UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE GEOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM GEOCIÊNCIAS

PREVALÊNCIA DE TRAÇOS DE PARASITAS EM MOLUSCOS MARINHOS: NOVOS PARADIGMAS DO CONTINENTE SUL-AMERICANO

VALENTINA SILVA DOS SANTOS

ORIENTADOR – Prof. Dr. Matias do Nascimento Ritter

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RESUMO

Ainda que raros, os traços de parasitismo oriundos do registro fóssil representam uma interação ubíqua na biosfera. O estudo da interação parasita-hospedeiro no registro fóssil é uma importante fonte de informações paleoecológicas. O objetivo principal deste trabalho é apurar valores para a taxa de prevalência de traços preservados em valvas de moluscos marinhos, ao longo do litoral norte do Rio Grande do Sul, Brasil, provenientes de setores atuais com comportamento de empilhamento predominante retrogradantes e progradantes. Além disto, verificar como se relaciona o tamanho corporal dos hospedeiros e a abundância dos traços, bem como qual o setor da valva ocorre o assentamento dos parasitas e como estes traços se distribuem entre os hospedeiros. A interação aqui encontrada, ocorre entre a espécie de bivalve *Donax hanleyanus* e parasitas da família Gymnophallidae. *D. hanleyanus* habita a zona de intermarés de praias dissipativas, chegando à idade adulta com tamanhos iguais ou superiores a 15 mm. Os parasitas trematódeos da família Gymnophallidae possuem ciclo de vida com até três hospedeiros, tendo espécies de bivalves como primeiro e, por vezes, segundo hospedeiro intermediário, finalizando seu ciclo de vida em uma ave ou mamífero. Os traços possibilitaram apurar valores maiores de prevalência e de abundância em espécimes de tamanhos maiores (adultos) de *D. hanleyanus*. Complementarmente, foi possível identificar o meio extra palial como local prioritário para o assentamento dos parasitas. Adicionalmente, identificamos um alto padrão de agregação de parasitas entre os hospedeiros e a não seletividade de valvas, o que nos permite destacar a eficácia do uso de traços como proxy para estudos no registro fóssil. Obtivemos um valor global de prevalência de 0,599, contudo, quando se trata dos setores, não há relação significativa com o padrão de empilhamento sedimentar. Tais dados nos indicam que a escala local e os fatores autogênicos atuantes se sobrepõem as características estratigráficas de empilhamento. Nosso estudo reforça a importância de pesquisas que visem compreender os padrões de parasitismo contidos no registro fóssil.

Palavras-chave: Interações ecológicas. Registro Fóssil. Moluscos. Litoral Norte do Rio Grande do Sul.

ABSTRACT

Traces of parasitism from the fossil record, despite being rare, represent a ubiquitous interaction in the biosphere. The study of parasite-host interaction in the fossil record has been an important source of paleoecological information. The main objective of this dissertation is to establish prevalence values for traces preserved in marine mollusk valves along the northern coast of Rio Grande do Sul, Brazil, from past to ongoing sectors with predominantly retrogradational and progradational patterns. In addition, we verify the relationship between host body size and the abundance of traces, as well as in which sector of the valve the parasites settle and how these traces are distributed among the hosts. The interaction occurs between the bivalve *Donax hanleyanus* and parasites of the family Gymnophallidae. *D. hanleyanus* inhabits the intertidal zone of dissipative beaches, reaching maturity with sizes of 15 mm or more. The trematode parasites of the Gymnophallidae family have a life cycle with up to three hosts, with a bivalve species as the first and sometimes second intermediate hosts, concluding their life cycle in a bird or a mammal. The traces made it possible to determine higher prevalence and abundance values in larger specimens (adults) of *D. hanleyanus*. Complementarily, it was possible to identify the extrapalial as a priority site for parasite settlement. Furthermore, we found a high pattern of parasite aggregation among hosts and non-selectivity of valves, which allows us to highlight the effectiveness of using traits as a proxy for studies in the fossil record. We obtained an overall prevalence of 0.599. However, there is no significant relationship between prevalence and sediment stacking pattern. These data indicate that the local scale and the acting autogenic factors overlap with the stratigraphic pattern. Our study reinforces the importance of understanding the patterns of parasitism in the fossil record.

Keywords: Ecological interactions. Fossil Record. Mollusks. North Coast of Rio Grande do Sul.

SUMÁRIO

ESTRUTURA DA DISSERTAÇÃO

Esta dissertação de mestrado está estruturada em torno de um artigo submetido em periódico classificado no estrato Qualis-CAPES como A2. A sua organização compreende os seguintes itens:

TEXTO INTEGRADOR:

Texto integrador composto pelos seguintes capítulos: a) introdução compreendendo considerações iniciais e a justificativa da pesquisa; b) objetivos gerais e específicos; c) estado da arte, no que concerne as espécies envolvidas; d) os materiais e métodos utilizados; e) a área de estudo e seu contexto geológico; f) resumo dos principais resultados e discussão; g) considerações finais; h) referências utilizadas.

ARTIGO:

Corpo Principal da Dissertação/Tese, constituído do artigo submetido ao periódico ***Paleobiology***, intitulado "***The power of location: prevalence of traces of parasites in marine mollusks reflects the spatial mixing within coast sectors with different stratigraphic scenarios***".

COMPLEMENTO:

Anexo compreendendo o e-mail de comprovação da submissão do artigo.

1 INTRODUÇÃO

1.1 Considerações Iniciais

As interações ecológicas possuem diferentes formas de classificação, podendo ser inferidas de acordo com o tipo de associação, força ou simetria (Morales-Castilla *et al*., 2015). Interações onde apenas um dos participantes se beneficia, como parasitismo e predação, são importantes ecologicamente e tem um papel fundamental na coevolução (Baumiller & Gahn, 2002). Embora a interação parasita-hospedeiro também demonstre o mecanismo de seleção natural, a interação presa-predador concentra a maior parte das investigações até o momento (e.g., Vermeij, 1977; Huntley & Kowaleski, 2007; Stanley, 2008). Isso se deve em razão do registro fóssil da interação presa-predador estar relativamente melhor representado (Klompmaker *et al*., 2019; Farrar *et al*., 2020).

