



UNIVERSIDADE FEDERAL DE SANTA CATARINA
COORDENADORIA ESPECIAL DE OCEANOGRAFIA
PROGRAMA DE PÓS-GRADUAÇÃO EM OCEANOGRAFIA

Beatriz Fernandes de Barros Bomfim Santana

**Biometria e biomassa de Uvigerinidae (Foraminifera) ao longo do Quaternário tardio no
talude continental do sul do Brasil**

Florianópolis

2020

Beatriz Fernandes de Barros Bomfim Santana

Biometria e biomassa de Uvigerinidae (Foraminifera) ao longo do Quaternário tardio no talude continental do sul do Brasil

Dissertação submetida ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Santa Catarina para a obtenção do título de Mestre em Oceanografia

Orientadora: Profa. Dra. Carla Bonetti

Coorientadora: Profa. Dra. Juliana Leonel

Florianópolis

2020

Ficha de identificação da obra elaborada pelo autor,
através do Programa de Geração Automática da Biblioteca Universitária da UFSC.

Santana, Beatriz

Biometria e biomassa de Uvigerinidae (Foraminifera) ao longo do Quaternário tardio no talude continental do sul do Brasil / Beatriz Santana ; orientador, Carla Bonetti, coorientador, Juliana Leonel, 2020.

48 p.

Dissertação (mestrado) - Universidade Federal de Santa Catarina, Centro de Ciências Físicas e Matemáticas, Programa de Pós-Graduação em Oceanografia, Florianópolis, 2020.

Inclui referências.

1. Oceanografia. 2. Paleoceanografia. 3. Biomassa. 4. Foraminíferos bentônicos. 5. Paleoprodutividade. I. Bonetti, Carla . II. Leonel, Juliana. III. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Oceanografia. IV. Título.

Beatriz Fernandes de Barros Bomfim Santana

Biometria e biomassa de Uvigerinidae (Foraminifera) ao longo do Quaternário tardio no talude continental do sul do Brasil

O presente trabalho em nível de mestrado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

Kalina Brauko, Dr. ^a
Universidade Federal de Santa Catarina

Prof. ^a Patrícia Eichler, Dr. ^a
Universidade do Sul de Santa Catarina

Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de mestre em Oceanografia.

Coordenação do Programa de Pós-Graduação

Prof.^a Carla Bonetti, Dr. ^a
Universidade Federal de Santa Catarina
Orientadora

Prof.^a Juliana Leonel, Dr. ^a
Universidade Federal de Santa Catarina
Coorientadora

Florianópolis, 2020

AGRADECIMENTOS

O processo de elaboração, desenvolvimento e escrita de um projeto acadêmico não é fácil. Esses 2 anos foram para mim o famoso mix de emoções: Muitos momentos felizes misturados à momentos de frustração total. Dito isso, gostaria de agradecer primeiramente a mim mesma: Burlar minha auto sabotagem e a famosa síndrome do impostor foi uma tarefa que exigiu muita conscientização interna. Lógico que não fiz tudo sozinha, sem o apoio da minha família que está longe de mim fisicamente e das muitas pessoas que encontrei nesses 2 anos e meio em Florianópolis a realização desse trabalho não seria possível.

Obrigada mãe e pai, eu não sei nem colocar em palavras quão grata eu sou por sempre estarem confiando em mim. Vocês são minhas inspirações e tenho muito orgulho em ser filha de vocês. Obrigada também as minhas orientadoras, Carla Bonetti e Juliana Leonel, por serem profissionais humanas muito incríveis e me inspirarem confiança. Por falar em pessoas humanas, obrigada por todos os conselhos que recebi dos amigos que fiz no mestrado, Karen, Karine, Cibelle, Danilo, Alex, Inaiê, Thaise, Pati, Lua, Thales, Júlia, Gabriel, Diego ... a lista é um pouco longa (ainda bem!), todos muito diferentes e que me proporcionaram muitas conversas sobre vida acadêmica. Sou muito grata por ter conhecido vocês e por tudo que compartilhamos: dos perrengues até as trilhas por essa ilha linda. Um obrigada gigantesco e muito especial para Thaíse, espero ser uma profissional como a que você vem se tornando. Obrigada por toda ajuda no R e até por ter me inspirado a gostar de programar.

Grata também aos amigos que fiz em Floripa, fora do laboratório, obrigada por terem sido como família para mim nas muitas vezes em que precisei de um escape: Carlos, Carol, Naldo, Digão, Vitinho, Tábata, Sol, Yanna, Caridá, Barreto, Thaíz, Léo, Henrique, Débora e Moa. Vocês e muitos outros que conheci por aqui representaram meus almoços de domingo na casa da minha avó e me ajudaram a lidar com esse processo. Obrigada também aos amigos de Aracaju que compartilham caminhos comigo desde a graduação: Ju, Bela, Gabi e as minhas amigas, unidas pelo desabafo: Giulia e Andrea. Tenho muito orgulho de vocês, de verdade, não duvidem do que vocês são capazes. Obrigada também aos amigos que não estão nesse processo, mas foram também muito importantes: Hannah, Larissa, Dani, Dudu, Neto, Carol, Namor, Mari, Laís, Leila, Mary, Carol. Amo vocês! Espero em breve estarmos todos juntos. Por fim, mas não menos importante: muito obrigada ao meu companheiro, Victor, por toda a paciência e por todo o apoio nesses anos, que venha uma nova aventura juntos!

Obrigada ao Programa de Pós-Graduação em Oceanografia da UFSC por todo o suporte, a Fapesc (Fundação de Amparo à Pesquisa de Santa Catarina) e a Capes (Coordenadoria de Apoio à Pesquisa de Ensino Superior) que forneceram a bolsa de estudos durante o desenvolvimento desse trabalho.

“We are all smart, distinguish yourself by being kind.”

Unknown author.

RESUMO

O objetivo desse trabalho consistiu em avaliar a distribuição e quantificar a biomassa de espécies da família Uvigerinidae, a fim de compreender a paleoprodutividade bentônica e, por consequência, como os ecossistemas marinhos responderam às variações ambientais. As amostras coletadas no talude continental da Bacia de Pelotas, cobrem os Estágios Isotópicos Marinhos EIM 5- EIM 1 (7,2-112,5 Ka BP) e refletem as alterações oceanográficas entre estágios glaciais e interglaciais. Oscilações nas massas de água influentes em cada período são refletidas no tamanho e na distribuição das testas de Uvigerinidae, devido às diferentes exigências ecológicas e aos micro-habitat de cada espécie identificada neste estudo. A biomassa acumulada desses indivíduos aumentou entre o EIM 3 – EIM 1, assim como a presença de testas maiores, provavelmente devido ao aumento da produtividade primária durante o período glacial e à influência de massas d'água mais frias e ricas em nutrientes, como a Água Profunda Circumpolar. Além de Uvigerinidae inferir mudanças no fluxo de matéria orgânica ao longo do tempo, os descritores métricos (comprimento, largura, volume, alongamento) e a biomassa acumulada, refletem também estratégias reprodutivas dos gêneros *Trifarina* e *Uvigerina*. Portanto, estimar biomassa, além de quantificar a biometria das testas, se mostrou uma metodologia importante para entender a ecologia das espécies e como estas responderam às mudanças ambientais.

Palavras-chave: Fauna bentônica, Paleoprodutividade, Atlântico Sul.

ABSTRACT

The present work aims to evaluate the family Uvigerinidae species distribution and biomass, in order to understand benthic paleoproductivity and consequently, how marine ecosystems answered to environmental variations. The samples collected from Pelotas Basin continental slope, cover MIS 5 – MIS 1 (7.2 – 112.5 Ka BP) and reflect the oceanographic changes between glacial and interglacial stages. Water masses oscillations in each period are reflected in Uvigerinidae tests distribution and size, due to the different ecological requirements and microhabitats for each species identified in this study. Beyond Uvigerinidae infers changes in organic matter flux through time, the metric descriptors and the accumulated biomass reflects the reproductive strategies for *Trifarina* and *Uvigerina* genus. Therefore, the biomass estimative, in addition to quantify the tests biomass, corresponded to an important methodology for understand the species ecology and how it answered to environmental changes.

Key words: Deep-sea Benthos, Paleoproductivity, South Atlantic.

LISTA DE FIGURAS

Figure 1. Map showing location of sediment core and bathymetry of the study area	23
Figure 2. Geometric model applied to estimate the volume of the tests. Abbreviations: d_one = depth, d_two = width, h = length.....	25
Figure 3. Relative abundance of the family Uvigerinidae expressed as a percentage of the total number of individuals in each sample, considering all taxa also richness and relative abundance of each uvigerinids species (as a percentage of the total individuals of the family Uvigerinidae) in the cores (a) SIS 188 e (b) SIS 249.....	26
Figure 4. Box plot showing the measures of variability (quartile method) for the biometrics descriptors (a) length, (b) width, (c) depth and (d) elongation index in the cores SIS 188 and SIS 249.....	27
Figure 5: Variability in the total biomass of uvigerinids along the time in the cores SIS 188 and SIS 249.....	29
Figure 6. Relationship between accumulated biomass and relative abundance of Uvigerinidae in the cores SIS 188 and SIS 249.....	30
Figure A1. Histograms showing the distribution of the classes of size for the length, width and depth of the uvigerinids tests measured in the cores SIS 188 (N=1247 individuals) e SIS 249 (N = 674 individuals).....	48
Figure A2. Histograms showing the distribution of elongation index classes of the uvigerinids tests measured in the cores SIS 188 and SIS 249.....	48
Figure A3: Plot of test length (μm) versus volume (μm^3) measures showing the best-fit polynomial regression curve and equation to describe this relationship.....	49

LISTA DE TABELAS

Table S1. Relative abundance of Uvigerinidae species identified in the cores SIS188 and SIS249.....	42
Table S2. Average and standard deviation of the biometrics descriptors of uvigerinids tests (n total = 1921) analyzed in the cores SIS188 and SIS249.....	44
Table S3. Spearman rank correlation coefficient between morphometric descriptors and total organic carbon, carbon and oxygen isotope ratios in the cores SIS 188 and SIS 249. (values of the rs – lower triangle; p value – upper triangle). N = 1923.....	47

LISTA DE ABREVIATURAS

AABW - Atlantic Bottom Water

AAIW – Antarctic Intermediate Water

AMOC – Atlantic Meridional Overturning Circulation

BC – Brazil Current

CAPES – Coordenação de Aperfeiçoamento de Pessoal de Nível Superior

CDW – Circumpolar Deep Water

CT – Computed Tomography

EIM – Estágio Isotópico Marinho

FAPESC- Fundação de Amparo à Pesquisa do Estado de Santa Catarina

HCL – Hydrochloric Acid

IODP – Integrated Ocean Drilling Program

Ka BP – 1000 years Before Present (events occurred prior to radiocarbon dating – 1950)

LCDW – Lower Circumpolar Deep Water

LGM – Late Glacial Maximum

MC – Malvinas Current

MIS – Marine Isotopic Stage

NADW – North Atlantic Deep Water

RMSE – Root-mean-square Deviation

SACW – South Atlantic Central Water

SIL-UCSC – Stable Isotope Laboratory – University of California, Santa Cruz

SEM – Scanning Electron Microscope

UFF – Universidade Federal Fluminense

UCDW – Upper Circumpolar Deep Water

V-PDB – Vienna Pee – Dee Belemnite

SUMÁRIO

1	INTRODUÇÃO GERAL.....	13
1.1	PRODUTIVIDADE OCEÂNICA E MUDANÇAS CLIMÁTICAS.....	13
1.2	FORAMINÍFEROS E <i>PROXIES</i> PALEOCEANOGRÁFICAS.....	14
1.3	FERRAMENTAS PARA INFERIR A PALEOPRODUTIVIDADE.....	16
2	JUSTIFICATIVA.....	17
2.1	PERGUNTAS DE PESQUISA.....	17
2.2	HIPÓTESE.....	17
2.3	OBJETIVOS.....	18
2.3.1	Objetivo geral.....	18
2.3.2	Objetivos específicos.....	18
3	Biometric and biomass analysis of Quaternary Uvigerinidae (Foraminifera) from Southern Brazilian continental slope.....	20
	Abstract.....	20
3.1	Introduction.....	21
3.2	Study Area.....	22
3.2.1	Geological and oceanographic settings.....	22
3.3	Material and Methods.....	23
3.3.1	Stable Isotopes, Age model and Geochemical data.....	23
3.3.2	Microfossil Processing.....	24
3.3.3	Morphometric Analysis and Biomass Estimative.....	24
3.4	Results.....	25
3.4.1	Richness and Abundance of Uvigerinidae Family.....	25
3.4.2	Morphometric Analysis.....	26
3.4.3	Volume, Biovolume and Biomass estimative.....	28
3.4.4	Analysis of Correlation.....	30
3.5	Discussion.....	30
3.5.1	Uvigerinidae species distribution as paleoceanographic indicators.....	30
3.5.2	Biometric variations of Uvigerinidae test.....	31
3.5.3	Biomass measures and changes through the time.....	32
3.6	Conclusion.....	33
	Acknowledgments.....	34
	References.....	35
	Appendix.....	42
3.4	CONCLUSÃO GERAL.....	51
	Referências.....	52

1. INTRODUÇÃO GERAL

1.1 PRODUTIVIDADE OCEÂNICA E MUDANÇAS CLIMÁTICAS

As alterações no clima da Terra afetam aspectos como a estrutura e produtividade dos ecossistemas globais. Previsões confiáveis da consequência das mudanças ambientais induzidas pelo homem são relevantes para entender os impactos dessas alterações nos ciclos ecossistêmicos. Dentre esses, o ecossistema marinho e o sistema atmosfera-oceano são fontes determinantes para compreensão das mudanças climáticas (Rost and Riebesell, 2004). Nesses sistemas, a produção primária realizada pelo fitoplâncton é um fator importante na regulação do clima, como produto do compartilhamento do dióxido de carbono entre o oceano e atmosfera (FALKOWSKI, WOODHEAD, 2013).

A produtividade primária reduz a concentração do CO₂ na superfície oceânica e parte do material orgânico gerado pelos organismos fotossintéticos serve de alimento para o zooplâncton e para outros organismos marinhos superiores. Uma parcela desse material que deixa a superfície, afunda em direção ao leito marinho (Sen Gupta and McNeil, 2012). A exportação do carbono, sequestra o dióxido de carbono atmosférico utilizado como matéria prima para os organismos fotossintetizantes e tem como produto final a biomassa de organismos fitodetrívoros. O processo responsável por transportar o carbono da superfície até o fundo marinho, contra um gradiente de concentração, é chamado de bomba biológica (Passow and Carlson, 2012).

Até o período industrial, a bomba biológica se mantinha próxima a um estado de equilíbrio entre o suprimento de nutrientes do oceano e a exportação de carbono para o assoalho oceânico (Petit et al., 1999). Ações antropogênicas como o desmatamento e a oxidação de combustíveis fósseis, interferem no balanço da bomba biológica, já que o oceano capta cerca de um terço dos gases estufa lançados através de ações humanas (Turley et al., 2010). O aumento progressivo de dióxido de carbono no oceano poderá provocar ao longo do tempo, por exemplo, a diminuição do pH marinho, causando interferências fisiológicas em diversos organismos (Raven et al., 2005). As mudanças no funcionamento da bomba biológica estão relacionadas com os ciclos de pressão atmosférica do dióxido de carbono durante períodos glaciais e interglaciais. Assim, o aumento das concentrações de CO₂ na atmosfera têm exaltado a importância de estudos relacionados ao ciclo do carbono e a bomba biológica (FALKOWSKI, WOODHEAD, 2013).

Um dos grandes objetivos das Ciências da Terra atualmente é desenvolver ferramentas para compreender o funcionamento do clima terrestre, através por exemplo, da reconstrução de cenários de mudança climáticas enfrentadas pelo planeta em períodos geológicos passados e, com isso, prever quais serão as consequências futuras das mudanças observadas hoje. (Weart, 2015)

Como já abordado, reconstruções no padrão de produtividade oceânica são de grande interesse pela sua relação com os ciclos do carbono, um importante gás na regulação climática (Sun et al., 2006). A reconstrução da variação espacial e temporal da produtividade primária e a sua associação com os ciclos de carbono orgânico, permitem compreender como fluxos de matéria orgânica funcionaram em um dado local. A análise de sedimentos marinhos antigos, principalmente os compostos por carbonato biogênico, sua relação com fluxos de matéria orgânica e com a produtividade primária oceânica, são objetivos comuns aos estudos de paleoprodutividade, os quais buscam por mudanças espaciais e temporais desses componentes biogênicos e por suas causas, principalmente com relação às variações no clima da Terra (Sun et al., 2006).

