018	0,0364	0,0064	0,0004
GR4	0,5630	0,7177	0,3018		0,2533	0,0917	0,0175
GR5	0,5319	0,4127	0,0364	0,2533		0,6722	0,3512
GR6	0,2563	0,1796	0,0064	0,0917	0,6722		0,6078
GR7	0,0758	0,0454	0,0004	0,0175	0,3512	0,6078	