Parasitismo costuma receber atenção apenas quando se torna danoso, porém a interação é globalmente conhecida (Marcogliese, 2004, 2005). Parasitas podem afetar a biologia, interferindo na reprodução, no crescimento e até mesmo provocar mudanças no comportamento do hospedeiro (Littlewood & Donovan, 2003; Marcogliese, 2004). Para além dos danos biológicos, os parasitas são capazes de intervir na estrutura das comunidades, podendo influenciar a riqueza das espécies, sobretudo aquelas bentônicas (Mouritsen & Poulin, 2002, 2005). Os parasitas são suscetíveis a mudanças climáticas, tendo a temperatura e a salinidade como principais fatores capazes de alterar o seu ciclo de vida (Studer *et al*., 2010; Byers, 2021). Contudo, mudanças como alteração do ciclo hidrológico e elevação do nível do mar podem modificar não apenas o ciclo de vida do parasita, como também do hospedeiro, carecendo de estudos que integrem ambos ciclos (Marcogliese, 2008, 2016).

Os trabalhos acerca do parasitismo no registro fóssil são escassos, por conta do baixo potencial de preservação, pois são animais de corpo mole. A maioria dos estudos são baseados no uso dos traços deixados em seus hospedeiros (Littlewood & Donovan, 2003). Os traços encontrados demonstram mecanismos de defesa produzidos por seus hospedeiros, reforçando que a interação ocorreu durante a vida do organismo parasitado (Huntley & De Baets, 2015). A variedade de traços é significativa. Recentemente, por exemplo, Marini *et al*. (2022) identificaram traços classificados como *U-shape* produzidos por *Caulostrepsis* sp. em bivalves da espécie *Mactra isabelleana* d'Orbigny, 1846, no litoral sul do Rio Grande do Sul, Brasil. O mesmo traço também já foi descrito para o braquiópode *Bouchardia rosea* (Mawe, 1823) na Baía de Ubatuba, SP (Rodrigues *et al*., 2008). Ainda na América do Sul, Ituarte *et al*. (2005) descreveram traços classificados como *igloo-shaped*, produzidos por parasitas trematódeos em valvas de bivalves recentes e holocênicos.

As interações entre parasitas trematódeos e moluscos bivalves, por meio do estudo dos traços, são relativamente bem conhecidas para o Hemisfério Norte, onde o registro estratigráfico do Holoceno tem permitido estabelecer relações entre eventos ambientais e taxas de prevalência de parasitismo (Huntley & Scarponi, 2012, 2021; Scarponi *et al*., 2017). Os estudos conduzidos no Mar Adriático, por exemplo, elucidaram seleção taxonômica, seletividade por tamanho dos hospedeiros e padrões de comportamento dos parasitas (Huntley & Scarponi, 2012, 2021). Recentemente, essas interações vêm recebendo muita atenção, devido aos dados obtidos a acerca da relação entre a taxa de prevalência e momentos de elevação relativa do nível do mar (Huntley *et al*., 2014; Scarponi *et al*., 2017) Considerando o cenário atual e futuro de mudanças climáticas e oscilações do nível do mar, este trabalho amplia a escala espacial desses estudos para o Hemisfério sul, demonstrando que fatores locais da dinâmica costeira podem obliterar padrões previamente encontrados.

1.2 Objetivos

O objetivo principal deste trabalho é estimar a prevalência dos traços de parasitas preservados em valvas de moluscos bivalves e compreender como a interação se comporta ao longo de setores costeiros com comportamento de empilhamento sedimentar atual progradante e retrogradante, no litoral norte do Rio Grande do Sul. Para tal, os seguintes objetivos específicos foram estabelecidos:

- Identificar as espécies de moluscos encontrados;
- Estimar o tamanho corporal das valvas coletadas;
- Estimar a abundância dos traços encontrados nas valvas coletadas;
- Verificar a localização e distribuição dos traços;
- Identificar padrões de parasitismo.

1.2 Estado da arte

1.2.1 Parasitas trematódeos

Os parasitas trematódeos possuem ciclo de vida complexo, com primeiro e segundo hospedeiro intermediários, terminando em um hospedeiro definitivo (Cribb *et al*., 2003). O primeiro hospedeiro é um bivalve, o segundo um gastrópode ou um bivalve, ou ainda um poliqueta e o hospedeiro definitivo comumente é uma ave (Galaktionov, 2007). Se tratando deste estudo, os traços usualmente encontrados são característicos da família Gymnophallidae (Huntley & Scarponi, 2012, 2015, 2021). Os parasitas desta família são normalmente encontrados na porção extra palial de seus hospedeiros bivalves, após serem ingeridos ou penetrarem no meio extra palial (Cribb *et al*., 2003; Ituarte *et al*., 2009).

1.2.2 Moluscos bivalves

O hospedeiro da interação aqui estudada é a espécie de bivalve *Donax hanleyanus* (Philippi, 1845). Os bivalves desta espécie estão distribuídos por toda costa do Atlântico Sul, de Caravelas, na Bahia (Brasil), até as praias de Buenos Aires, na Argentina (Cardoso & Veloso, 2003; Thompson & De Bock, 2009). A espécie é filtradora e habita a zona intermarés, escavando profundidades superficiais (Gianuca, 1985; Gil & Thomé, 2004; Delgado & Defeo, 2007). *D. hanleyanus* é conhecido por habitar praias com diversos estados morfodinâmicos (Celentano *et al*., 2022), residindo em ambientes com alta energia, exposto a ondas e com alto fluxo de sedimentos (Marcomini *et al*., 2002; Thompson & De Bock, 2009). Estes bivalves são classificados de acordo com o seu tamanho, entre recrutas (1 a 5 mm), juvenis (5,5 a 15 mm) e adultos (>15 mm) (Defeo & De Alava, 1995). Diversos trabalhos relacionam a classe dos indivíduos com o estado morfodinâmico do local onde ocorrem (e.g., Herrmann *et al*., 2009; Risoli *et al*., 2022). Para as praias do Uruguai, essa relação está mais ligada ao tamanho dos indivíduos, onde adultos possuem maior abundância em setores reflectivos, enquanto tamanhos menores são mais abundantes em praias dissipativas (Delgado & Defeo, 2007). Contudo, para as praias brasileiras, Cardoso & Veloso (2003) não identificaram essa relação, muito embora verificaram efeitos negativos na abundância da espécie devido à sua coocorrência com o crustáceo *Emerita brasiliensis* Schmitt, 1935. Está coocorrência regula a abundância de *D. hanleyanus*, fato também verificado para o bivalve *Amarilladesma mactroides* (Reeve,

1854) (Herrmann *et al*., 2009). Em ambos os casos, este padrão ocorre devido à competição por alimento e por local de colonização (Defeo & De Alava, 1995). Ademais, recentemente, Bom & Colling (2022) demonstraram o uso de *D. hanleyanus* e *A. mactroides* como indicadores de distúrbios ocasionados por veículos que ocupam a linha de praia, sendo a classe dos recrutas a mais impactada.