Pelo fato das medições diretas do fluxo do carbono para o oceano profundo não poderem ser feitas para períodos passados, as reconstruções são realizadas a partir de registros geoquímicos e micropaleontológicos no sedimento marinho. Existe uma grande variedade de métodos qualitativos ou quantitativos que podem ser aplicados, idealmente de modo conjunto, em busca de um detalhamento melhor para inferir mudanças na produtividade marinha ao longo do tempo (PAYTAN, 2009).

1.2 FORAMINÍFEROS E *PROXIES* PALEOCEANOGRÁFICOS

Em trabalhos que envolvem estudos paleoceanográficos e de reconstrução climática, um dos grupos mais utilizados como *proxy* corresponde aos foraminíferos; protistas unicelulares de ampla distribuição e boa preservação no registro fóssil, englobados por uma carapaça que pode ser constituída por partículas aglutinadas ou por minerais, como calcita, aragonita ou sílica (ARMSTRONG, BRASIER, 2005; BURONE, HELENA, *et al.*, 2011). Dados obtidos a partir da análise da abundância e riqueza de espécies ao longo de testemunhos, da morfologia e da composição geoquímica da sua carapaça são utilizados nessas reconstruções (Duleba et al., 2003).

A estrutura da comunidade de foraminíferos bentônicos, a composição de espécies e o tamanho dos organismos refletem, entre outros fatores, o fornecimento de matéria orgânica para o sedimento marinho, já que o fluxo de carbono representa uma fonte de alimento para a comunidade bentônica e por isso são considerados *proxies* confiáveis em estudos de paleoceanografia e paleoprodutividade (Gooday, 2003; Sun et al., 2006). A disponibilidade de matéria orgânica e a concentração de oxigênio, são os principais fatores que controlam a abundância e a distribuição de foraminíferos bentônicos no oceano profundo (FONTANIER, C, MACKENSEN, *et al.*, 2006, ENGE, WITTE, *et al.*, 2014, ALMEIDA, MELLO, *et al.*, 2015). Essa afirmação embasa o modelo trófico-óxico estabelecido por JORISSEN, STIGTER, WIDMARCK (1995) o qual infere que espécies que habitam meios oligotróficos e bem oxigenados estão presentes nos sedimentos superficiais e compõem grande parte das espécies com hábitos epifaunais. Já em ambientes eutróficos e dióxicos, a assembleia de foraminíferos é predominantemente dominada por táxons de infauna. Espécies que compreendem a epifauna ou infauna rasa se beneficiam da matéria orgânica lábil, já organismos infaunais estão relacionados à matéria orgânica refratária (Gooday, 2003). Assim, a análise da abundância e riqueza de populações epi ou infaunais é positivamente correlacionada com estimativas de fluxo de carbono anuais para um determinado local (PAYTAN, 2009).

Uma importante fonte de alimento corresponde a camada de fitodetritos presente no assoalho oceânico, que se forma tipicamente em períodos de picos de produtividade primária sazonais (Gooday, 2003). A maioria das espécies de *Uvigerina* são consideradas *proxies* de baixa oxigenação e alta quantidade de matéria orgânica depositada no fundo marinho (Kawagata et al., 2006). Com isso, a investigação de uvigerinídeos representa uma importante estratégia para identificar períodos e variações na produtividade oceânica. NOMAKI, YAMAOKA, SHYRAIAMA (2007) apontam que diferenças na abundância ou biomassa de foraminíferos bentônicos do gênero *Uvigerina*, também refletem a preferência alimentar e os aspectos ecológicos frente à picos de matéria orgânica.

Análises isotópicas em testas de foraminíferos são amplamente utilizadas em reconstruções paleoceanográficas, já que as variações na composição isotópica de carbono e oxigênio são relacionadas às variações paleoambientais, de modo que espécies de foraminíferos secretam suas testas em equilíbrio com a água do mar, ou seja, são registradas nelas as características isotópicas das massas d'água (Zerfass and Andrade, 2008). A razão entre ^{18}O / ^{16}O em conchas carbonáticas permite inferir condições da temperatura no oceano profundo, já a proporção $^{13}\text{C}/^{12}\text{C}$ está relacionada a processos fisiológicos, tais como a fotossíntese, ambas

podem ser usadas como *proxies* de paleoprodutividade e configurações de massas d'água (SCHMIEDL, GERHARD, PFEILSTOCKER, *et al.*, 2004, FONTANIER, C, MACKENSEN, *et al.*, 2006). O ^{12}C é preferencialmente utilizado na fotossíntese, assim, o aumento de valores de $\delta^{13}\text{C}$ no carbonato mineralizado por microfósseis marinhos, indica um empobrecimento de isótopos leves, o que é interpretado como um aumento da produtividade fitoplanctônica (WEFER, *et al.*, 1999, ZERFASS, ANDRADE, 2008).

1.3 FERRAMENTAS PARA INFERIR A PALEOPRODUTIVIDADE

Diante do que foi exposto, as variações na riqueza e abundância de espécies de foraminíferos bentônicos fitodetrítivas, aliada à sua biomassa, são *proxies* importantes para inferir processos que interferem no fluxo do carbono ao longo do tempo geológico (VOLKER ALTENBACH, STRUCK, 2001, LOUBERE, JACOBSEN, *et al.*, 2011).

Dentre outras definições, a biomassa pode ser representada pela quantidade de carbono orgânico e o volume da testa (Murray and Alve, 2000). Pode ser expressa por diversas medidas, devido à variedade de métodos de inferência (FREITAS, 2019). No entanto, esses métodos muitas vezes apresentam problemas que dificultam seu uso, seja por destruírem a carapaça para sua medição, por sua difícil aplicação e calibração ou pelo seu custo. Assim, uma alternativa corresponde ao cálculo da biomassa a partir do biovolume, que associa formas geométricas como uma representação da forma da carapaça (MURRAY, 2006; MOVELLAN, SCHIEBEL, *et al.*, 2012; FREITAS, 2019). FREITAS (2019) propõe que a automatização da estimativa do biovolume pode reduzir o esforço e facilitar a obtenção desse dado com menor subjetividade (acuidade visual) e uma maior precisão.

Características geométricas e suas variações tanto geográficas como temporais em estudos paleontológicos permitem identificar interferências em processos ecológicos e fisiológicos, como tamanho da população e taxas metabólicas (Hunt and Roy, 2006). Pela sua abundância no ambiente marinho e pela sua carapaça mineralizada, foraminíferos bentônicos são organismos ideais para investigar os possíveis parâmetros oceanográficos que interferem no seu tamanho ou crescimento, como por exemplo a relação entre a razão de área-volume e temperatura, oscilações no fluxo de matéria orgânica e concentração de oxigênio (Keating-Bitonti and Payne, 2016).

Portanto, para utilizar as medidas de biomassa e abundância de foraminíferos bentônicos, em particular de uvigerinídeos como *proxies*, é necessário que estes mostrem correlações com parâmetros abióticos. Assim, nesse trabalho, fatores abióticos como carbonato

biodetrítico nos sedimentos, isótopos de carbono e oxigênio em testas de *Uvigerina*, distribuição e características das massas d'água são associados à abundância, riqueza e biometria dos taxa estudados.

2. JUSTIFICATIVA

O estudo de condições climatológicas e oceanográficas passadas permite inferir como estas irão se comportar no futuro, principalmente devido aos impactos antropogênicos causados não somente na atualidade, mas desde o período industrial. Mudanças climáticas ocasionadas pelos efeitos do aquecimento global, já podem ser testemunhadas em cenários de eventos extremos atuais. A previsão de mudanças climáticas globais, baseada em eventos passados, serve como um alerta para os impactos de episódios futuros. Assim, espera-se que a análise de *proxies* como a biomassa, abundância e características paleoecológicas dos foraminíferos bentônicos contribua para a compreensão das respostas biológicas à regulação climática, ciclo do carbono, variações nos picos de paleoprodutividade e mudanças no comportamento de massas d'água de fundo.

2.1 PERGUNTAS DE PESQUISA

- A abundância relativa das espécies da família Uvigerinidae, responde às variações na disponibilidade do carbono durante os eventos climáticos do Quaternário Tardio no talude da bacia de Pelotas?
- Quais fatores paleoecológicos e paleoceanográficos podem influenciar na variação da biomassa de Uvigerinidae entre os testemunhos analisados?
- A variação na morfologia e biometria das testas analisadas refletem as oscilações dos parâmetros ambientais?

2.2 HIPÓTESE

A abundância, a biomassa e a riqueza de foraminíferos bentônicos da família Uvigerinidae respondem positivamente, em escala milenar, ao aumento da produtividade primária decorrente de mudanças climáticas e do maior input de nutrientes no ambiente marinho associadas aos períodos mais frios ao longo do Quaternário Tardio na Bacia de Pelotas.

2.3 OBJETIVOS

2.3.1. Objetivo Geral

Inferir variações nos padrões de circulação oceânica e de flutuações na produtividade primária a partir de proxies bióticos analisados na Família Uvigerinidae (foraminíferos bentônicos) em testemunhos coletados no talude continental da Bacia de Pelotas ao longo do Quaternário tardio.

2.3.2. Objetivos Específicos

- Avaliar a abundância relativa e riqueza de uvigerinídeos ao longo dos testemunhos e discutir mudanças em sua distribuição ao longo dos últimos 112 ka BP¹;
- Relacionar descritores métricos das testas (tamanho, alongamento e volume) com variações nas condições ecológicas e oceanográficas ao longo dos testemunhos;
- Identificar períodos de maior enriquecimento orgânico dos sedimentos e redução das condições de oxigenação a partir da determinação da abundância e biomassa de uvigerinídeos.

¹ A sigla Ka BP significa “Kilo annum/thousand years before present”. É usada para especificar eventos que ocorreram antes da origem prática da datação por radiocarbono na década de 1950. BP refere-se também ao período em que testes com armas nucleares interferiram na composição isotópica do carbono na atmosfera.

BIOMETRIC AND BIOMASS ANALYSIS OF QUATERNARY UVIGERINIDAE
(FORAMINIFERA) FROM SOUTHERN BRAZILIAN CONTINENTAL SLOPE

Este capítulo apresenta o conteúdo do artigo que compõe esta dissertação e foi submetido à revista *Marine micropaleontology* em 14 de junho de 2020

3. Biometric and biomass analysis of Quaternary Uvigerinidae (Foraminifera) from Southern Brazilian continental slope

Beatriz Fernandes de Barros Bomfim Santana^{1,2*}, Thaise R. Freitas³, Juliana Leonel² and Carla Bonetti^{2*}

1 Postgraduate Program in Oceanography, Center of Physical, Mathematics and Oceanography Sciences, Federal University of Santa Catarina, CEP: 88040-000, Florianópolis, Santa Catarina, Brazil. E-mail address: beatriz_fbbs@yahoo.com.br

2 Coastal Oceanography Laboratory (LOC), Federal University of Santa Catarina, CEP 88061-600, Florianópolis, Santa Catarina, Brazil. Email address: carla.bonetti@ufsc.br

3 Department of Geosciences, University of Oslo, P.O. Box 1047 Blindern, 0316 Oslo, Norway
Email address: thaisericoardo.freitas@gmail.com

* Corresponding author: Carla Bonetti. Email address: carla.bonetti@ufsc.br

Highlights

- Higher relative abundance of Uvigerinids and smaller test size characterize a warmer period between MIS 5 and MIS 3
- *Trifarina angulosa* higher dominance is linked to periods of NADW stronger influence; near-bottom currents strengthen and lower marine productivity
- Richness of Uvigerinidae family increases as Circumpolar Deep-Water advances northward during MIS 2, highlighting the occurrence of *Uvigerina peregrina* and *Uvigerina mediterranea*
- Accumulated biomass peaked during last glacial stage with major contribution of *Uvigerina hispidocostata* and *Uvigerina peregrina*

Abstract

Relative abundance, test size, elongation index, volume, and biomass variations of Uvigerinidae species were analyzed in 1921 tests from 42 samples of two cores recovered from continental slope of the Western South Atlantic. Variations in Uvigerinids distribution and their tests metrics are discussed based on main climatic and oceanographic changes through the last glacial cycle. Higher dominance of *Trifarina angulosa* during the interglacial stages suggests that this species is favored by a stronger influence of NADW - North Atlantic Deep Water (warm, nutrient-poor, and oxygen-rich water mass) and currents near-bottom. The increase in CDW - Circumpolar Deep Water (oxygen enriched and nutrient depleted water mass) influence during the glacial stage is related to higher uvigerinids richness, larger and less elongated tests, and increasing in the accumulated biomass. Moreover, the results obtained reveal the potential usefulness of these test metric, based on high taxonomic level (Family), to identify major changes in ocean circulation and carbon flows to the seafloor through time. A regression model was also formulated to convert test length to total test volume for Uvigerinidae, which can facilitate the data acquisition in future studies, expanding their use as paleoceanographical proxies.

Keywords: Southern Atlantic, Uvigerina, Paleoproductivity

3.1 Introduction

Climate oscillations during the late Quaternary had a powerful impact in oceanographic processes, such as nutrient cycling, carbon sequestration, oceanic circulation, marine productivity and oxygen availability (Sweetman et al., 2017; Violante, 2017; Kandiano et al., 2019). Changes in the marine productivity pulses and water column stability derived from climatic shifts have the potential to alter the amount and quality of the organic matter that reaches the seafloor, with consequences for the benthic food web, biodiversity and distribution patterns (Chiessi et al., 2015; Sweetman et al., 2017; Mazurkiewicz et al., 2020). In the Western South Atlantic region, changes in species composition, abundance, body size and other geochemical descriptors of deep-sea benthic foraminifera, as other marine communities, reflect these paleoceanographic shifts (Nagai et al., 2009; Almeida et al., 2015; Rodrigues et al., 2018; Ovsepyan et al., 2019). Moreover, microfossil populations of coccolithophorids, planktonic and benthic foraminiferids have been used to explain these environmental variations and trends in the southern Brazilian continental slope during the last 130 ka (MIS 5 to MIS 1) (eg. Leonhardt et al., 2013; Portilho-Ramos et al., 2014; Ferreira, et al., 2014; Almeida et al., 2015; Chiessi et al., 2015; Petró et al., 2016; Rodrigues et al., 2018; Petró et al., 2018; Petró and Burone, 2018; Schmitt et al., 2019)

Uvigerinidae is one of the most dominant deep-sea benthic foraminifera family found throughout the oceans. The genus *Uvigerina* has an elongate test, with triserial to biserial coiling in initial portion and uniserial in later growth stages, and a neck in terminal position of the aperture. Another important genus is *Trifarina*, that has an elongate, thin, and translucent test with a triangular shape. The key characteristics used to distinguish Uvigerinidae is the test size, the length/width ratio, the chamber arrangement and test shape (Schonfeld, 2006; Schweizer, 2006). The shape diversity in benthic foraminifera species is usually related to epifaunal or infaunal habit, habitat characteristics (Jorissen, 1999), water column and sediment depth and temperature (Boltovskoy and Wrigth, 1976; Corliss and Fois, 1990), as to light intensity and water motion (Hallock, 1979; Hohenegger, 2009). As test shape is influenced by environmental characteristics its phenotypic expression can evidence dominant factors in a given region (Healy-Williams and Williams, 1981).

The area/volume ratio of *Uvigerina peregrina* tests decreases in high dissolved oxygen concentrations and increases in lower concentrations (Keating-Bitonti and Payne, 2017), whereas high abundance, of *Uvigerina peregrina* alongside smaller body size (63-150µm) and biomass is a response to higher food availability (Nomaki et al., 2005). Most *Uvigerina* species preferentially occupy shallow infaunal niches (Corliss and Emerson, 1990; Morigi et al., 2001; Licari et al., 2003), which are the best microhabitats conditions for *Uvigerina mediterranea* and *Uvigerina peregrina* reproduction due to a seasonal phytodetritus enrichment. (Fontanier et al., 2006). However, they can migrate downward through the sediment layers, searching for more favorable ecological conditions. (Loubere et al., 1995; Schmiedl et al., 2000, Geslin et al., 2004). The intermittent organic matter flux to the ocean floor favors opportunistic Uvigerinids reproductive strategy (Koho et al., 2008; Schmiedl et al., 2010; Enge et al., 2014).

Understanding ecological and temporal patterns of Uvigerinidae is, therefore, essential for organic carbon flux estimation and paleoproductivity reconstructions, as well as changes in paleobathymetry and circulation patterns (Van Der Zwaan et al., 1999; Gooday and Hughes, 2002; Gooday, 2003; Geslin et al., 2004; Hess and Kuhnt, 2005; Das Manisha et al., 2018). Besides their paleoecological applications, the Uvigerinids, mainly *Uvigerina peregrina*, provide a good record of ocean geochemical properties (e.g. stable oxygen and carbon isotopes), by building their tests in isotope equilibrium with seawater (Fontanier et al., 2006; Schonfeld,

2006), which linked to population dynamics and biometric analysis have been used to understand the variability of bottom water masses and paleoproductivity oscillations along the Late Holocene in southeast Brazilian coast (Dias et al., 2013).

Foraminiferal biomass and biometric features have been the subject of many scientific studies for several decades. These metrics are strongly dictated by changes in temperature (Schmidt et al., 2003; Keating-Bitonti and Payne, 2016), organic carbon flux to the sea floor (Caralp, 1989; Korsun et al., 1998; Bhaumik et al., 2014) and oxygen availability (Gerlach et al., 1985; Hannah et al., 1994; Kaiho, 1999; Kaiho et al., 2006; Geslin et al., 2011). In addition, size strongly influence whether calcification will increase or decrease with acidification in marine carbonate systems, therefore, this metric plays a critical role in predicting foraminiferal response to future climatic changes (Corliss, 1979; Henehan et al., 2017). Based on these general evidences, the purpose of this study is to evaluate abundance, size (length, width, depth), and biomass variations of Uvigerinidae species along two sediment cores retrieved from Pelotas basin continental slope. The data and knowledge gained from this study will contribute to a better understanding of Uvigerinidae size-dependent response to climatic and oceanographic changes through Late Quaternary in the Western South Atlantic region.

3.2 Study Area

3.2.1 Geological and oceanographic settings

The Pelotas Basin is located between 28°30'S to 34°S, bound by the Florianópolis High in the north and the Polônio High in the south, and reaches up to 2000 meters depth (Morales et al., 2017). Sediment cores have been retrieved from the northern sector of the basin (Figure 1), that is characterized by a low-gradient continental shelf (shelf break ~ 180 m). Muddy and sandy-bioclastic sediments characterize the transitional facies between the outer shelf and upper slope (Rocha et al., 1975). The surface sediments types (fine sand to very fine silt) in the region are composed by siliciclastic sediments and authigenic phosphorites from diverse sources (Mahiques et al., 2019).

Tropical Water (TW) and South Atlantic Central Water (SACW) presently influence the Southwestern Atlantic in the upper layer. The deeper water column layer is influenced by the Antarctic Intermediate Water (AAIW), Upper Circumpolar Deep Water (UCDW), North Atlantic Deep Water (NADW), Lower Circumpolar Deep Water (LCDW) and Antarctic Bottom Water (AABW) (Campos et al., 1995; Stramma and England, 1999). The AABW is cold, rich in nutrients and poor in oxygen concentration and the NADW is warm, rich in oxygen and poor in dissolved nutrients. UCDW and LCDW are described with low oxygen concentration and salinity and high dissolved nutrients (Stramma and England, 1999). The warm Brazilian current (BC) and the cold Malvinas Current (MC) contour the South America continental margin in opposite directions. The encounter of these currents forms the Brazil-Malvinas Confluence region (also known as South Atlantic Convergence Zone), which moves from 30° to 46°S due climatic seasonal variations and local winds stress (Wainer et al., 2000). The major drivers of the ocean productivity in the area are related to this convergence zone, as well as La Plata Plume and continental shelf upwelling (Gonzalez-Silveira et al., 2006).

Major changes in ocean circulation during the Quaternary are associated with glacial - interglacial cycles, as consequence of relative sea level fluctuations and disturbances in the strength of the Atlantic Meridional Overturning Circulation (Rüthemann et al., 1999). During the last deglaciation, periods of decreased strength of the AMOC are associated with warmer

sea surface temperatures in the South Atlantic. During the Last Glacial Maximum, an increase ocean productivity is directly linked to a higher input of terrigenous sediments and the BC offshore displacement in the Brazilian upper continental margin (24° - 25°S) (Nagai et al., 2010), whereas a high surface productivity in Santos Basin during glacial periods is related to La Plata River plume, alongside a shelf-break upwelling and higher flux of eolian dust (Almeida et al., 2015). For the same region, the influence of oceanographic physical parameters, for example, periods of enhanced SE trade winds, may have caused peaks of low sea surface temperature (SST) around 70, 50-45 and 20 Ka BP (Petró et al., 2016).

SIS 188 and SIS 249 cores location in the Southwest Atlantic Ocean

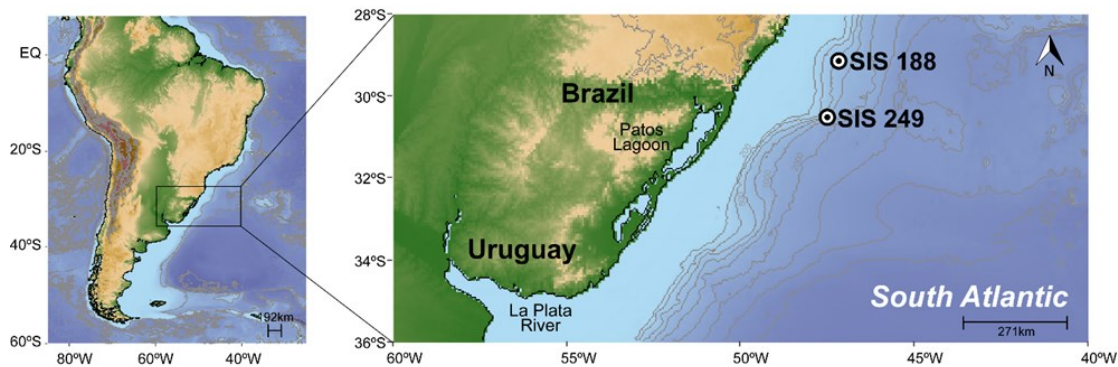


Figure 1. Map showing location of sediment core and bathymetry of the study area

3.5 Materials and Methods

Samples were selected from two piston cores, SIS 188 (29°13'16.266"SS, 47°17'1.761"W; 1.514 m depth, 3.65 m long) and SIS 249 (30°5'6.39"SS, 47°5'35, 63"W; 2.091 m depth, 1.94 m long), retrieved at Pelotas Basin slope by Fugro Brasil. The samples were collected in 10 cm intervals, 1 cm slice and started at 21 cm from the top of SIS 188, and at 50 cm from the top of SIS 249. Both cores have similar sedimentological characteristics: relative proportion of detrital mud ranged from 71.2 % to 94.4% and carbonate content between 10.1% and 38.1% (Petró, 2018).

3.3.1 Stable Isotopes, Age model and Geochemical data

The age models used in this research were proposed and/or described previously by Petró, (2018); Rodrigues, (2018) and Duque-Castaño et al. (2019). They are based on the foraminifera oxygen isotope curve (Lisiecki and Stern, 2016) using AMS 14C on foraminifera as control points. The analyses were performed at Radiocarbon Laboratory of the Universidade Federal Fluminense (UFF) and Stable Isotope Laboratory of the University of California, Santa Cruz (SIL-UCSC). Isotope data are reported relative to the Vienna Pee-Dee Belemnite (V-PDB) standard. The detrital mud content was determined by laser diffraction particle size analyzer after the extraction of carbonate. The carbonate content was determined by the weight loss after a reaction with hydrochloric acid (HCL) 10%. More information about the analytical processing and results can be found in Petró, (2018), Rodrigues et al. (2018) and Lopes et al. (*submitted*).

3.3.2 Microfossil Processing

For this study, benthic foraminifera were picked from 16 samples of SIS 249 and 26 samples of SIS 188. A minimum of 300 individuals were counted from the sand fraction ($> 63\mu\text{m}$) of each sampling interval. All Uvigerinids specimens (1921 tests) from the cores were analyzed. Details about sample processing for analysis of total benthic foraminifera assemblage composition is described in Schmitt et al. (2019). For taxonomic classification Loeblich and Tappan, (1988); Bornmalm, (1996); Schonfeld, (2006); Schweizer, (2006); Milker and Schmiedl, (2012); Aturamu, (2016) and WoRMS (2020) – World Register of Marine Species were used as references.

3.3.3 Morphometric Analysis and Biomass estimative

The uvigerinidae photomicrographs were acquired using the stereomicroscope Zeiss Axio Zoom V16 (max magnification - 644x) with the AxioVision software support. The program allows the capture of a series of images with defined focus range while providing the distance between this range measured by the microscope (the z-axis). This measurement allows the thickness degree calculation and infer some metabolic responses to oxygen stress. Also, an elongation index (width/depth) proposed by Blott and Pye, (2008) was used for analyze growth patterns and its relation with abiotic changes through time.

Although foraminiferal assemblages provide reliable data for statistical analysis with small sample volumes (Mojathid et al., 2008), the acquisition of statistically significant body size data is time consuming. Thus, efforts to assess these metrics in a faster, accurate and reproducible way has been a long-standing goal (Briguglio et al., 2013). With the objective to retrieve uvigerinidae tests size and biomass measurements, this study uses the open source R package *forImage* (v0.1.0, Freitas, 2019) developed specifically for the study of foraminifera. This package allows the measurement of test outline, giving values of area, major and minor axis distance (length and width), and retrieves the z-axis (depth) distance measured by the microscope. The first module of this package corresponds to the image analysis and individual measurement, through the *measure* function. The second module consists of volumetric calculations and biomass estimative through the functions: *volume.total*, *bio.volume* and *biomass*. The geometric model selected to calculate uvigerinidae test was *cone + half ellipsoid* (Figure 2). The available geometric models in the package are associated with the shape of several foraminifera genus. Considering that foraminiferal tests are not entirely occupied by protoplasm (Gerlach et al., 1985 ; Altenbach, 1987; Hannah et al., 1994; Geslin et al., 2011), in this study, the average value of 70.57% of cell occupancy ($n = 95$ of *Angulogerina*, see Freitas, 2019) was used to estimate the biovolume. The biovolume was converted to cell carbon content (biomass, expressed in $\mu\text{gC}_{\text{org. ind}}^{-1}$) using the cell density of $0.089 \text{ pgC}_{\text{org.}} \mu\text{m}^{-3}$ proposed by Michaels et al., (1995) as carbon conversion factor.

A polynomial regression analysis for all tests smaller than $500 \mu\text{m}$ ($n = 1863$), was performed to investigate the relationship between test length and volume. This statistical technique consisted of creating a “best fit” line through of the available data points, using a least square method to define parameters estimates. The accuracy of the model was evaluated using the following statistical indicators: Test F; normality residuals’ distribution and root-mean-square error – RMSE. Relationships among biometric measures and geochemical descriptors were tested using Spearman's rank correlation coefficient (r_s) and assuming as significant correlation p values < 0.05 . The Mann Kendall Trendal Test was used to identify a possible

tendency in the samples. The data were analyzed using PAST software version 3.25 (Hammer et al., 2001) .

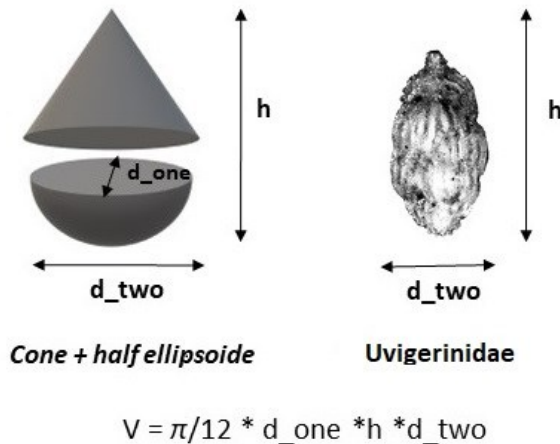


Figure 2. Geometric model applied to estimate the volume of the tests. Abbreviations: d_one = depth, d_two = width, h = length

3.4 Results

3.4.1 Richness and Abundance of Uvigerinidae family

Uvigerinidae is second only to by Cassidulinidae as the most abundant family in the sediment cores. The relative abundance of uvigerinids in core SIS 188 varies between 5.6 % (20.9 ka BP) and 31.6 % (27.8 ka BP), with average of the 17.6%. For core SIS 249, the highest value (30.3 %) is registered in its base (112.5 ka BP) and the lowest (9.3 %), at 59.04 ka BP, with an average of 15.3 % (Figure 3). A total number of six uvigerinids species were identified in the study area. *Trifarina angulosa*, *Uvigerina auberiana*, *Uvigerina mediterranea*, *Uvigerina peregrina*, *Uvigerina hispidocostata* and *Uvigerina dirupta* in SIS 188, only *Uvigerina dirupta* did not occurred in the SIS 249 core (Figure 3). Although the number of species fluctuates throughout the cores, there is an increasing trend towards the top of the core SIS 188, with more frequent higher richness values between 26.1 and 7.2 ka BP. The assemblage in both cores is dominated by *Trifarina angulosa*. It represents more than 60% of all uvigerinids from SIS 249 (exception to 84.1 ka BP sample) and from SIS 188 samples before 20 ka BP. Abundance of *Uvigerina mediterranea*, *Uvigerina peregrina* and *Uvigerina hispidocostata* increases towards the top of SIS 188 core while the dominance of *Trifarina angulosa* decreases. Relative abundance of all uvigerinids are presented in Appendix 1. (Table A1).

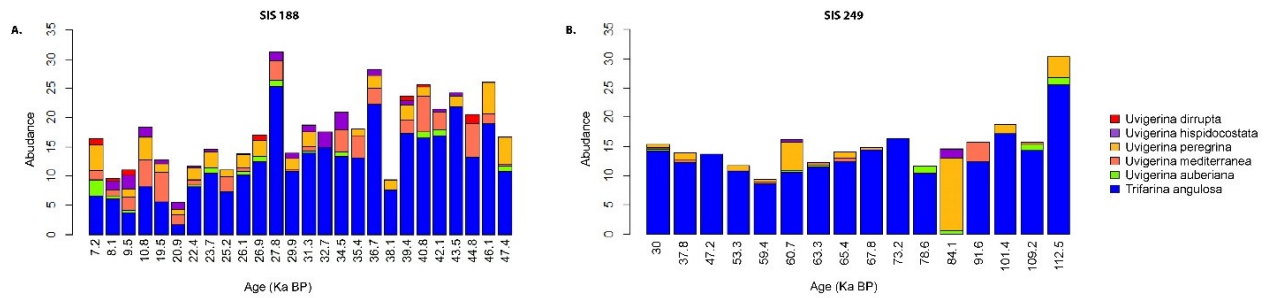


Figure 3: Relative abundance of the family Uvigerinidae expressed as a percentage of the total number of individuals in each sample, considering all taxa also richness and relative abundance of each uvigerinid species (as a percentage of the total individuals of the family Uvigerinidae) in the cores (a) SIS 188 and (b) SIS 249.

3.4.2 Morphometric Analysis

A total of 1247 individuals from SIS 188 and 674 from SIS 249 were measured and analyzed (Appendix 1 - Table A2; Appendix A2 – Figure A1). The specimens test length, width, depth and elongation index were analyzed to assess its response to environmental changes through time. Samples from the SIS 188 were generally marked by a wider range of test sizes (individuals larger than 500 μm represent less than 5% of the uvigerinids in this core), while samples from SIS 249 have a more restricted variability (tests larger than 500 μm were not found in this core). Although size heterogeneity throughout the cores, it is possible to identify an increasing trend in the importance of the larger tests upwards (MIS 3 to MIS 1) in core SIS 188 (Mann Kendall Test: $S = -143$, p value = 0.002) and from MIS 3 to MIS 5 (towards the base of the core) in core SIS 249 (Mann Kendall Test: $S = 58$, p value = 0.01).