1.2.3 Trematódeos-Bivalves

Ruiz & Lindeberg (1989) foram pioneiros ao utilizar os traços induzidos por trematódeos em valvas de bivalves como fonte de informações paleoecológicas e evolutivas. O registro mais antigo de traços de trematódeos em bivalves data do início do Eoceno (~56 Ma) na Inglaterra, sugerindo um ambiente marinho raso com aves se alimentando de bivalves (Todd & Harper, 2011).

O tipo de estrutura produzida como mecanismo de defesa pelos hospedeiros pode variar de acordo com a localização do estabelecimento do parasita e da espécie do hospedeiro (Ituarte *et al*., 2005; Vázquez *et al*., 2006). Contudo, traços classificados como *pits* e *igloo-shapes* podem ser considerados diagnósticos dos trematódeos da família Gymnophallidae para hospedeiros fósseis e modernos (Huntley & De Baets, 2015). Os *pits* foram primeiramente descritos por Ruiz & Lindeberg (1989) para o Eoceno (Luteciano), tendo sua distribuição recentemente estendida até o Ipresiano (Todd & Harper, 2011). Este traço é caracterizado por elevações ovaladas, e demonstram mais uma forma de tentar encapsular o parasita (Huntley & De Baets, 2015) (Figs. 1A e 1B). Existem registros de *igloo-shapes* em bivalves de água doce datados do Cretáceo norte americano, onde os autores consideram um novo marco para o entendimento da evolução e da ecologia dos trematódeos (Rogers *et al*., 2018). Este traço representa a tentativa do hospedeiro de isolar o parasita, sendo caracterizado por uma cobertura circular, por vezes alongada e com uma abertura lateral (Ituarte *et al*., 2001; Ituarte *et al*., 2005) (Figs. 1C e D).

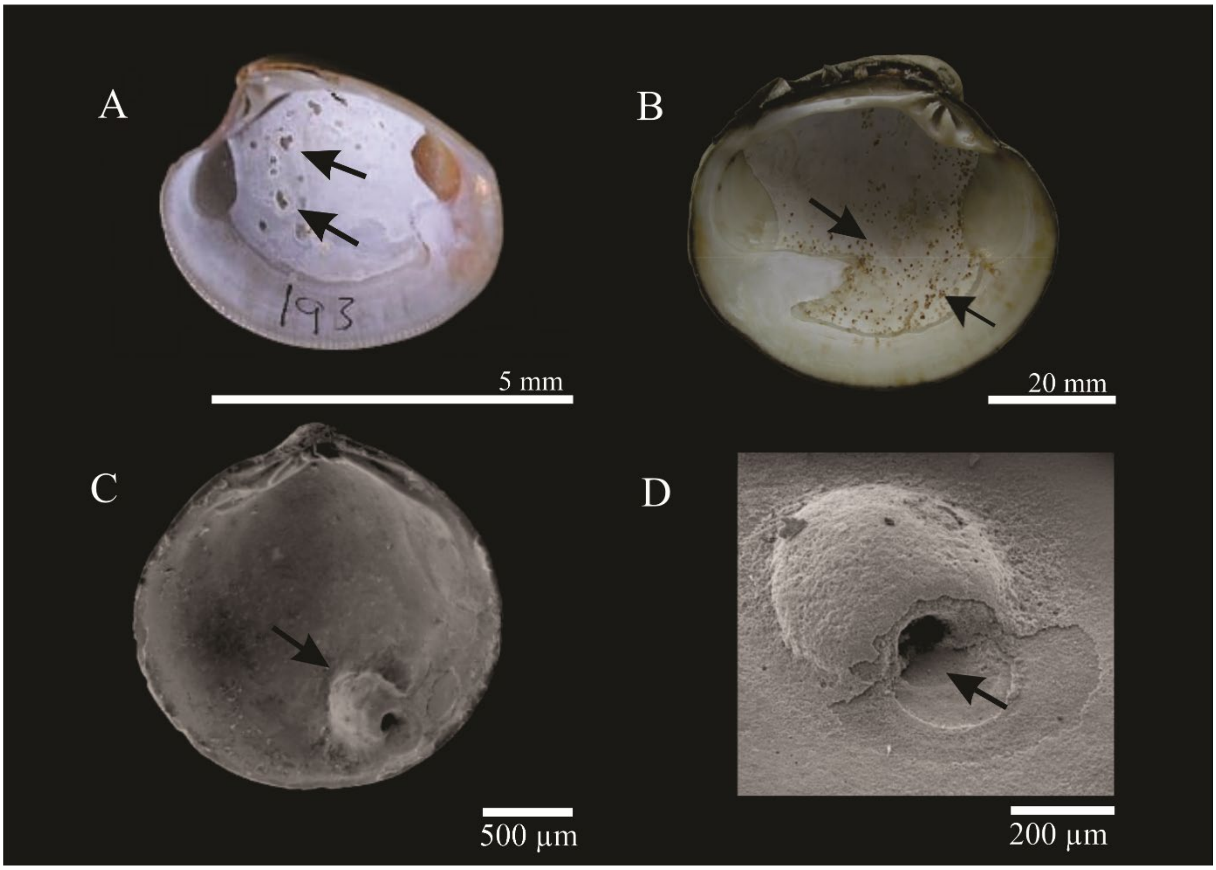

Figura 1 - Diferentes tipos de traços relacionados as espécies de bivalves. A) Vista do interior da valva do bivalve *Chamalea gallina*, exibindo os traços do tipo *pits* de parasitas trematódeos, provenientes do Holoceno da Itália (cortesia de Daniele Scarponi. B) Vista do interior da valva de *Leukoma thaca* com *pits* com coloração marrom alaranjada (modificada de Montenegro *et al*., 2021). *C) Igloo-shape* no interior da valva recente *de Neolepton bennetti* originaria das Ilhas Malvinas (modificada de Ituarte *et al*., 2005). D) Imagem de microscopia eletrônica de varredura da valva de *Cyamiomactra* sp. exibindo a abertura do traço tipo *igloo-shape* (modificada de Ituarte *et al*., 2005).