Variations in the morphological features of the uvigerinids were also analyzed according to the tests' elongation index, based on width/length ratios (Appendix 2 – Figure A2). Adopting the nominal classification proposed by Blott and Pye (2008) for sedimentary particles, 45% of the tests from SIS 188 belong to the “*not elongate*” class (ratio values between 0.8 and 1.0) and 39% were classified as “*slightly elongate*” (values between 0.6 and 0.8). For core SIS 249, 40% of the tests were classified as “*slightly elongate*”, while the remaining were considerate “*moderately elongate*” (28% with values 0.4 to 0.6) and “*not elongate*” classes (29% with values 0.8 to 1.0). It is possible to identify a decreasing trend (MIS 3 to MIS 1) in the elongation values for SIS 188 ($S = 141$; $p = 0.002$; Figure 4), meaning that the tests are slightly more elongated during MIS 1. No statistically significant trend is observed for core SIS 249 ($S = -40$; $p = 0.078$; Figure 4)

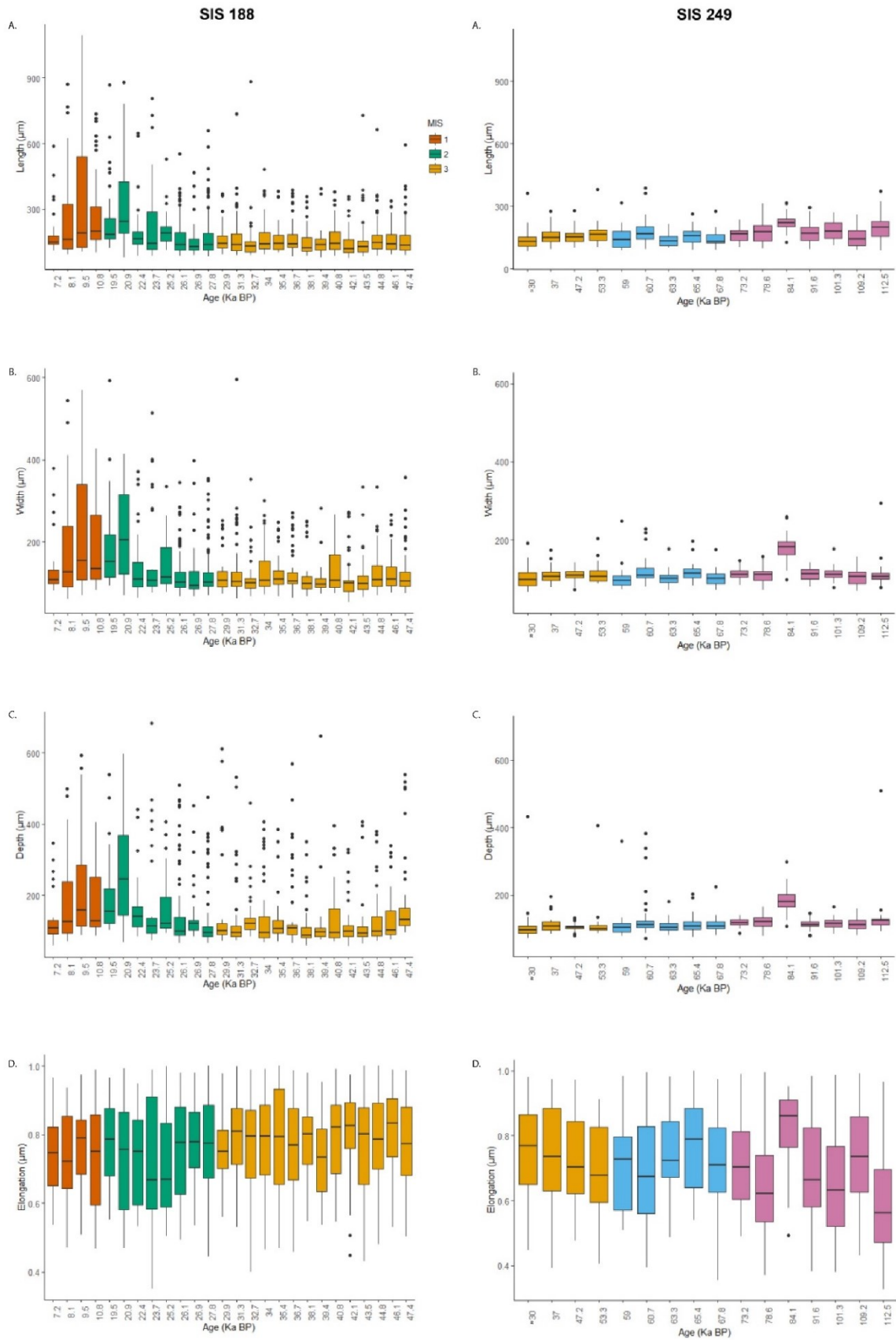


Figure 4. Box plot showing the measures of variability (quartile method) for the biometrics descriptors (a) length, (b) width, (c) depth and (d) elongation index in the cores SIS 188 and SIS 249.

3.4.3 Volume, Biovolume and Biomass estimative

The measured length, width and depth of each specimen were used to calculate the test volume based on the geometric model that best resemble the Uvigerinidae test. Test volumes range from $7.64E+04$ to $9.50E+07 \mu\text{m}^3$ (median $4.68E+05 \mu\text{m}^3$) in core SIS 188 and from $1.11E+05$ to $1.41E+07$ (median $6.25E+05 \mu\text{m}^3$) in core SIS 249.

The relationship between test length (μm) and volume (μm^3) is plotted in Figure A3 (Appendix 2). The measures of length explain 89% of the volume variance. Polynomial regression (2 degree) presented in Equation 1 provides the best approximation of the relationship between test length and volume (F: 7642.5; p value < 0.05),

$$\text{Volume } (\mu\text{m}^3) = 112.09 * (\text{length})^2 - 22462 * (\text{length}) + 1.3E10^6$$

The root mean squared error (RMSE), used as a measure of the differences between predicted values and observed values (i.e., size of the errors of estimative) is $8.10E5105 \mu\text{m}^3$. This equation has general applicability for Uvigerinidae family test volume from the measurement of a single linear dimension (i.e. test length), which implies less analytical effort.

Assuming that cell occupancy corresponds to 70.57 % of the total test volume in uvigerinids (see Freitas, 2019), biovolumes in this study range between $5.39E+04$ and $6.70E+07 \mu\text{m}^3$ with median of $3.30E+05 \mu\text{m}^3$ in SIS 188 and from $7.80E+04$ to $9.93E+06 \mu\text{m}^3$ with median of $4.41E+05 \mu\text{m}^3$ in SIS 249. Biovolume results were converted into carbon biomass, adopting $0.089 \text{ pg C}_{\text{org}} \mu\text{m}^{-3}$ as cell density (Michaels et al., 1995). Accumulated biomass represents the sum of all individual biomass of each sample. The lower accumulated biomass values were measured in the core SIS 249, fluctuating from $0.8 \mu\text{g C}_{\text{org}}$ at 63.3 ka BP with a maximum of $4.1 \mu\text{g C}_{\text{org}}$ at 78.7 ka BP and lower variability throughout the core (median $1.4 \mu\text{g C}_{\text{org}}$). In contrast, SIS 188 values ranged from $1.9 \mu\text{g C}_{\text{org}}$ (39.4 ka BP) to $55.3 \mu\text{g C}_{\text{org}}$ (20.9 ka BP), with median of $5.5 \mu\text{g C}_{\text{org}}$. It is worth mentioning the marked biomass increase towards the core top (Mann Kendall Test: S = -150, p value = 0.001). During the end of the MIS 2 and beginning of the MIS 1 the accumulated biomass values are predominantly above $10 \mu\text{g C}_{\text{org}}$ (Figure 5).

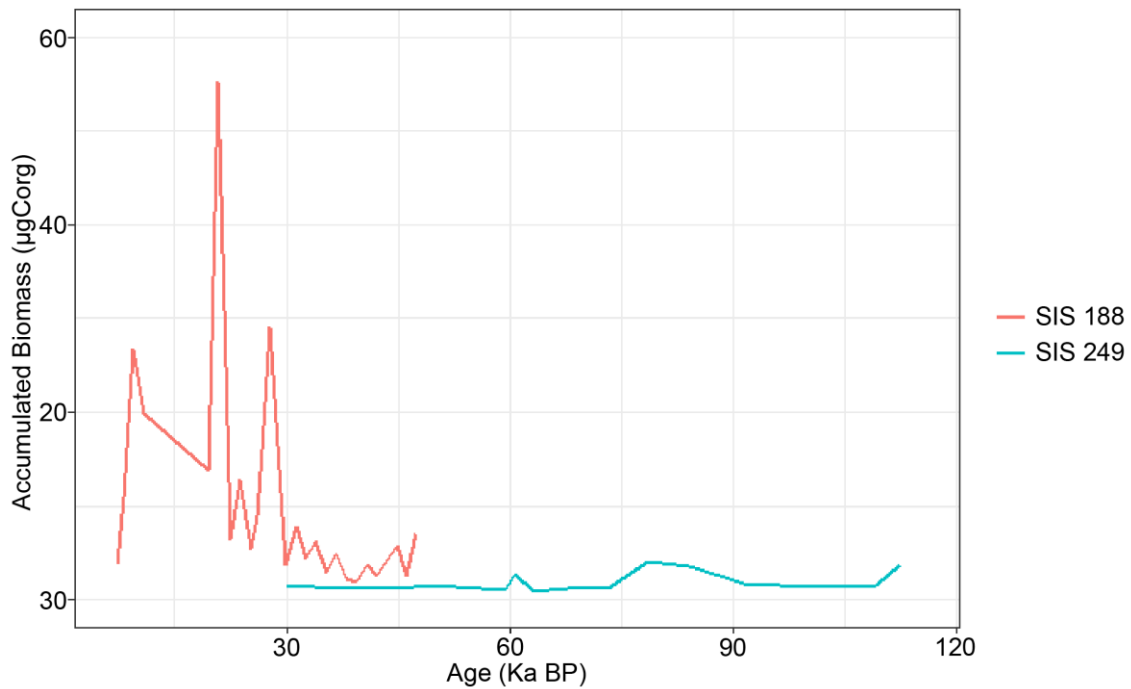


Figure 5: Variability in the total biomass of uvigerinids along the time in the cores SIS 188 and SIS 249

Although SIS 188 has the highest uvigerinids accumulated biomass and relative abundance values, no relationship was observed between these two descriptors (Figure 6). In other words, the samples with the highest percentage of the Uvigerinidae family were not necessarily those with the highest biomass of these taxa. For example, the samples at 20.9 ka BP and 9.5 ka BP in SIS 188, have the highest biomass values ($> 20 \mu\text{g C}_{\text{org}}$) and the lowest relative abundance values ($< 15\%$). On the contrary, a sample from the base of SIS 249 (112.5 ka BP) has relative abundance $> 30\%$ and biomass $< 5 \mu\text{g C}_{\text{org}}$.

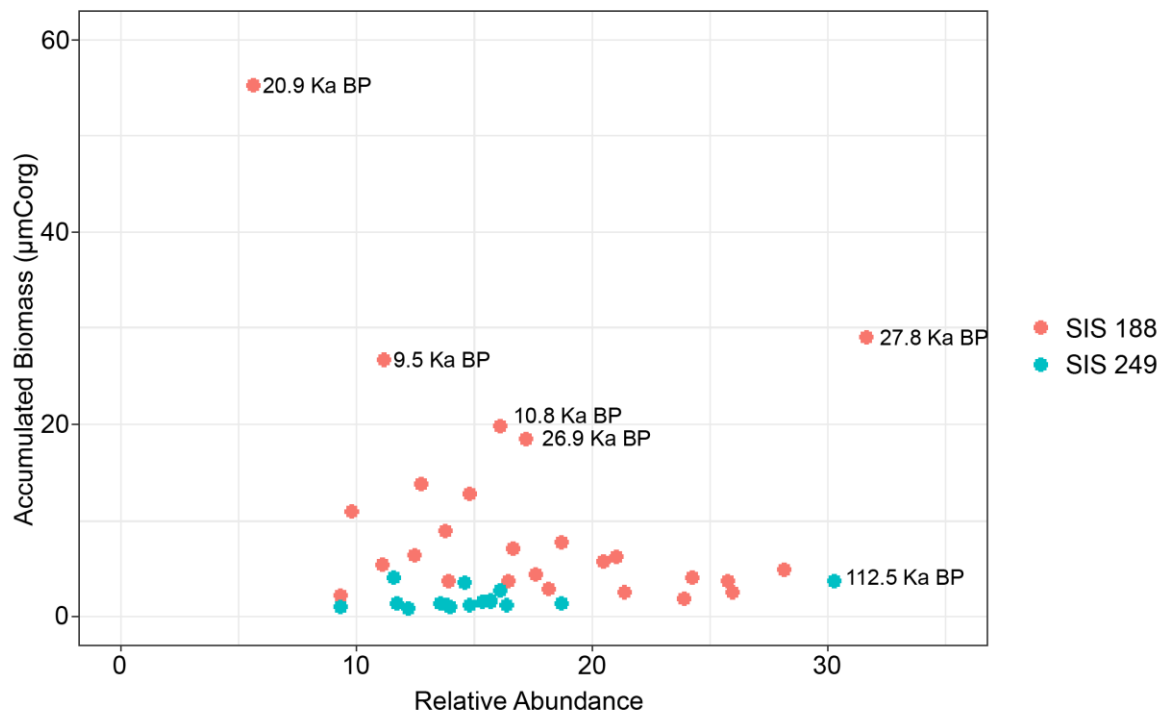


Figure 6. Relationship between accumulated biomass and relative abundance of *Uvigerinidae* in the cores SIS 188 and SIS 249.

3.4.4 Analyses of Correlation

A correlation analysis between biological and geochemical variables was carried out to assess the environmental relationship with the observed morphometric and biomass patterns. The results of the Spearman correlation analysis are presented in Table A3 (Appendix 1). Among the variables analyzed, only carbonate biotrititic content (%), stable carbon ($\delta^{13}\text{C}_{\text{Uvig}}$ - ‰) and oxygen ($\delta^{18}\text{O}_{\text{Uvig}}$ - ‰) isotopic composition of *Uvigerina* presented a significant correlation (p value < 0,05) with *Uvigerinids* biometric descriptors. Carbonate content is negatively correlated with relative abundance of *Uvigerinids* ($r_s = -0.45$, $p = 0.013$) and positively with test length ($r_s = 0.48$, $p = 0.007$). The $\delta^{13}\text{C}_{\text{Uvig}}$ is inversely correlated with *uvigerinids* abundance ($r_s = -0.32$, $p = 0.040$) and elongation index ($r_s = -0.47$, $p = 0.002$). The $\delta^{18}\text{O}_{\text{Uvig}}$ is positively correlated with the elongation index, ($r_s = 0.57$). The $\delta^{18}\text{O}_{\text{Uvig}}$ is the only variable correlated to the accumulated biomass ($r_s = 0.36$). The higher ratio values in MIS 2 and MIS 1 coincides with the biomass peaks observed in SIS 188.

3.5 Discussion

3.5.1 Uvigerinidae species distribution as paleoceanographic indicators

According to the adopted age models, the cores embrace interglacial and glacial periods through the Marine Isotopic Stages MIS 5 to MIS 1. During most of these periods, Uvigerinidae plays a significant role in the total benthic foraminifera assemblage, second only to Cassidulinidae (particularly *Globocassidulina subglobosa*) in abundance on both cores. Most species of the Uvigerinidae family are considered part of the infauna. They are adapted to organic matter-rich environments, with high bacterial concentration, and capable of living in low oxygenated areas (Schweizer et al., 2005; Schonfeld, 2006; Das et al., 2018). These characteristics are also described for some Cassidulinidae species (Murray, 2006; Ovsepyan et al., 2019). The high abundances of these families, associated to other ecological proxies derived from foraminifera studies, point to the dominance of eutrophic conditions in the study area, as previously discussed by Rodrigues et al. (2018) and Schmitt et al. (2019).

Most of the biological descriptors analyzed in this study responded to changes in oceanic circulation and carbon flux fluctuations during the interval from MIS 5 to MIS 1. The decrease in the relative abundance of uvigerinids (mainly in *Trifarina angulosa*) upward cores is probably related to general trend towards climate cooling from MIS 5 to MIS 2 (Petró, 2018; Schmitt et al., 2019). During this time interval, changes in nutrient input caused an increase in superficial waters primary productivity, which had its peak during the MIS 2 (Schmitt et al., 2019). These trophic conditions favored the development of epifaunal populations (*Alabaminella weddellensis* and *Epistominella exigua*) and consequently reduced the relative importance of infaunal species like uvigerinids in the study area.

Within the Uvigerinidae family, *Trifarina angulosa* is the dominant species in all samples, except at 84.1 ka BP (SIS 249). Its dominance may suggest that this site is impacted by strong currents, which is consistent with the absence of arborescent foraminifera (*Rhadamina* and *Rhizammina*) observed in the samples. This finding is also commented by Yamashita et al. (2016) for the deeper stations of the São Paulo Bight. According to Morigi et al. (2012) physical parameters, especially currents, can benefit oligotypical associations dominated by resistant species like *Cibicides lobatulus*, *Cibicides refulgens* and *Trifarina angulosa*. Beyond higher energy environments, *Trifarina angulosa* is capable to live in cold waters and oxic to suboxic conditions (Das et al., 2018). The decrease in the relative abundance of this species towards the Holocene, simultaneously with the increase in the richness of uvigerinids, notably the larger participation of *Uvigerina peregrina* and *Uvigerina mediterranea*, suggest marked changes in paleoceanographic conditions.

Some studies have showed differences within Uvigerinidae ecological niches, bathymetric distribution, food and substrate preferences, even though this family is generally associated to high surface productivity, dysoxic bottom waters and organic carbon rich sediments. (Fontanier et al., 2003; Geslin et al., 2004; Schweizer et al., 2005; Das et al., 2018). *Uvigerina peregrina*, an important species in this study, is found in regions of high and sustained flux of organic matter. It seems to feed on more degraded organic matter than *Uvigerina mediterranea*, which occupies more superficial niches in the sediment probably due to its preference for fresh labile organic matter (De Rijk et al., 2000; Schmiedl et al., 2000; Geslin et al., 2004). *Uvigerina hispidocostata* is associated to high and continuous food supply, with low seasonality (Jayaraju et al., 2010). *Uvigerina dirupta* and *Uvigerina auberiana* represent environments with low oxygen concentrations (Wilson and Costelloe, 2011; Machain-Castillo et al., 2019). Therefore,

the increase in richness and abundance of other Uvigerinidae species, besides *Trifarina angulosa*, towards the SIS 188 core top, mainly during 20.9 to 7.2 ka BP suggest higher and continuous organic flux during glacial periods, as well as dysoxic conditions.

3.5.1 Biometric variations of Uvigerinidae test

Studies of foraminiferal size using two (length and width) or three dimensions (plus depth) allow to evaluate morphological ratios, volume and biomass variations and have shown to be useful as metrics for understanding paleoceanographic changes and biodiversity dynamic in multi-timescale patterns (Keating-Bitonti and Payne, 2016; Hsiang et al., 2016). The higher variability in tests size observed in SIS 188 samples from MIS 2 to MIS1, simultaneously to a richness increase, which may suggest reproductive and life strategies diversification in order to explore the increase in food supply during glacial stages, as inferred from coccolithophorids record (Leonhardt et al., 2013). Molina (2019) also observed differences in *Uvigerina peregrina* volume and size with respect to changes in food availability. *Uvigerina mediterranea* and *Uvigerina peregrina* optimum growth under eutrophic conditions is also reported by Schumacher et al. (2010). On the contrary, the lower food available from MIS 5 to MIS 3 (SIS 249) can be associated to occurrence of smaller tests and high dominance of *T. angulosa*.

The higher ocean surface fertility during the last glacial stage is associated with carbonate deposition and larger uvigerinids tests, but contrasts with the decrease in uvigerinids relative abundance. This result may reflect changes in the foraminifer's species assemblages due to abrupt oceanographic changes, that occurred in this period, as discussed by Schmitt et al. (2019).

Although in stressful environments foraminifera size tend to decrease as a reproductive strategy or an attempt to decrease metabolic demand, not all species display the same patterns of morphological variations due to environment shifts. For example, *Bolivina spissa* from Santa Monica Basin shows no test volume response to a decrease in dissolved oxygen concentrations, while the test volume of *Uvigerina peregrina* increases (Keating-Bitonti and Payne, 2017). Moreover, it is important to consider that the size distribution observed can be also influenced by the high dominance of one species (*Trifarina angulosa*). Which explains the size distribution regularity, and uniform elongation values through core SIS 249 (with no significant trends), whereas the significant size shift in SIS 188 increases alongside the number of species.

The lowest elongation index mean value was observed for *Uvigerina hispidocostata* tests (0.6), while lowest sample values (all tests combined) were found between MIS 5 to MIS 3, an interval characterized by *Trifarina angulosa* dominance. Higher elongation values (0.8) are associated to lower values of $\delta^{13}\text{C}_{\text{Uvig}}$ (negative correlation) and higher $\delta^{18}\text{O}_{\text{Uvig}}$ (positively correlated), suggesting that under stronger influence of CDW (cold, nutrient and $\delta^{18}\text{O}$ -enriched, and $\delta^{13}\text{C}$ depleted water mass) predominate Uvigerinids with rounded tests. Schweizer et al., (2005) and Schonfeld (2006) have already considered the width:length ratio (here called as elongation index) as a significant morphological criteria in discriminating *Uvigerina* morphotypes. Nevertheless, the interpretation based on isotope measurements should be used with caution considering the factors influencing stable isotope composition of deep-sea benthic foraminifera. The isotope variability observed within and between cores can be a result of vital effects, changes in organic carbon sources contributing to the pore water carbon reservoir, ontogenetic variations, among others (Loubere, 1995; Theodor et al., 2016).

In summary, the larger size, volume and less equant uvigerinids tests observed upwards in core SIS 188 (MIS 3 to MIS 1) may be interpreted as a morphometric proxy of more favorable conditions, as well as a consequence of the partial replacement of the population of *Trifarina* by *Uvigerina*.

3.5.3 Biomass measures and changes through the time

Nomaki et al. (2015) discuss alternatives to individual foraminifera biomass calculations, among them, the test volume is mentioned either by morphometrically measuring the test external surface (using photomicrographs acquired by stereomicroscopies or SEM - Scanning Electron Microscope) or by mapping the inner volume with a micro-X-ray Computed Tomography (micro-CT). The first alternative, associated with the approximation of the test shape to a three-dimensional geometric model, proved to be efficient to identify variations in the behavior of the accumulated biomass through glacial and interglacial periods. The test length use for calculating volume and consequently infer biomass in *Uvigerina* species is also reported by Molina (2019).

The uvigerinids biomass peaked during MIS 2, dominated by the large-sized *Uvigerina hispidocostata* and *Uvigerina peregrina*. The data suggested that these benthic species increase following phytoplankton blooms during the glacial periods. Nevertheless, Uvigerinidae population density does not follow this pattern. The higher numbers of uvigerinids per sample were found during warmer periods (MIS 5 to MIS 3), when the accumulated biomass was lower due to the dominance of small-sized individuals of *Trifarina angulosa*. Inverse pattern between biovolume and abundance was also observed by Lesen, (2005) studying seasonal distribution of *Fursenkoina pontoni* in South San Francisco Bay.

Besides the abrupt increasing in the Uvigerinidae biomass observed in the present study during the MIS 2, changes in the composition of the foraminiferal assemblages (higher abundance of family Cibicididae) and an increasing trend in the importance of epifaunal species towards the colder periods were observed by Schmitt et al. (2019) and Rodrigues et al. (2018) for the same cores. These authors attributed these foraminiferal behaviors as responses to the increase in the volume of Circumpolar Deep Water flowing through the study area. Peterson and Lohman, (1982) also associated *Uvigerina peregrina* with the two branches of CDW in cores recovered from Rio Grande Rise area and proposed that its records can be used as indicators of past changes in the advances/retreats of the NADW and CDW. The decrease in rich oxygen NADW influence from MIS 3 to MIS 2, allowing the oxygen-poor CDW advances to lower latitudes (Bickert and Wefer, 1996), has affected the nature and amount of food supply and oxygen concentration in the South Atlantic sea floor. Besides the presence of the nutrient rich CDW during the Last Glacial Maximum, others factors such as the increasing in the terrigenous input to continental slope due the lower sea level and strengthening of the SE winds transporting iron-rich dust, contributed to the increasing in the superficial marine productivity, higher influx of organic matter and dysoxia at the sea floor (Mahiques et al., 2007; Nagai et al., 2010; Leonhardt et al., 2013). All these features may have provided different food sources for the uvigerinids, increasing the biomass of these eutrophic species (De Rijk et al., 2000).

3.5 Conclusion

The higher abundance of Uvigerinidae family during all time interval covered by this research, point to the dominance of eutrophic conditions in the study area. Nevertheless, changes in the uvigerinids richness, species abundances, test size, and biomass through the two cores from Southern Atlantic continental slope suggest fluctuations in the deep-sea circulation and carbon flux during the last 112 ka, with major changes occurring in the glacial stage MIS 2.

The dominance of *Trifarina angulosa* and smaller tests are interpreted as indicators of stronger currents near-bottom and less food availability for deep-sea benthos, conditions which prevailed during interglacial stages. As the climate cooling began, at about 30 ka BP, changes in sea level and ocean circulation (retraction of NADW and advance of CDW northwards) promoted an increase in surficial primary productivity and consequent intensification of the carbon flow to the bottom. During this time, there was a simultaneous increase in uvigerinids richness and in tests size mean, with higher elongation index values and peaks of accumulated biomass. Thus, these features may be considered as indicators of more intense and sustained phytoplankton blooms. *Uvigerina peregrina* and *Uvigerina hispidocostata* are among the species that were favored by the organic enrichment and dysoxic conditions of the last glacial period.

It was demonstrated that volume measure, associated with the approximation of the test shape to a three-dimensional geometric model and the use of computational routines to automate the measurements and convert volume into biovolume and into biomass, allowed to identify variations in the behavior of the accumulated biomass through glacial and interglacial periods. To encourage other researchers to include foraminifera biomass as one more proxy in their studies, a length-to-volume conversion equation is also proposed, which allows satisfactory precision estimate. This alternative is aimed to researchers who do not have equipment available to measure tests depth and/or choose to reduce the time dedicated to the acquisition of these measures.

The results from the present study are important to show how Uvigerinidae responds to variations in the water masses and organic flux through time, acting, therefore, as proxies for ecological and environmental reconstructions. A greater understanding of the responses of important taxa based on size metric and biomass may enhance our ability to interpret micropaleontologic data and might enable us to refine the use of these proxies at higher taxonomic levels (for example, at family level as is the case of this study) for modelling paleoceanographic processes.

Acknowledgments

This study was financially supported by CAPES - Coordination for the Improvement of Higher Education Personnel (IODP-CAPES Program, process 88887.116800/2016-0). The research that originated this article is part of the first author's master's study developed in the Graduation Program in Oceanography/UFSC and supported by FAPESC scholarship (Research and Innovation Support Foundation of Santa Catarina State, process 23038.013359/2017-71). The authors also acknowledge the technical staff of the LCME - Central Electronic Microscopy Laboratory (Federal University of Santa Catarina)

References

- Almeida, F.K. De, Mello, R.M. De, Costa, K.B., Toledo, F.A.L., 2015. The response of deep-water benthic foraminiferal assemblages to changes in paleoproductivity during the Pleistocene (last 769 . 2 kyr), western South Atlantic Ocean. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 440, 201–212. <https://doi.org/10.1016/j.palaeo.2015.09.005>
- Altenbach, A. V., 1987. The measurement of organic carbon in foraminifera. *J. Foraminifer. Res.* 17, 106–109. <https://doi.org/10.2113/gsjfr.17.2.106>
- Aturamu, A., 2016. Taxonomic notes on some members of genus *uvigerina* from the deep offshore Eastern Niger delta Nigeria. *Br. J. Earth Sci. Res.* 4, 1–16.
- Bhaumik, A.K., Gupta, A.K., Clemens, S.C., Mazumder, R., 2014. Functional morphology of *Melonis barleeanum* and *Hoeglundina elegans*: A proxy for water-mass characteristics. *Curr. Sci.* 106, 1133–1140.
- Bickert, T., Wefer, G., 1996. Late Quaternary Deep Water Circulation in the South Atlantic : Reconstruction from Carbonate Dissolution and Benthic Stable Isotopes, in: Wefer, G., Berger, W.H., Siedler, G., Webber, D. (Eds.), *The South Atlantic: Present and Past Circulation*. Springer-Verlag Berlin Heidelberg, pp. 599–620. https://doi.org/10.1007/978-3-642-80353-6_30
- Blott, S.J., Pye, K., 2008. Particle shape: A review and new methods of characterization and classification. *Sedimentology* 55, 31–63. <https://doi.org/10.1111/j.1365-3091.2007.00892.x>
- Boltovskoy, E., Wright, R., 1976. Recent Foraminifera, Igarss 2014. <https://doi.org/10.1007/978-94-017-2860-7>
- Bornmalm, L., 1996. Taxonomy and paleoecology of late Neogene benthic foraminifera from the Caribbean Sea and eastern equatorial Pacific Ocean, Lethaia. <https://doi.org/10.1111/j.1502-3931.1996.tb01875.x>
- Briguglio, A., Hohenegger, J., Less, G., 2013. Paleobiological applications of three-dimensional biometry on larger benthic foraminifera: A new route of discoveries. *J. Foraminifer. Res.* 43, 72–87. <https://doi.org/10.2113/gsjfr.43.1.72>
- Burone, L., Helena, S., Mello, D., 2011. Benthic foraminiferal distribution on the southeastern Brazilian shelf and upper slope 159–179. <https://doi.org/10.1007/s00227-010-1549-7>
- Campos, E.J., Miller, J., Muller, T.J., Peterson, R.G., 1995. Physical Oceanography of the Southwest Atlantic Ocean. *Oceanography* 8, 87–91.
- Caralp, M.H., 1989. Size and morphology of the benthic foraminifer *Melonis barleeanum*: relationships with marine organic matter. *J. Foraminifer. Res.* 19, 235–245. <https://doi.org/10.2113/gsjfr.19.3.235>
- Chiessi, C.M., Mulitza, S., Mollenhauer, G., Silva, J.B., Groeneveld, J., Prange, M., 2015. Thermal evolution of the western South Atlantic and the adjacent continent during Termination 1. *Clim. Past* 11, 915–929. <https://doi.org/10.5194/cp-11-915-2015>
- Corliss, B.H., 1979. Size variation in the deep-sea benthonic foraminifer *Globocassidulina subglobosa* (Brady) in the Southeast Indian Ocean. *J. Foraminifer. Res.* 9, 50–60. <https://doi.org/10.2113/gsjfr.9.1.50>
- Corliss, B.H., Emerson, S., 1990. Distribution of rose bengal stained deep-sea benthic foraminifera from

- the Nova Scotian continental margin and Gulf of Maine. *Deep Sea Res. Part A, Oceanogr. Res. Pap.* 37, 381–400. [https://doi.org/10.1016/0198-0149\(90\)90015-N](https://doi.org/10.1016/0198-0149(90)90015-N)
- Corliss, B.H., Fois, E., 1990. Morphotype Analysis of Deep-Sea Benthic Foraminifera from the Northwest Gulf of Mexico. *Palaios* 5, 589. <https://doi.org/10.2307/3514864>
- Da Costa Portilho-Ramos, R., Barbosa, C.F., Rios-Netto, A.M., 2014. Planktonic Foraminiferal Variations in the Southwestern Atlantic Since the Last Glacial-Interglacial Cycle. *Palaios* 29, 38–44. <https://doi.org/10.2110/palo.2012.104>
- Das, M., Singh, R.K., Vats, N., Holbourn, A., Mishra, S., Farooq, S.H., Pandey, D.K., 2018. Changes in the distribution of Uvigerinidae species over the past 775 kyr: Implications for the paleoceanographic evolution of the Japan Sea. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 507, 201–213. <https://doi.org/10.1016/j.palaeo.2018.07.019>
- De Rijk, S., Jorissen, F.J., Rohling, E.J., Troelstra, S.R., 2000. Organic flux control on bathymetric zonation of Mediterranean benthic foraminifera. *Mar. Micropaleontol.* 40, 151–166. [https://doi.org/10.1016/S0377-8398\(00\)00037-2](https://doi.org/10.1016/S0377-8398(00)00037-2)
- Dias, B.B., Galliza, L., Barbosa, C.F., Luiza, A., 2013. Late Holocene Productivity In The Southeast Brazilian continental shelf. *Central European Geology*, vol.56, no 2-3, 2013, p.125+. Accessed 20 May 2020.
- Duque-Casntaño, M.L., Leonhardt, A., Pivel, M.A.G., 2019. Morphometric analysis in the shells of planktonic foraminifera *Orbulina universa*: a source for paleoceanographic information? *Brazilian J. Oceanogr.* 67, 1–17.
- Enge, A.J., Witte, U., Kucera, M., Heinz, P., 2014. Uptake of phytodetritus by benthic foraminifera under oxygen depletion at the Indian margin (Arabian Sea). *Biogeosciences* 11, 2017–2026. <https://doi.org/10.5194/bg-11-2017-2014>
- Ferreira, F., Frontalini, F., Leão, C.J., Leipnitz, I.I., 2014. Changes in the water column structure and paleoproductivity in the western South Atlantic Ocean since the middle Pleistocene: Evidence from benthic and planktonic foraminifera. *Quat. Int.* 352, 111e123-123. <https://doi.org/10.1016/j.quaint.2014.07.061>
- Fontanier, Christophe, Jorissen, F., Anschutz, P., Chaillou, G., 2006. Seasonal variability of benthic foraminiferal faunas at 1000 M depth in the Bay of Biscay. *J. Foraminifer. Res.* 36, 61–76. <https://doi.org/10.2113/36.1.61>
- Fontanier, C., Jorissen, F.J., Chaillou, G., David, C., Anschutz, P., Lafon, V., 2003. Seasonal and interannual variability of benthic foraminiferal faunas at 550 m depth in the Bay of Biscay 50, 457–494. [https://doi.org/10.1016/S0967-0637\(02\)00167-X](https://doi.org/10.1016/S0967-0637(02)00167-X)
- Fontanier, C, Mackensen, A., Jorissen, F.J., Anschutz, P., Licari, L., Griveaud, C., 2006. Stable oxygen and carbon isotopes of live benthic foraminifera from the Bay of Biscay : Microhabitat impact and seasonal variability 58, 159–183. <https://doi.org/10.1016/j.marmicro.2005.09.004>
- Freitas, T. R., 2019. Método automatizado para estimativa da biomassa de foraminíferos bentônicos. Dissertação (Mestrado em Oceanografia) – Universidade Federal de Santa Catarina, Florianópolis.
- Freitas, 2019. An R package for foraminiferal test measurement and biomass estimation. GitHub repository, <https://github.com/ThaiseRF/forImage>
- Gerlach, S., Hahn, A., Schrage, M., 1985. Size spectra of benthic biomass and metabolism. *Mar. Ecol. Prog. Ser.* 26, 161–173. <https://doi.org/10.3354/meps026161>
- Geslin, E., Heinz, P., Jorissen, F., Hemleben, C., 2004. Migratory responses of deep-sea benthic foraminifera to variable oxygen conditions: Laboratory investigations. *Mar. Micropaleontol.* 53, 227–243. <https://doi.org/10.1016/j.marmicro.2004.05.010>