Os trematódeos, principalmente aqueles da família Gymnophallidae, são encontrados infestando bivalves atuais, como demonstram os estudos realizados envolvendo os bivalves *Tagelus plebeius* ([Lightfoot], 1786) e *Leukoma thaca* (Molina, 1782) (Fig. 1B) (Ituarte *et al*., 2001; Vázquez *et al*., 2006; Montenegro *et al*., 2021). Em consonância com os estudos citados, traços encontrados no registro fóssil e em valvas recentes, provenientes de associações mortas, são similares aos encontrados em estudos atuais, caso da espécie *Chamelea gallina* (Linnaeus, 1758) (Fig. 1) (Ituarte *et al*., 2005; Huntley & Scarponi, 2012, 2015, 2021).

2 MATERIAL E MÉTODOS

2.1 Área de estudo

A área estudo se concentra entre os municípios de Torres, ao norte; e Balneário Dunas Altas, pertencente ao município de Palmares do Sul, ao sul. Estes municípios compõem o setor norte da Planície Costeira do Rio Grande do Sul (PCRS), sul do Brasil.

A costa atual da PCRS é levemente ondulada com orientação NE-SW, em um total de 620 km (Tomazelli & Villwock, 2000; Rosa, 2012). Possui um regime de micromarés com uma amplitude média de 0,5 metros regida por condições astronômicas (Dillenburg *et al.*, 2009). As praias são classificadas como dissipativas a intermediárias, experimentando ondas de *swell* e ondas formadas por ventos locais, que acabam por controlar o transporte e a deposição dos sedimentos (Tomazelli & Villwock, 1992; Dillenburg *et al.*, 2000, 2009). O padrão de vento é bimodal, com predomínio de vento oriundo de NE, durante os meses de setembro e março. Durante os meses de abril e agosto predominam vento de S e SW (Dillenburg *et al.*, 2009). O clima na Planície Costeira, conforme classificação de Köppen (1948), varia entre climas temperados a subtropicais. As chuvas são bem distribuídas, porém no litoral norte ocorrem as maiores precipitações devido à proximidade com as escarpas da Serra Geral (Dillenburg *et al.*, 2009).

2.2 Contexto Geológico

A PCRS exprime a porção emersa da Bacia de Pelotas, concentrando sedimentos majoritariamente terrígenos desde sua formação no Cretáceo Inferior, abrigando um dos registros mais completos de sedimentação do Quaternário brasileiro (Tomazelli *et al.*, 2000).

A PCRS possui dois sistemas deposicionais: o Sistema de Leques Aluviais e o Sistema Laguna-Barreira. O Sistema de Leques Aluviais se originou pelos processos de transporte, como por exemplo, a queda de blocos que se desprenderam da encosta de terras mais altas, e que escalonam para depósitos transportados e assentam-se em aluviões (Vilwock & Tomazelli, 2007).

Segundo Tomazelli & Villwock (2000), os Sistemas Laguna-Barreira se formaram devido aos ciclos de oscilações glácio-eustáticas, durante máximos transgressivos no Quaternário. O Sistema Laguna-Barreira I é o mais antigo (325 ka) e o mais interior, sendo formado durante o primeiro evento transgressivo-regressivo no Pleistoceno, possuindo suas praias próximas a borda da bacia (Tomazelli & Villwock, 2000; Lopes *et al*., 2010; Rosa, 2012). Sua formação está ligada ao depósito de sedimento eólicos sobre o embasamento (Tomazelli & Villwock, 2000, 2005; Lopes *et al*., 2010; Rosa, 2012).

O Sistema Laguna-Barreira II foi formado no segundo evento transgressivo-regressivo durante o Pleistoceno, tendo sua idade estimada em 200 ka, tendo papel na formação da Lagoa Mirim (Tomazelli; *et al*., 2000; Lopes *et al*., 2010, 2014; Rosa, 2012). O Sistema Laguna-Barreira III representa o terceiro evento transgressivo-regressivo do Pleistoceno, há 125 ka, sendo a barreira mais bem preservada e responsável pela formação da Lagoa dos Patos e Mirim (Tomazelli *et al*., 2000). Este sistema conta com diversos afloramentos contento icnofósseis de *Ophiomorpha*, indicando um nível de mar de aproximadamente 6-8 metros acima do atual (Tomazelli & Dillenburg 2007; Rosa *et al*., 2017).

O Sistema Laguna-Barreira IV é o mais recente, tendo se formado no decorrer do Holoceno, cerca de 7 ka, durante as fases finais da Transgressão Marinha Pós-Glacial, tendo seu pico transgressivo há ~6 ka, com o nível do mar 1-4 metros acima do atual (Angulo *et al*., 2006; Barboza *et al*., 2021). Este sistema ocupa toda a extensão da costa atual, possuindo projeções em direção à bacia e reentrâncias em direção ao continente, que acabam por influenciar o padrão deposicional da costa (Dillenburg *et al*., 2000, 2009; Dillenburg & Barboza 2014; Rosa *et al*., 2017).

Dillenburg *et al.* (2009) subdividiram a costa em cinco setores, baseado em dados já publicados de outros autores, com adição de imagens aéreas e de satélite. Dois dos setores abrangem a área abordada neste trabalho. O setor que abrange a área de Torres à Tramandaí exibe uma linha de costa côncava, indicando uma barreira regressiva, que durante a progradação foi recoberta por diversos campos de dunas (Dillenburg *et al*., 2000, 2009; Dillenburg & Barboza, 2014). Em sua porção leste, este setor tem em sua estratigrafia depósitos eólicos sobre depósitos praiais, onde a progradação se deu pelo aporte positivo de sedimentos, devido ao embaiamento do local (Dillenburg *et al*., 2000; Travessas *et al*., 2005).

O setor que compreende a área de Tramandaí à Mostardas, a linha de costa é convexa em direção à bacia, com dunas transgressivas que chegam até a barreira Pleistocênica. Esse setor tem um comportamento retrogradacional. No trecho que corresponde ao Balneário Jardim do Éden, lamas lagunares afloram, evidenciando erosão (Dillenburg *et al*., 2000, 2009; Travessas *et al*., 2005). Estes indicativos demonstram um balanço negativo de sedimentos, em momentos em que a erosão foi mais elevada que o ritmo de subida do nível do mar (Dillenburg *et al*., 2000, 2009; Travessas *et al*., 2005).

2.3 Coleta de dados

Em onze pontos foram realizadas coletas entre os municípios de Tramandaí e Balneário Dunas Altas, em Palmares do Sul, sendo denominada de área sul, onde predominam setores com comportamento atual retrogradacional (Fig. 2).

Figura 2 - Localização dos pontos de coleta do setor sul (modificada de Santos, 2020).

Outros dezesseis pontos foram coletados entre os munícipios de Imbé e Torres, sendo denominada área norte, onde predominam setores progradacionais (Fig. 3). Para ambos setores o mesmo protocolo foi seguido: a cada 5 km na face da praia, com o uso de um quadrante de 1 m² (Fig. 4), foram coletados todos os moluscos presentes na superfície (até 1 cm) e armazenados em potes. Após o campo, as amostras foram lavadas, dispostas em bandejas para secagem e novamente acondicionadas em potes com a identificação do ponto de coleta no Laboratório de Sedimentologia (UFRGS-CECLIMAR). Todo material está sendo tombado na coleção científica de Malacologia do Museu de Ciências Naturais (MUCIN), UFRGS – CECLIMAR.

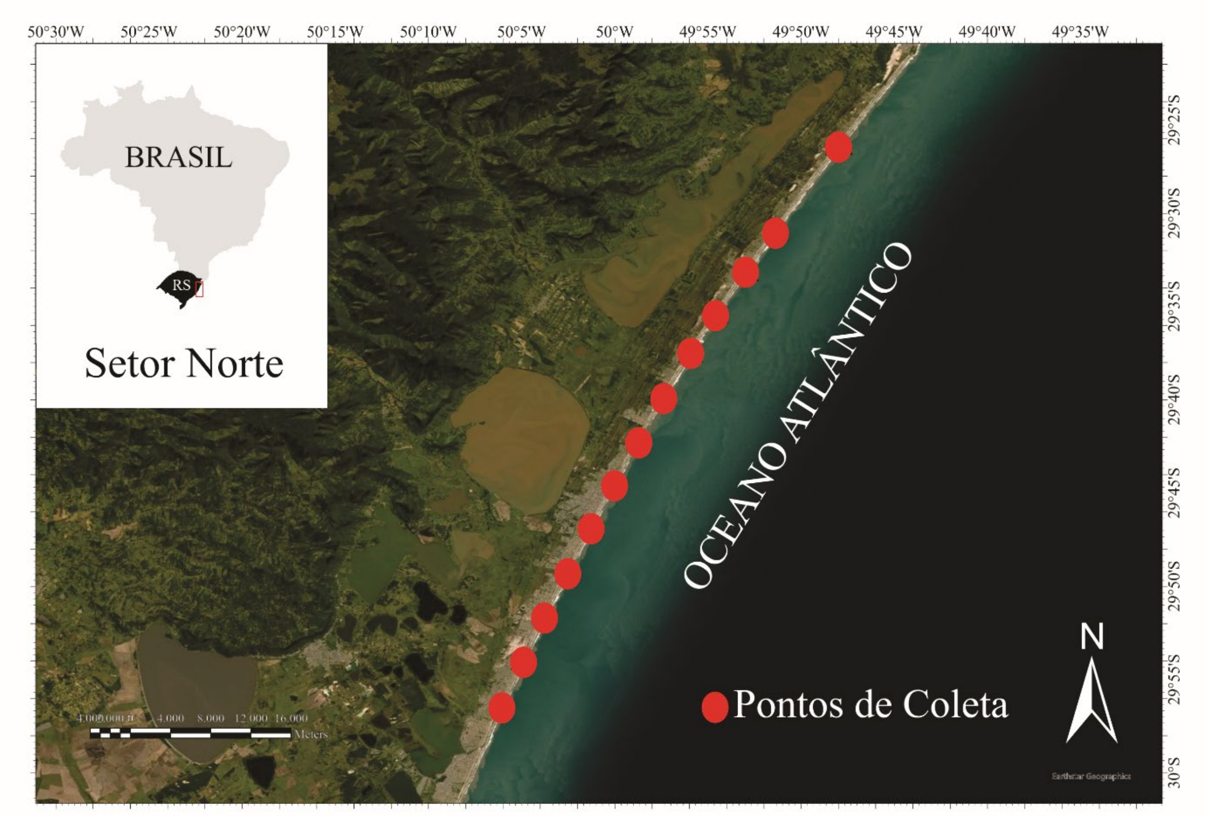

Figura 3 - Localização dos pontos de coleta do setor norte (modificada de Santos, 2020).

Os espécimes de moluscos encontrados foram identificados ao menor nível taxonômico exequível, de acordo com Wiggers (2003), Pimpão (2004) e Rios (2009). Para todas as conchas foram tomadas medidas de comprimento (C) e altura (H) máxima, em milímetros (Fig. 5), por meio de um paquímetro digital, com erro de até 0,1 mm. A partir dessas medidas, o tamanho corporal para cada indivíduo foi estimado, através da média geométrica, de acordo com Kosnik *et al*. (2006). O tamanho corporal foi calculado para todas as valvas com baixo grau de fragmentação (<10%, Zuschin *et al*., 2003).

Figura 4 - Quadrante de 1 m² utilizado para coletada dos moluscos presentes na superfície (até 1 cm).