- Geslin, E., Risgaard-Petersen, N., Lombard, F., Metzger, E., Langlet, D., Jorissen, F., 2011. Oxygen respiration rates of benthic foraminifera as measured with oxygen microsensors. *J. Exp. Mar. Bio. Ecol.* 396, 108–114. <https://doi.org/10.1016/j.jembe.2010.10.011>
- Gonzalez-Silvera, A., Santamaria-del-Angel, E., Millán-Núñez, R., 2006. Spatial and temporal variability of the Brazil-Malvinas Confluence and the La Plata Plume as seen by SeaWiFS and AVHRR imagery. *J. Geophys. Res. Ocean.* 111, 1–17. <https://doi.org/10.1029/2004JC002745>
- Gooday, I., 2003. Benthic Foraminifera (Protista) as Tools in Deep-water Palaeoceanography : Environmental Influences on Faunal Characteristics 46.
- Gooday, A.J., Hughes, J.A., 2002. Foraminifera associated with phytodetritus deposits at a bathyal site in the northern Rockall Trough (NE Atlantic): seasonal contrasts and a comparison of stained and dead assemblages 46.
- Hallock, P., 1979. Trends in test shape with depth in large, symbiont-bearing foraminifera. *J. Foraminifer. Res.* 9, 61–69. <https://doi.org/10.2113/gsjfr.9.1.61>
- Hammer, Ø., David, A.T.H., Paul, D.R., 2001. Past: Paleontological Statistics Software Package For Education And Data Analysis. *Palaeontol. Electron.* 4, 1352–1357.
- Hannah, F., Rogerson, A., Laybourn-Parry, J., 1994. Respiration rates and biovolumes of common benthic foraminifera (Protozoa). *J. Mar. Biol. Assoc. United Kingdom* 74, 301–312. <https://doi.org/10.1017/S0025315400039345>
- Healy-Williams, N., Williams, D.F., 1981. Fourier analysis of test shape of planktonic foraminifera. *Nature* 289, 485–487.
- Henehan, M.J., Evans, D., Shankle, M., Burke, J.E., Foster, G.L., Anagnostou, E., Chalk, T.B., Stewart, J.A., Alt, C.H.S., Durrant, J., Hull, P.M., 2017. Size-dependent response of foraminiferal calcification to seawater carbonate chemistry. *Biogeosciences* 14, 3287–3308. <https://doi.org/10.5194/bg-14-3287-2017>
- Hess, S., Kuhnt, W., 2005. Neogene and Quaternary paleoceanographic changes in the southern South China Sea (Site 1143): the benthic foraminiferal record 54, 63–87. <https://doi.org/10.1016/j.marmicro.2004.09.004>
- Hohenegger, J., 2009. Functional shell geometry of symbiont-bearing benthic Foraminifera. *Galaxea, J. Coral Reef Stud.* 11, 81–89. <https://doi.org/10.3755/galaxea.11.81>
- Hsiang, A.Y., Elder, L.E., Hull, P.M., 2016. Towards a morphological metric of assemblage dynamics in the fossil record: A test case using planktonic foraminifera. *Philos. Trans. R. Soc. B Biol. Sci.* 371. <https://doi.org/10.1098/rstb.2015.0227>
- Jayaraju, N., Reddy, B.C.S.R., Reddy, K.R., Reddy, A.N., 2010. Deep-Sea Benthic Foraminiferal Distribution in South West Indian Ocean: Implications to Paleoecology. *Int. J. Geosci.* 01, 79–86. <https://doi.org/10.4236/ijg.2010.12011>
- Jorissen, F.J., 1999. Benthic foraminiferal microhabitats below the sediment-water interface. *Mod. Foraminifera* 161–179.
- Kaiho, K., 1999. Effect of organic carbon flux and dissolved oxygen on the benthic foraminiferal oxygen index (BFOI). *Mar. Micropaleontol.* 37, 67–76. [https://doi.org/10.1016/S0377-8398\(99\)00008-0](https://doi.org/10.1016/S0377-8398(99)00008-0)
- Kaiho, K., Takeda, K., Petrizzo, M.R., Zachos, J.C., 2006. Anomalous shifts in tropical Pacific planktonic and benthic foraminiferal test size during the Paleocene-Eocene thermal maximum. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 237, 456–464. <https://doi.org/10.1016/j.palaeo.2005.12.017>
- Kandiano, E., Werner, K., Juliane, M., Thomas M, C., 2019. Editorial: Paleoceanographic Conditions in High Northern Latitudes During Quaternary Interglaciations. *Front. Earth Sci.* 7.

<https://doi.org/10.3389/feart.2019.00207>

- Keating-Bitonti, C.R., Payne, J.L., 2017. Ecophenotypic responses of benthic foraminifera to oxygen availability along an oxygen gradient in the California Borderland. *Mar. Ecol.* 38, 1–16. <https://doi.org/10.1111/maec.12430>
- Keating-Bitonti, C.R., Payne, J.L., 2016. Physicochemical controls on biogeographic variation of benthic foraminiferal test size and shape. *Paleobiology* 42, 595–611. <https://doi.org/10.1017/pab.2016.7>
- Koho, K.A., García, R., Stigter, H.C. De, Epping, E., Koning, E., Kouwenhoven, T.J., Zwaan, G.J. Van Der, 2008. Progress in Oceanography Sedimentary labile organic carbon and pore water redox control on species distribution of benthic foraminifera: A case study from Lisbon – Setúbal Canyon (southern Portugal). *Prog. Oceanogr.* 79, 55–82. <https://doi.org/10.1016/j.pocean.2008.07.004>
- Korsun, S., Hald, M., Panteleeva, N., Tarasov, G., 1998. Biomass of foraminifera in the St. Anna trough, russian arctic continental margin. *Sarsia* 83, 419–431. <https://doi.org/10.1080/00364827.1998.10413701>
- Leonhardt, A., Toledo, F.A.L., Coimbra, J.C., 2013. The productivity history in the Southwestern Atlantic as inferred from coccolithophore record for the last 130 kyr. *Rev. Bras. Paleontol.* 16, 361–374. <https://doi.org/10.4072/rbp.2013.3.02>
- Lesen, A.E., 2005. Relationship between benthic foraminifera and food resources in South San Francisco Bay, California, USA. *Mar. Ecol. Prog. Ser.* 297, 131–145.
- Licari, L., Schumacher, S., Wenzhofer, F., Zabel, M., Mackensen, A., 2003. Communities and microhabitats of living benthic foraminifera from the Tropical East Atlantic: Impact of different. *J. Foraminifer. Res.* 33, 10–31.
- Lisiecki, L.E., Stern, J. V., 2016. Regional and global benthic $\delta^{18}\text{O}$ stacks for the last glacial cycle. *Paleoceanography* 31, 1368–1394. <https://doi.org/10.1002/2016PA003002>
- Loeblich, A.R., Tappan, H., 1988. *Foraminiferal Genera and Their Classification*. Springer Science+Business Media New York.
- Lopes, R.R.; Bonetti, C.; Santos, G.S.; Pivel, M.A.G.; Petró, S.M.; Caron, F.; Bonetti, J. Late Pleistocene sediment accumulation on the lower slope off the Rio Grande Terrace, southern Brazilian Continental Margin, (submitted).
- Loubere, P., 1995. Benthic foraminiferal microhabitat selection, carbon isotope values, and association with larger animals: a test with 83–95.
- Machain-Castillo, M.L., Ruiz-Fernández, A.C., Gracia, A., Sanchez-Cabeza, J.A., Rodríguez-Ramírez, A., Alexander-Valdés, H.M., Pérez-Bernal, L.H., Nava-Fernández, X.A., Gómez-Lizárraga, L.E., Almaraz-Ruiz, L., Schwing, P.T., Hollander, D.J., 2019. Natural and anthropogenic oil impacts on benthic foraminifera in the southern Gulf of Mexico. *Mar. Environ. Res.* 149, 111–125. <https://doi.org/10.1016/j.marenvres.2019.06.006>
- Mahiques, M.M., Fukumoto, M.M., Silveira, I.C.A., Figueira, R.C.L., Bicego, M.C., Lourenço, R.A., Mello-E-Sousa, S.H., 2007. Sedimentary changes on the Southeastern Brazilian upper slope during the last 35,000 years. *An. Acad. Bras. Cienc.* 79, 171–181. <https://doi.org/10.1590/S0001-37652007000100018>
- Mahiques, M.M., Alcántara-Carrió, J., Lobo, F.J., Schattner, U., dos Santos, R.F., Cazzoli y Goya, S., Ramos, R.B., Natorf de Abreu, J.G., Pereira de Souza, L.A., Lopes Figueira, R.C., Bicego, M.C., 2019. The building, shaping, and filling of an Upper Slope Terrace: the Rio Grande Terrace, SW Atlantic. *Solid Earth Discuss.* 25, 1–27. <https://doi.org/10.5194/se-2018-140>

- Mazurkiewicz, M., Górska, B., Renaud, P.E., Włodarska-Kowalczyk, M., 2020. Latitudinal consistency of biomass size spectra - benthic resilience despite environmental, taxonomic and functional trait variability. *Sci. Rep.* 10, 1–12. <https://doi.org/10.1038/s41598-020-60889-4>
- Michaels, A.F., Caron, D.A., Swanberg, N.R., Howse, F.A., 1995. Primary productivity by symbiont-bearing planktonic sarcodines (Acantharia, Radiolaria, Foraminifera) in surface waters near Bermuda. *J. Plankton Res.* 17, 103–129. <https://doi.org/10.1093/plankt/17.1.103>
- Milker, Y., Schmiedl, G., 2012. A taxonomic guide to modern benthic shelf foraminifera of the western Mediterranean sea. *Palaeontol. Electron.* 15. <https://doi.org/10.26879/271>
- Mojtahid, M., Jorissen, F., Pearson, T.H., 2008. Comparison of benthic foraminiferal and macrofaunal responses to organic pollution in the Firth of Clyde (Scotland). *Mar. Pollut. Bull.* 56, 42–76. <https://doi.org/10.1016/j.marpolbul.2007.08.018>
- Molina, G.S., 2019. Resposta dos foraminíferos bentônicos indicadores de paleoprodutividade às variações no transporte de carbono orgânico no talude continental da Bacia de Santos nos últimos 130.000 anos. Monografia (Graduação em Oceanografia) – Universidade Estadual do Rio de Janeiro.
- Morales, E., Chang, H.K., Soto, M., Corrêa, F.S., Veroslavsky, G., Ana, H.D.S., Conti, B., Daners, G., 2017. Tectonic and stratigraphic evolution of the Punta del Este and Pelotas basins (offshore Uruguay).
- Morigi, C., Jorissen, F.J., Gervais, A., Guichard, S., Borsetti, M., 2001. Benthic foraminiferal faunas in surface sediments off NW Africa : relationship with organic flux to the ocean floor. *J. Foraminifer. Res.* 31, 350–368.
- Morigi, C., Sabbatini, A., Vitale, G., Pancotti, I., Gooday, A.J., Duineveld, G.C.A., De Stigter, H.C., Danovaro, R., Negri, A., 2012. Foraminiferal biodiversity associated with cold-water coral carbonate mounds and open slope of SE Rockall Bank (Irish continental margin-NE Atlantic). *Deep. Res. Part I Oceanogr. Res. Pap.* 59, 54–71. <https://doi.org/10.1016/j.dsr.2011.10.004>
- Movellan, A., Schiebel, R., Zubkov, M. V., Smyth, A., Howa, H., 2012. Protein biomass quantification of unbroken individual foraminifers using nano-spectrophotometry. *Biogeosciences* 9, 3613–3623. <https://doi.org/10.5194/bg-9-3613-2012>
- Murray, J., 2006. *Ecology and Applications of Benthic Foraminifera*. Cambridge University Press.
- Nagai, R.H., Sousa, S.H.M., Burone, L., Mahiques, M.M., 2009. Paleoproductivity changes during the Holocene in the inner shelf of Cabo Frio, southeastern Brazilian continental margin: Benthic foraminifera and sedimentological proxies. *Quat. Int.* 206, 62–71. <https://doi.org/10.1016/j.quaint.2008.10.014>
- Nagai, R.H., Sousa, S.H.M., Lourenço, R.A., Bicego, M.C., Mahiques, M.M., 2010. Paleoproductivity changes during the Late Quaternary in the southeastern Brazilian upper continental margin of the Southwestern Atlantic. *Brazilian J. Oceanogr.* 58, 31–41.
- Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Kitazato, H., 2005. Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: In situ tracer experiments. *Limnol. Oceanogr.* 50, 134–146. <https://doi.org/10.4319/lo.2005.50.1.0134>
- Nomaki, H., Toyofuku, T., Tsuchiya, M., Matsuzaki, T., Uematsu, K., Tame, A., 2015. Three-dimensional observation of foraminiferal cytoplasmic morphology and internal structures using uranium-osmium staining and micro-X-ray computed tomography. *Mar. Micropaleontol.* 121, 32–40. <https://doi.org/10.1016/j.marmicro.2015.09.003>
- Ovsepyan, Y.S., Averkina, N.O., Taldenkova, E.E., 2019. The Importance of Foraminifera of the Family Cassidulinidae for the Late Quaternary Paleoenvironmental Reconstructions Based on Sediment Cores from the Laptev Sea. *Paleontol. J.* 53, 894–898.