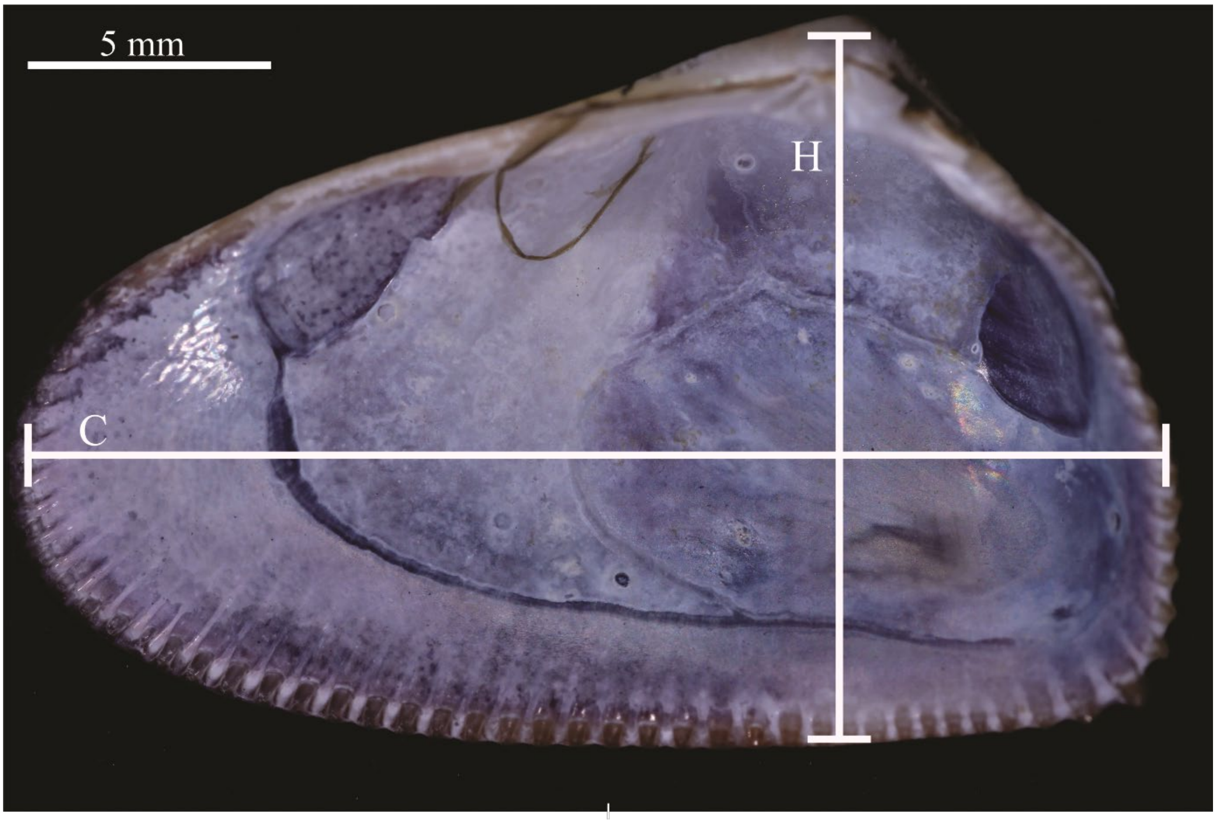

Figura 5 - Medidas do tamanho corporal (altura – H; comprimento – C) de uma valva direita (v.d.) do molusco bivalve *Donax hanleyanus*.

Todas as valvas foram observadas em microscópio estereoscópio quanto a presença de qualquer tipo de traço que indique a presença de parasitas. Além da busca e identificação, os traços encontrados também foram quantificados e seu local de ocorrência registrado (interior da linha palial, seio palial, cicatrizes dos músculos adutores e nas margens da valva). Para assegurar que apenas indivíduos fossem contabilizados, o número de organismos foi estimado como o número de valvas fechadas mais as valvas desarticuladas que apresentaram a maior frequência: diretas ou esquerdas.

2.4 Análise de dados

A prevalência de infestação foi calculada por meio da divisão do número total de indivíduos infestados pelo número total de espécimes (para cada setor da costa e para cada amostra) (Huntley & Scarponi 2012). Um intervalo de confiança de 95% foi estimado para cada amostra através da função “*prop.test*” do pacote básico do R (R Core Team, 2022). Para comparar a prevalência entre os setores, foi realizado teste não paramétrico de Mann-Whitney-Wilcoxon, após transformação em arco seno (Huntley & Scarponi, 2015).

As medidas obtidas para tamanho e comprimento, foram comparadas por meio de uma regressão de eixo principal reduzido (RMA, do inglês, *reduced major axis regression*), considerando possíveis erros de mensuração em ambos os eixos (Smith, 2009). A RMA foi executada usando o pacote “lmodel2” do R com 9999 permutações (Legendre, 2018). Para verificar a seletividade quanto ao tamanho corporal dos hospedeiros, foi conduzido o teste *t* para comparar o tamanho corporal médio dos indivíduos com traços com aqueles sem traços preservados. Uma vez que teste *t* é sensível ao tamanho amostral (Holland, 2019), a amostra com maior *n* amostral relativo foi reamostrada ao tamanho da menor amostra sem substituição, previamente a realização do teste. Esse mesmo teste foi realizado separadamente para os setores da costa (progradante e retrogradante).

A abundância de traços, aqui chamados de *pits*, foi calculada como o número total de *pits* em uma valva. Quanto a abundância relativa, o cálculo foi feito pela divisão do número total de *pits* da amostra dividido pelo número total de indivíduos (Huntley & Scarponi, 2021). O cálculo para estimar a ocorrência da agregação foi realizado por meio da razão entre a variância e a média da abundância de traços (Wilson *et al.*, 2002). Através de um modelo de regressão linear usando transformação logarítmica, obtivemos a inclinação da reta entre a variância e a abundância média (Shaw & Dobson, 1995; Wilson *et al*., 2002; Johnson & Hoverman, 2014). Valores de inclinação maiores que um comprovam a ocorrência da agregação dos parasitas entre hospedeiros (Wilson *et al*., 2002). A assimetria da distribuição da abundância do número de traços por concha foi realizada utilizando a função "skewness" do pacote "moments" do R (Komsta & Novomestky, 2022).

3 RESULTADOS E DISCUSSÃO

Embora obtivemos um total de 22 espécies, apenas a espécie *D. hanleyanus* apresentou traços da interação com trematódeos, caracterizados por seu formato ovalado e bordas finas elevadas representando a tentativa do hospedeiro ainda vivo de isolar o parasita. Organismos infestados estão propensos a serem manipulados de alguma forma pelos parasitas, para que assim, eles completem seu ciclo de vida (Poulin, 2010). Esse fato foi demonstrado em organismos infestados de *Tagelus plebeius* ([Lightfoot], 1786), onde os parasitas foram responsáveis por um aumento na frequência de filtração, tornando, devido à sua exposição mais frequente, mais vulnerável aos predadores (Addino *et al*., 2010).

D. hanleyanus é uma das principais fontes de alimento de diversas aves marinhas na costa do RS, entre elas o piru-piru (*Haematopus palliatus* (Temminck, 1820)) (Linhares *et al*., 2021). Ao mesmo tempo que a predação por aves marinhas é fundamental para o ciclo de vida do parasita, pode também se tornar um viés de preservação negativa, fragmentando as valvas onde se encontram os traços (e.g., Cadée 1989, 1994, 1995; Zuschin *et al*., 2003).

O valor de prevalência total de parasitismo foi de 0,599. Quanto aos setores, a prevalência para o setor predominantemente progradante foi de 0,639, enquanto para o setor predominantemente retrogradante foi de 0,540. Nossos resultados são levemente mais elevados do que aqueles obtidos por Scarponi *et al*. (2017) e por Huntley & Scarponi (2021). Apesar do setor predominantemente progradante apresentar valores de prevalência levemente mais expressivos, quando comparados ao setor predominantemente retrogradante, eles se mostraram estatisticamente similares (p = 0.083). Nossos dados parecem demonstrar uma relação fraca entre padrões de empilhamento sedimentar atual e valores de prevalência, em dissonância com aqueles demonstrados para o Mar Adriático (Scarponi *et al*., 2017; Huntley & Scarponi, 2021).

A linha de costa do Rio Grande do Sul possui projeções onde a maior energia de onda propicia elevados valores de erosão, originando uma barreira retrogradacional. Já os embaiamentos são atingidos por ondas de menor energia e, assim, geram uma barreira progradacional (Dillenburg *et al*., 2000; Martinho *et al*., 2010; Dillenburg & Barboza, 2014; Rosa *et al*., 2017). O aporte de sedimentos para a costa também é baixo, pois a descarga de sedimentos se encontra represada em lagoas originadas pelo sistema de laguna-barreira (Tomazelli *et al*., 1998). Ao longo da costa, há a ocorrência de ondulações oriundas de sul, que embora menos frequentes, transportam mais de 30% de sedimento em direção nordeste, viabilizando a deriva litorânea (Tomazelli & Villwock 1992; Lima *et al*., 2001; Toldo *et al*., 2006). Portanto, o balanço de sedimentos da costa é altamente influenciado pela topografia antecedente e pela deriva litorânea (Dillenburg *et al*., 2000). Ainda, a quantidade de sedimentos carreados no transporte longitudinal é maior onde a linha de costa possui projeções; menor onde há embaiamentos (Martinho *et al*., 2009). Todos estes fatores parecem demonstrar que a morfologia da costa, em conjunto com a deriva litorânea, é determinante para o entendimento dos valores de prevalência de parasitismo obtidos para a costa do Rio Grande do Sul. A deriva litorânea resultante de sudoeste para nordeste, que atua por toda extensão da costa, é capaz de realizar transporte não apenas de sedimentos, mas também de bioclastos, dessa forma, podendo deslocar as valvas do setor retrogradacional, em direção ao setor progradacional. Destacamos ainda que estes padrões (deriva litorânea e topografia antecedente) têm influenciado a evolução da barreira Holocênica durante os últimos 5 ka (Dillenburg *et al*., 2000; Martinho *et al*., 2009; Dillenburg & Barboza, 2014).

Referente a distribuição dos traços, alguns padrões se sobrepõem, como o padrão de agregação dos parasitas. Agregação se manifesta quando muitos indivíduos possuem um número reduzido de parasitas, enquanto poucos indivíduos abrigam um elevado número (Shaw & Dobson, 1995; Shaw *et al*., 1998). O valor que obtivemos para a inclinação da curva de regressão foi de 2.029, resultado relativamente alto, quando comparado a estudos prévios sobre o tema (*e.g.*, Johnson & Hoverman, 2014; Huntley & Scarponi, 2021). Diversos fatores heterogênicos influenciam a agregação dos parasitas, entre eles, sexo, idade, condição corporal e genética do hospedeiro (Wilson *et al*., 2002). Contudo, é importante considerar a sazonalidade e o momento em que o hospedeiro está exposto ao parasita, pois os processos tendem a ocorrer em conjunto com os fatores heterogênicos (Wilson *et al.*, 2002; Raffel *et al.*, 2011). A agregação pode apontar como a população está estruturada, pois populações onde o valor de agregação é alto, os parasitas são capazes de atuar como reguladores do crescimento populacional (Anderson & May, 1978; Adler & Kretzschmar, 1992).

No que concerne aos traços encontrados, podemos inferir diversas informações. A média do tamanho corporal dos indivíduos infestados foi de 16,45 mm, enquanto para os indivíduos não infestados foi de 15,71 mm. Estes dados demonstram que os indivíduos infestados são relativamente maiores, quando comparados aos indivíduos não infestados. Com relação a quantidade de traços, constatamos um declínio no número de traços quando o hospedeiro atinge o tamanho corporal de 20 mm. Este padrão, entre intensidade de parasitas e a idade do hospedeiro, pode estar atrelado a aquisição de imunidade, morte ou predisposição à infestação por parte do hospedeiro (Hudson & Dobson, 1995; Wilson *et al.*, 2002; Raffel *et al.*, 2011). Não existe preferência de traços entre a valvas direitas ou esquerdas, corroborando com as proposições elaboradas por Huntley (2007).