<https://doi.org/10.1134/S0031030119090119>

- Peterson, L., Lohman, G., 1982. Major Change in Atlantic Deep and Bottom Waters 700,000 yr Ago: Benthonic Foraminiferal Evidence from the South Atlantic. *Quat. Res.* 17, 26–38.
- Petró, S.M., 2018. Dissolução de foraminíferos Quaternários do Atlântico Sul: da perda de CaCo₃ ao ganho de informação paleoceanográfica 158.
- Petró, S.M., Burone, L., 2018. Changes in water masses in the late Quaternary recorded at Uruguayan Continental Slope. *Journal Sediment. Environ.* 3, 280–289. <https://doi.org/10.12957/jse.2018.39156>
- Petró, S.M., Pivel, M.A.G., Coimbra, J.C., 2016. Implicações da dissolução de carbonato de cálcio pelágico para reconstruções paleoceanográficas do Quaternário. *Quat. Environ. Geosci.* 7, 14–25. <https://doi.org/10.5380/abequa.v7i1-2.46419>
- Rocha, J., Milliman, J.D., Santana, C.I., Vicalvi, M.A., 1975. Upper continental margin sedimentation off Brazil. *Contributions to Sedimentology*.
- Rodrigues, A.R., Pivel, M.A.G., Schmitt, P., de Almeida, F.K., Bonetti, C., 2018. Infaunal and epifaunal benthic foraminifera species as proxies of organic matter paleofluxes in the Pelotas Basin, south-western Atlantic Ocean. *Mar. Micropaleontol.* 144, 38–49. <https://doi.org/10.1016/j.marmicro.2018.05.007>
- Rühlemann, C., Müller, P.J., Schneider, R.R., 1999. Organic carbon and carbonate as paleoproductivity proxies: examples from high and low productivity areas of the tropical Atlantic. *Use proxies Paleoceanogr. examples from South Atl.* 315–344. https://doi.org/10.1007/978-3-642-58646-0_12
- Schmidt, D.N., Renaud, S., Bollmann, J., 2003. Response of planktic foraminiferal size to late Quaternary climate change. *Paleoceanography* 18, 1–12. <https://doi.org/10.1029/2002PA000831>
- Schmiedl, G., De Bovée, F., Buscail, R., Charrière, B., Hemleben, C., Medernach, L., Picon, P., 2000. Trophic control of benthic foraminiferal abundance and microhabitat in the bathyal Gulf of Lions, western Mediterranean Sea. *Mar. Micropaleontol.* 40, 167–188. [https://doi.org/10.1016/S0377-8398\(00\)00038-4](https://doi.org/10.1016/S0377-8398(00)00038-4)
- Schmiedl, G., Kuhnt, T., Ehrmann, W., Emeis, K.C., Hamann, Y., Kotthoff, U., Dulski, P., Pross, J., 2010. Climatic forcing of eastern Mediterranean deep-water formation and benthic ecosystems during the past 22 000 years. *Quat. Sci. Rev.* 29, 3006–3020. <https://doi.org/10.1016/j.quascirev.2010.07.002>
- Schmitt, P., Rodrigues, A.R., Bonetti, C., 2019. Anuário do Instituto de Geociências - UFRJ Sucessão de Associações de Foraminíferos Bentônicos como Indicadoras de Variações Paleoceanográficas no Terraço de Torres (RS - Brasil) Durante o Quaternário Tardio Succession of Benthic Foraminiferal Assemblage 42, 387–395.
- Schonfeld, J., 2006. Taxonomy and distribution of the *Uvigerina peregrina* plexus in the tropical to northeastern Atlantic. *J. Foraminifer. Res.* 36, 355–367.
- Schumacher, S., Jorissen, F.J., Mackensen, A., Gooday, A.J., Pays, O., 2010. Ontogenetic effects on stable carbon and oxygen isotopes in tests of live (Rose Bengal stained) benthic foraminifera from the Pakistan continental margin. *Mar. Micropaleontol.* 76, 92–103. <https://doi.org/10.1016/j.marmicro.2010.06.002>
- Schweizer, M., 2006. Evolution and molecular phylogeny of Cibicides and Uvigerina (Rotaliida, Foraminifera).
- Schweizer, M., Pawlowski, J., Duijnste, I.A.P., Kouwenhoven, T.J., 2005. Molecular phylogeny of the foraminiferal genus *Uvigerina* based on ribosomal DNA sequences 57, 51–67. <https://doi.org/10.1016/j.marmicro.2005.07.001>

- Stramma, L., England, M., 1999. On the water masses and mean circulation of the South Atlantic Ocean. *Geophys. Res.* 104, 20863–20883.
- Sweetman, A.K., Thurber, A.R., Smith, C.R., Levin, L.A., Mora, C., Wei, C.L., Gooday, A.J., Jones, D.O.B., Rex, M., Yasuhara, M., Ingels, J., Ruhl, H.A., Frieder, C.A., Danovaro, R., Würzberg, L., Baco, A., Grupe, B.M., Pasulka, A., Meyer, K.S., Dunlop, K.M., Henry, L.A., Roberts, J.M., 2017. Major impacts of climate change on deep-sea benthic ecosystems. *Elementa* 5. <https://doi.org/10.1525/elementa.203>
- Theodor, M., Schmiedl, G., Jorissen, F., Mackensen, A., Theodor, M., 2016. Stable carbon isotope gradients in benthic foraminifera as proxy for organic carbon fluxes in the Mediterranean Sea 6385–6404. <https://doi.org/10.5194/bg-13-6385-2016>
- Van Der Zwaan, G.J., Duijnste, I.A.P., Den Dulk, M., Ernst, S.R., Jannink, N.T., Kouwenhoven, T.J., 1999. Benthic foraminifera: Proxies or problems? A review of paleocological concepts. *Earth Sci. Rev.* 46, 213–236. [https://doi.org/10.1016/S0012-8252\(99\)00011-2](https://doi.org/10.1016/S0012-8252(99)00011-2)
- Violante, R.A., 2017. The Argentina Continental Margin A Potential Paleoclimatic- Paleoceanographic Archive for the Southern Ocean.
- Volker Altenbach, A., Struck, U., 2001. On the coherence of organic carbon flux and benthic foraminiferal biomass. *J. Foraminif. Res.* 31, 79–85. <https://doi.org/10.2113/0310079>
- Wainer, I., Gent, P., Goni, G., 2000. Annual cycle of the Brazil-Malvinas confluence region in the National Center for Atmospheric Research Climate System Model. *J. Geophys. Res. Ocean.* 105, 26167–26177. <https://doi.org/10.1029/1999jc000134>
- Wilson, B., Costelloe, A., 2011. Benthonic foraminiferal paleoecology of the pleistocene in DSDP hole 148, Aves Ridge, eastern Caribbean Sea. *J. Foraminif. Res.* 41, 363–370. <https://doi.org/10.2113/gsjfr.41.4.363>
- WoRMS Editorial Board .2020. World Register of Marine Species. Available from <https://www.marinespecies.org> at VLIZ. Accessed 2020-06-16. doi:10.14284/17
- Yamashita, C., Nagai, R.H., Martins, M.V., Vicente, T., Sousa, S.H.M., Frontalini, F., Palóczy, A., Mahiques, M.M., Godoi, S., Montova-Montes, I., Figueira, R.C., 2016. On the interplay between hydrodynamics, bottom morphology, sedimentary processes and benthic foraminifera assemblages in the São Paulo bight (Brazil, SW Atlantic). *J. Sediment. Environ.* 1, 326–347. <https://doi.org/10.12957/jse.2016.25990>

Appendix 1

Core	Age (Ka BP)	<i>Trifarina angulosa</i>	<i>Uvigerina auberiana</i>	<i>Uvigerina mediterranea</i>	<i>Uvigerina peregrina</i>	<i>Uvigerina hispidocostata</i>	<i>Uvigerina dirrupta</i>
SIS188	7.2	40.0	16.7	10.0	26.7	0.0	6.7
SIS188	8.1	63.2	5.3	10.5	0.0	15.8	5.3
SIS 188	9.5	33.3	4.2	20.8	12.5	20.8	8.3
SIS 188	10.8	50.8	0.0	13.8	24.6	10.8	0.0
SIS 188	19.5	43.2	0.0	40.9	11.4	4.5	0.0
SIS 188	20.9	28.7	0.0	32.7	17.8	19.8	1.0
SIS 188	22.4	70.3	2.7	8.1	16.2	2.7	0.0
SIS 188	23.7	71.0	6.5	0.0	19.4	3.2	0.0
SIS 188	25.2	67.4	0	21.7	10.9	0	0
SIS 188	26.1	71.8	4.2	4.2	18.3	0.0	1.4
SIS 188	27.8	75.8	3.0	10.1	7.1	4.0	0.0
SIS 188	29.9	77.4	0.0	3.2	12.9	6.5	0.0
SIS 249	30.0	91.7	2.1	2.1	4.2	0.0	0.0
SIS 188	31.1	74.5	2.1	4.3	12.8	6.4	0.0
SIS 188	32.7	84.4	0.0	0.0	0.0	15.6	0.0
SIS 188	34.1	63.9	3.3	18.0	0.0	14.8	0.0
SIS 188	35.4	77.5	0.0	15.0	7.5	0.0	0.0
SIS 188	36.7	78.8	0.0	9.6	7.7	3.8	0.0
SIS 249	37.1	87.9	0.0	3.0	9.1	0.0	0.0

Core	Age (Ka BP)	<i>Trifarina angulosa</i>	<i>Uvigerina auberiana</i>	<i>Uvigerina mediterranea</i>	<i>Uvigerina peregrina</i>	<i>Uvigerina hispidocostata</i>	<i>Uvigerina dirrupta</i>
SIS 188	39.4	75.0	0.0	10.7	10.7	0.0	3.6
SIS 188	40.8	65.2	0.0	26.1	6.5	0.0	2.2
SIS 188	42.1	76.7	4.7	16.3	0.0	2.3	0.0
SIS188	43.5	90.2	0.0	0.0	7.8	2.0	0.0
SIS 188	44.8	65.2	0.0	27.3	0.0	0.0	7.6
SIS 188	46.1	73.3	0.0	6.7	20.0	0.0	0.0
SIS 249	47.2	100.0	0.0	0.0	0.0	0.0	0.0
SIS 188	47.4	63.6	5.5	3.6	27.3	0.0	0.0
SIS 249	53.3	100.0	0.0	0.0	0.0	0.0	0.0
SIS 249	59.4	95.8	0.0	0.0	4.2	0.0	0.0
SIS 249	60.7	67.5	2.5	2.5	25.0	2.5	0.0
SIS 249	63.4	88.2	0.0	2.9	8.8	0.0	0.0
SIS 249	65.5	80.8	7.7	3.8	7.7	0.0	0.0
SIS 249	67.8	97.6	0.0	0.0	2.4	0.0	0.0
SIS 249	73.2	100.0	0.0	0.0	0.0	0.0	0.0
SIS 249	78.7	89.9	10.1	0.0	0.0	0.0	0.0
SIS 249	84.1	0.0	3.7	0.0	85.2	11.1	0.0
SIS 249	91.6	79.1	0.0	0.0	20.9	0.0	0.0
SIS 249	101.4	70.6	0.0	26.5	2.9	0.0	0.0
SIS 249	109.2	88.9	4.4	2.2	4.4	0.0	0.0
SIS 249	112.5	85.2	4.9	0.0	0.0	9.9	0.0

Table A1. Relative abundance of Uvigerinidae species identified in the cores SIS188 and SIS249.

Core	Age (Ka BP)	number of tests	length (μm)		width (μm)		depth (μm)		elongation		volume (μm^3)		biomass ($\mu\text{gC.cm}^{-3}$)	
			mean \pm stdev		mean \pm stdev		mean \pm stdev		mean \pm stdev		mean \pm stdev		mean \pm stdev	
SIS 188	7.2	30	190.92	109.23	139.58	75.85	131.27	71.10	0.74	0.11	2E+06	4E+06	0.12	0.25
SIS 188	8.1	19	284.56	260.09	191.41	154.24	187.79	139.37	0.73	0.14	9E+06	2E+07	0.58	1.09
SIS 188	9.5	24	360.50	342.37	235.43	178.34	233.67	175.02	0.75	0.14	2E+07	3E+07	1.11	1.96
SIS 188	10.8	65	267.16	172.58	183.57	95.40	185.15	98.23	0.73	0.15	5E+06	8E+06	0.31	0.48
SIS 188	19.5	44	244.08	149.26	184.43	97.87	193.52	100.93	0.78	0.12	5E+06	1E+07	0.31	0.75
SIS 188	20.9	101	319.10	182.68	218.27	98.67	268.94	136.00	0.73	0.16	9E+06	1E+07	0.55	0.71
SIS 188	22.4	37	195.21	125.64	140.17	80.09	167.41	94.79	0.74	0.14	3E+06	6E+06	0.17	0.39
SIS 188	23.7	31	245.05	205.71	160.38	118.17	178.42	150.67	0.73	0.18	7E+06	2E+07	0.41	0.95
SIS 188	25.2	46	199.10	72.47	142.11	59.34	156.80	78.90	0.71	0.15	2E+06	3E+06	0.12	0.20
SIS 188	26.1	71	178.41	99.38	129.22	63.53	153.45	116.65	0.76	0.14	2E+06	4E+06	0.13	0.23
SIS 188	26.9	53	154.53	76.63	120.37	63.48	140.43	71.66	0.78	0.11	1E+06	3E+06	0.09	0.21
SIS 188	27.8	99	175.14	106.17	126.69	62.82	129.45	85.46	0.76	0.15	2E+06	4E+06	0.11	0.23
SIS 188	29.9	31	167.08	72.92	126.25	53.22	164.10	148.45	0.77	0.11	1E+06	3E+06	0.12	0.23
SIS 249	30.0	48	136.47	44.89	100.50	24.56	106.15	50.89	0.76	0.13	520335	1E+06	0.03	0.07
SIS 188	31.3	47	175.89	113.46	137.19	89.74	135.47	104.03	0.79	0.13	3E+06	9E+06	0.16	0.57
SIS 188	32.7	45	156.52	119.61	114.82	52.28	140.69	66.18	0.78	0.13	2E+06	6E+06	0.10	0.35
SIS 188	34.05	61	174.74	88.29	130.08	54.30	140.33	98.66	0.78	0.13	2E+06	3E+06	0.10	0.17
SIS 188	35.4	40	163.09	69.22	123.39	43.88	131.10	70.40	0.78	0.15	520335	1E+06	0.07	0.12

Core	Age (Ka BP)	number of tests	length (μm)		width (μm)		depth (μm)		elongation		volume (μm^3)		biomass ($\mu\text{gC.cm}^{-3}$)	
			mean \pm stdev	mean \pm stdev	mean \pm stdev	mean \pm stdev	mean \pm stdev	mean \pm stdev	mean \pm stdev	mean \pm stdev				
SIS 188	36.7	52	169.08	79.99	124.05	50.22	143.94	106.03	0.76	0.14	1E+06	3E+06	0.09	0.16
SIS 249	37.08	33	156.93	41.80	110.30	19.08	112.27	23.63	0.73	0.16	7E+05	1E+06	0.03	0.02
SIS 188	38.01	32	151.58	73.31	117.13	54.23	119.03	72.88	0.79	0.12	1E+06	2E+06	0.07	0.12
SIS 188	39.4	28	154.42	70.29	108.72	41.75	123.36	109.55	0.73	0.13	1E+06	3E+06	0.07	0.17
SIS 188	42.1	43	143.0	69.3	112.29	53.23	118.16	63.05	0.80	0.12	910354	2E+06	0.06	0.10
SIS 188	43.5	51	158.12	108.58	110.28	47.34	118.31	80.48	0.76	0.15	1E+06	4E+06	0.08	0.24
SIS 188	44.8	66	168.73	89.92	125.94	50.10	133	79.63	0.78	0.13	1E+06	3E+06	0.09	0.19
SIS 188	46.1	30	163.23	68.73	131.83	55.88	141.30	81.65	0.82	0.12	1E+06	2E+06	0.09	0.12
SIS 249	47.23	48	154.68	35.36	108.88	14.79	104.02	11.35	0.73	0.14	5E+05	2E+05	0.03	0.01
SIS 188	47.4	55	169.12	93.91	125.86	57.88	174.78	113.74	0.77	0.13	2E+06	5E+06	0.13	0.29
SIS 249	53.3	27	170.78	53.14	113.4	25.35	113.59	59.8	0.69	0.14	8E+05	1E+06	0.05	0.09
SIS 249	59.04	25	149.38	53.07	102.48	53.07	112.04	53.81	0.71	0.14	7E+05	1E+06	0.04	0.09
SIS 249	60.7	40	179.70	59.10	121.0	36.38	132.98	66.08	0.70	0.16	1E+06	2E+06	0.07	0.10
SIS 249	63.36	32	129.74	32.67	103.9	19.15	109.00	19.41	0.75	0.13	5E+05	3E+05	0.03	0.02
SIS 249	65.48	27	159.42	42.64	118.24	24.55	114.59	28.61	0.77	0.15	6E+05	5E+05	0.04	0.03
SIS 249	67.83	42	143.22	34.90	100.68	19.48	112.17	22.71	0.72	0.14	5E+05	3E+05	0.03	0.02

Core	Age (Ka BP)	number of tests	length (μm)		width (μm)		depth (μm)		elongation		volume (μm^3)		biomass ($\mu\text{gC.cm}^{-3}$)	
			mean \pm stdev	mean \pm stdev	mean \pm stdev	mean \pm stdev	mean \pm stdev	mean \pm stdev	mean \pm stdev	mean \pm stdev				
SIS 249	73.21	32	163.50	34.87	112.92	14.84	119.28	12.49	0.71	0.14	6E+05	2E+05	0.04	0.01
SIS 249	78.6	99	179.48	55.64	108.81	17.34	120.46	18.76	0.65	0.17	1E+06	7E+05	0.04	0.02
SIS 249	84.1	27	221.63	44.10	180.35	34.74	184.96	39.62	0.82	0.12	3E+06	2E+06	0.13	0.07
SIS 249	91.63	44	111.70	14.45	173.88	47.22	114.14	16.24	0.68	0.16	1E+06	6E+05	0.04	0.02
SIS 249	101.39	35	183.08	46.74	112.98	17.22	117.09	17.42	0.65	0.17	1E+06	6E+05	0.04	0.02
SIS 249	109.21	46	152.61	50.70	104.61	20.97	113.83	17.12	0.72	0.16	9E+05	6E+05	0.03	0.02
SIS 249	112.5	69	195.05	52.90	109.32	26.25	125.77	48.62	0.59	0.15	1E+06	2E+06	0.05	0.11

Table A2. Average and standard deviation of the biometrics descriptors of uvigerinids tests (n total = 1921) analyzed in the cores SIS188 and SIS249

	Detrital mud (%)	Carbonate (%)	$\delta^{13}\text{C}$ Uvig (‰)	d^{18}O \Uvig (‰)	Uvigerinidae %	Length (μm)	Elongation Index	Volume (μm^3)	Accumulated Biomass ($\mu\text{gC}\cdot\text{cm}^3$)
Detrital mud (%)		0.131	0.485	0.257	0.703	0.989	0.465	0.731	0.200
Carbonate (%)	-0.3		0.000	0.013	0.013	0.007	0.138	0.113	0.551
$\delta^{13}\text{C}$ Uvig (‰)	-0.1	0.7		0.002	0.040	0.256	0.002	0.883	0.653
$\delta^{18}\text{O}$ \Uvig (‰)	0.2	-0.4	-0.5		0.107	0.481	0.000	0.144	0.020
Uvigerinidae %	-0.1	-0.5	-0.3	0.3		0.269	0.061	0.783	0.878
Length (μm)	0.0	0.5	0.2	-0.1	-0.2		0.192	0.000	0.000
Elongation Index	0.1	-0.3	-0.5	0.6	0.3	-0.2		0.125	0.137
Volume (μm^3)	0.1	0.3	0.0	0.2	0.0	0.8	0.2		0.000
Accum Biomass ($\mu\text{gC}\cdot\text{cm}^{-3}$)	0.2	0.1	-0.1	0.4	0.0	0.7	0.2	0.9	

Table A3. Spearman rank correlation coefficient between morphometric descriptors and total organic carbon, carbon and oxygen isotope ratios in the cores SIS 188 and SIS 249. (values of the r_s – lower triangle; p value – upper triangle).

N=1923

Appendix 2.

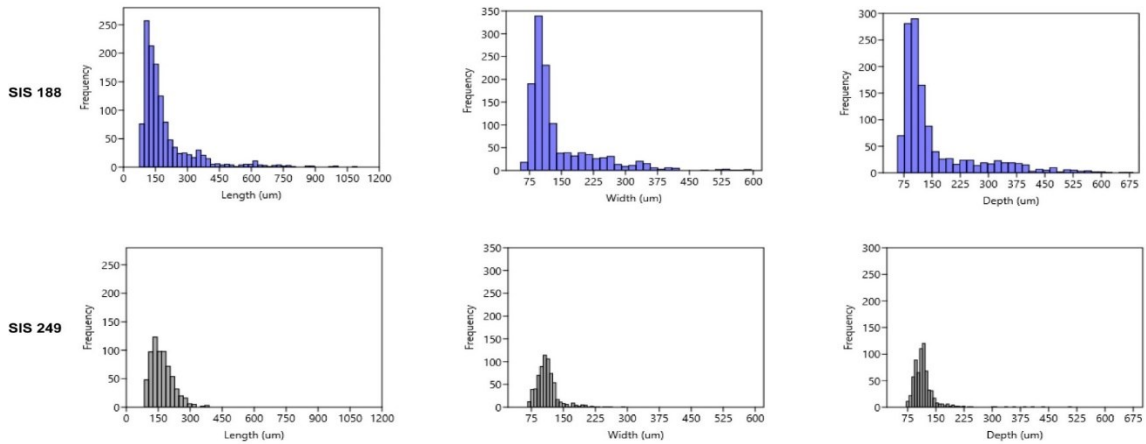


Figure A1. Histograms showing the distribution of the classes of size for the length, width and depth of the uvigerinids tests measured in the cores SIS 188 (N=1247 individuals) e SIS 249 (N = 674 individuals)

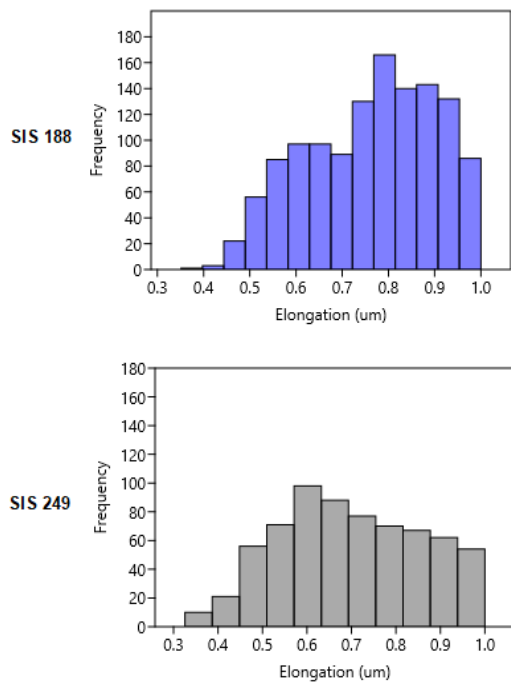


Figure A2. Histograms showing the distribution of elongation index classes of the uvigerinids tests measured in the cores SIS 188 and SIS 249.

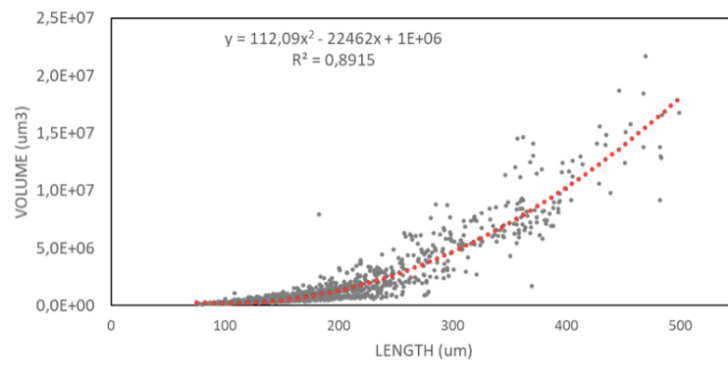


Figure A3: Plot of test length (μm) versus volume (μm^3) measures showing the best-fit polynomial regression curve and equation to describe this relationship.

Supplementary Data – Taxonomic List

Kingdom Chromista

Subkingdom Harosa

Infrakingdom Rhizaria

Phylum Foraminifera

Class Globothalamea

Order ROTALIIDA Lankester 1885

Family UVIGERINIDAE Haeckel, 1894

Subfamily UVIGERININAE Haeckel, 1894

Genus *Uvigerina* d'Orbigny, 1826*Uvigerina peregrina* Cushman, 1923*Uvigerina mediterranea* Hofker 1932*Uvigerina hispidocostata* Cushman & Todd 1945*Uvigerina dirupta* Todd 1948*Uvigerina auberiana* d'Orbigny 1939

Genus TRIFARINA Cushman, 1923

Trifarina angulosa Williamson, 1858

3 CONCLUSÃO GERAL

Esse trabalho permitiu investigar ferramentas para estimar variações oceanográficas e de produtividade primária ao longo do Quaternário tardio, contribuindo para ampliar o conhecimento sobre os processos de transferência de carbono da superfície oceânica para o fundo marinho como a bomba biológica, um importante regulador no clima da Terra. A biomassa de foraminíferos bentônicos da família Uvigerinidae, composta em sua maioria por espécies detritívoras, ou seja, que são afetadas pela quantidade matéria orgânica depositada no fundo oceânico, se mostrou um *proxie* para identificar os picos de produção primária durante o último estágio glacial. A redução da produtividade primária e maior dependência trófica de matéria orgânica refratária levou a redução da biomassa e aumento da dominância de *Trifarina angulosa* nos estágios interglaciais. Outros descritores bióticos obtidos a partir do estudo desta família, como tamanho e alongamento das testas também permitiram discutir oscilações na intensidade das correntes, oxigenação e nos nutrientes dissolvidos decorrentes de mudanças na distribuição das massas de água atuantes na região ao longo do tempo. Além de qualificar a biomassa de Uvigerinidae como um *proxy* para inferir oscilações na produtividade primária ao longo do tempo, as características ecológicas e morfológicas a nível de família e espécie, também correspondem à *proxies* referentes a mudanças ambientais, como oscilações nas correntes de fundo e identificação de processos sazonais na produtividade primária.

Referências

- ARMSTRONG, H.; BRASIER, M. D.; BRASIER, M. D. 2005. *Microfossils*. [s.l.] Blackwell Pub.
- ALMEIDA, F. K. De, MELLO, R. M. De, COSTA, K. B., *et al.* "The response of deep-water benthic foraminiferal assemblages to changes in paleoproductivity during the Pleistocene (last 769 . 2 kyr), western South Atlantic Ocean", **Palaeogeography, Palaeoclimatology, Palaeoecology**, v. 440, p. 201–212, 2015. DOI: 10.1016/j.palaeo.2015.09.005. Disponível em: <http://dx.doi.org/10.1016/j.palaeo.2015.09.005>.
- BURONE, L., HELENA, S., MELLO, D. "Benthic foraminiferal distribution on the southeastern Brazilian shelf and upper slope", p. 159–179, 2011. DOI: 10.1007/s00227-010-1549-7. .
- DULEBA, W., PETRI, S., COIMBRA, J. C. S. "Foraminíferos, Tecamebas e Ostracodes Sub-Recentes e Fósseis do Quaternário do Brasil", **Revista do Instituto de Geociências - USP**, p. 1–24, 2003. .
- ENGE, A. J., WITTE, U., KUCERA, M., *et al.* "Uptake of phytodetritus by benthic foraminifera under oxygen depletion at the Indian margin (Arabian Sea)", **Biogeosciences**, v. 11, n. 7, p. 2017–2026, 2014. DOI: 10.5194/bg-11-2017-2014.
- FALKOWSKI, P. G., AND A. D. WOODHEAD. "Primary productivity and biogeochemical cycles in the sea", Springer Science & Business Media. 2013.
- FONTANIER, C., MACKENSEN, A., JORISSEN, F. J., *et al.* "Stable oxygen and carbon isotopes of live benthic foraminifera from the Bay of Biscay : Microhabitat impact and seasonal variability", v. 58, p. 159–183, 2006. DOI: 10.1016/j.marmicro.2005.09.004.
- FREITAS, T. R. "Método automatizado para estimativa da biomassa de foraminíferos bentônicos". Dissertação (Mestrado em Oceanografia) – Universidade Federal de Santa Catarina, Florianópolis. 2019.
- GOODAY, I. "Benthic Foraminifera (Protista) as Tools in Deep-water Palaeoceanography : Environmental Influences on Faunal Characteristics", v. 46, 2003. .
- HUNT, G., ROY, K. "Climate change, body size evolution, and Cope's Rule deep-sea ostracodes", **Proceedings of the National Academy of Sciences of the United States of America**, v. 103, n. 5, p. 1347–1352, 2006. DOI: 10.1073/pnas.0510550103. .
- JORISSEN, F. J., STIGTER, H. C. De, WIDMARK, J. G. V. "A conceptual model explaining benthic foraminiferal microhabitats", v. 26, 1995. .
- KAWAGATA, S., HAYWARD, B. W., GUPTA, A. K. "Benthic foraminiferal extinctions linked to late Pliocene-Pleistocene deep-sea circulation changes in the northern Indian Ocean (ODP Sites 722 and 758)", **Marine Micropaleontology**, v. 58, n. 3, p. 219–242, 2006. DOI: 10.1016/j.marmicro.2005.11.003. .

- KEATING-BITONTI, C. R., PAYNE, J. L. "Physicochemical controls on biogeographic variation of benthic foraminiferal test size and shape", **Paleobiology**, v. 42, n. 4, p. 595–611, 2016. DOI: 10.1017/pab.2016.7. .
- LOUBERE, P., JACOBSEN, B., KLITGAARD KRISTENSEN, D., *et al.* "The structure of benthic environments and the paleochemical record of foraminifera", **Deep-Sea Research Part I: Oceanographic Research Papers**, v. 58, n. 5, p. 535–545, 2011. DOI: 10.1016/j.dsr.2011.02.011. Disponível em: <http://dx.doi.org/10.1016/j.dsr.2011.02.011>.
- MOVELLAN, A., SCHIEBEL, R., ZUBKOV, M. V., *et al.* "Protein biomass quantification of unbroken individual foraminifera using nano-spectrophotometry", **Biogeosciences**, v. 9, n. 9, p. 3613–3623, 2012. DOI: 10.5194/bg-9-3613-2012. .
- MURRAY, J. W., ALVE, E. "Major aspects of foraminiferal variability (standing crop and biomass) on a monthly scale in an intertidal zone", **Journal of Foraminiferal Research**, v. 30, n. 3, p. 177–191, 2000. DOI: 10.2113/0300177. .
- NOMAKI, H., YAMAOKA, A., SHIRAYAMA, Y., *et al.* "Deep-sea benthic foraminiferal respiration rates measured under laboratory conditions", **Journal of Foraminiferal Research**, v. 37, n. 4, p. 281–286, 2007. DOI: 10.2113/gsjfr.37.4.281. .
- PASSOW, U., CARLSON, C. A. "The biological pump in a high CO₂ world", **Marine Ecology Progress Series**, v. 470, n. 2, p. 249–271, 2012. DOI: 10.3354/meps09985.
- PAYTAN A. "Ocean Paleoproductivity". In: Gornitz V. (eds) *Encyclopedia of Paleoclimatology and Ancient Environments*. Encyclopedia of Earth Sciences Series. Springer, Dordrecht. 2009
- PETIT, J. R., RAYNAUD, D., BASILE, I., *et al.* "Climate and atmospheric history of the past 420 , 000 years from the Vostok ice core , Antarctica", 1999. .
- ROST, B., RIEBESELL, U. "Coccolithophores and the biological pump: responses to environmental changes", **Coccolithophores**, p. 99–125, 2004. DOI: 10.1007/978-3-662-06278-4_5. .
- SCHMIEDL, G., PFEILSTICKER, M., HEMLEBEN, C., *et al.* "Environmental and biological effects on the stable isotope composition of recent deep-sea benthic foraminifera from the western Mediterranean Sea", **Marine Micropaleontology**, v. 51, n. 1–2, p. 129–152, 2004. DOI: 10.1016/j.marmicro.2003.10.001. .
- SEN GUPTA, A., MCNEIL, B. **Variability and Change in the Ocean**. Second Edition. [S.l.], Elsevier B.V., 2012. Disponível em: <http://dx.doi.org/10.1016/B978-0-12-386917-3.00006-3>.
- SUN, X., CORLISS, B. H., BROWN, C. W., *et al.* "The effect of primary productivity and seasonality on the distribution of deep-sea benthic foraminifera in the North Atlantic", v. 53, p. 28–47, 2006. DOI:

10.1016/j.dsr.2005.07.003. .

TURLEY, C., EBY, M., RIDGWELL, A. J., *et al.* "The societal challenge of ocean acidification", **Marine Pollution Bulletin**, v. 60, n. 6, p. 787–792, 2010. DOI: 10.1016/j.marpolbul.2010.05.006. .

VOLKER ALTENBACH, A., STRUCK, U. "On the coherence of organic carbon flux and benthic foraminiferal biomass", **Journal of Foraminiferal Research**, v. 31, n. 2, p. 79–85, 2001. DOI: 10.2113/0310079. .

WEART, S. **Climate and Climate Change: History of Scientific Work on Climate Change**. Second Edition. [S.l.], Elsevier, 2015. v. 2. Disponível em: <http://dx.doi.org/10.1016/B978-0-12-382225-3.00491-6>.

WEFER, G., BERGER, W. H., BIJMA, J., & FISCHER, G. "Clues to Ocean History: a Brief Overview of Proxies. Use of Proxies in Paleoceanography", 1–68. doi:10.1007/978-3-642-58646-0_1. 1999

ZERFASS, G. de S. dos A., ANDRADE, E. D. J. "Foraminíferos e Bioestratigrafia: uma abordagem didática", **Terrae Didatica**, v. 3, n. 1, p. 18–35, 2008. .