O meio extra palial abriga cerca de 70% dos traços de trematódeos, seguido pelo setor que demarca o seio palial na parte posterior, 25,5%, com cerca de 3,4 % dos traços na margem da concha, e raros no músculo adutor posterior (0,8 %) e anterior (0,3%). Os parasitas da família Gymnophallidae tendem a colonizar o meio extra palial quando metacercárias (Lauckner, 1983; Ituarte *et al.*, 2001; Cremonte & Ituarte, 2003; Cremonte, 2004). Para o setor da valva com a segunda maior ocorrência de traços (25,5%), que abrange a porção posterior do seio palial, autores como Lauckner (1983) e Ituarte *et al.* (2009) identificaram metacercárias próximas ao seio palial, em locais correspondentes a setorização utilizada neste trabalho, em hospedeiros que possuíam altos níveis de infestação e em idade avançada.

4 CONSIDERAÇÕES FINAIS

A interação parasita-hospedeiro está presente em moluscos bivalves coletados em setores progradantes e retrogradantes do litoral sul do Brasil, identificados por meio dos traços correspondentes aos produzidos por metacercárias da família

Gymnophallidae. Esses traços foram encontrados apenas nas valvas do molusco bivalve *Donax hanleyanus*. Isso reforça que existe seleção taxonômica exercida pelos parasitas. É a primeira vez que estes traços são descritos para conchas vazias do litoral brasileiro. O valor geral de prevalência é relativamente mais alto quando comparado aos estudos prévios sobre o tema. Nosso estudo aponta que fatores locais da costa exercem controle sobre a resolução espacial e assim, influenciam os padrões de prevalência associados ao comportamento da linha de costa atual e possivelmente o registro fóssil resultante.

Com nossos dados demonstramos ainda que os parasitas trematódeos selecionam seus hospedeiros pelo seu tamanho corporal, até o tamanho de 20 mm, quando a quantidade de traços declina. Verificamos que os parasitas estão altamente agregados entre os seus hospedeiros. Dados como a não seletividade de valvas e no que concerne a agregação, reforçam o uso dos traços como um proxy valioso para o estudo da interação no registro fóssil. Constatamos que há um local preferencial de assentamento das metacercárias, o meio extra palial, padrão este já conhecido para bivalves modernos.

Ponderando sobre a quantidade de informações retiradas do registro fóssil, podemos inferir como os parasitas respondem as mudanças climáticas e também aquelas ocorridas no ambiente em momentos de variações no nível relativo do mar, e assim, tornar exequível medidas de conservação e preservação dos serviços ecossistêmicos, pertinentes a manutenção da sociedade, frente as consequências do aquecimento global em curso. Sumariamente, os resultados apresentados e discutidos aqui reforçam a importância de estudos que avaliem de forma quantitativa a interação parasitismo-hospedeiro, visto a enorme gama de informações que podemos inferir em um cenário de mudanças globais.

REFERÊNCIAS

Addino, M., Lomovasky, B.J., Cremonte, F. & Iribarne, O. 2010. Infection by gymnophallid metacercariae enhances predation mortality of SW Atlantic stout razor clam *Tagelus plebeius*. *Journal of Sea Research*, 63(2): 102-107.

Adler, F.R. & Kretzschmar, M. 1992. Aggregation and stability in parasite—host models. *Parasitology*, 104(2): 199-205.

Anderson, R.M. & May, R.M. 1978. Regulation and stability of host-parasite population interactions. *Journal of Animal Ecology*, 47(1): 219-247.

Angulo, R.J., Lessa, G.C. & de Souza, M.C. 2006. A critical review of mid-to late-Holocene sea-level fluctuations on the eastern Brazilian coastline. *Quaternary Science Reviews*, 25(5-6): 486-506.

Ansell, A.D. 1983. The biology of the genus *Donax*. *In*: McLachlan, A. & Erasmus, T. (Eds.). *Sandy beaches as ecosystems.* Port Elizabeth, South Africa, p. 607-635.

Barboza, E.G., Dillenburg, S.R., Ritter, M.N., Angulo, R.J., Silva, A.B., Rosa, M.L.C.D.C. & Souza, M. C. 2021. Holocene sea-level changes in southern Brazil based on high-resolution radar stratigraphy. *Geosciences*, 11(8): 326.

Baumiller, T.K. & Gahn, F.J. 2002. Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid-crinoid interaction. *The Paleontological Society Papers*, 8: 195-210.

Bom, F.C. & Colling, L.A. 2022. The bivalves *Amarilladesma mactroides* and *Donax hanleyanus* as bioindicators of the impact of vehicles on Cassino Beach, southern Brazil. *Anais da Academia Brasileira de Ciências*, 94.

Byers, J.E. 2021. Marine parasites and disease in the era of global climate change. *Annual Review of Marine Science*, 13: 397-420.

Cadée, G.C. 1989. Size-selective transport of shells by birds and its palaeoecological implications. *Palaeontology*, 32: 429–437.

Cadée, G.C. 1994. Eider, shelduck, and other predators, the main producers of shell fragments in the Wadden Sea. *Palaeontology*, 37: 181–202.

Cadée, G.C. 1995. Birds as producers of shell fragments in the Wadden Sea, in particular the role of the Herring gull. *Geobios*, 18: 77–85.

Cardoso, R. & Veloso, V. 2003. Population dynamics and secondary production of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) on a high-energy, subtropical beach of Brazil. *Marine Biology*, 142: 153-162.

Celentano, E., Gómez, J., Lercari, D., de Álava, A. & Defeo, O. 2022. Unravelling the role of local and large-scale factors in structuring sandy beach populations: the wedge clam *Donax hanleyanus*. *Marine Ecology Progress Series*, 696: 29-42.

Cremonte, F. 2004. Life cycle and geographic distribution of the gymnophallid *Bartolius pierrei* (Digenea) on the Patagonian coast, Argentina. *Journal of Natural History*, 38(13): 1591-1604.

Cremonte, F. & Ituarte, C. 2003. Pathologies elicited by the gymnophallid metacercariae of *Bartolius pierrei* in the clam *Darina solenoides*. *Journal of the Marine Biological Association of the United Kingdom*, 83(2): 311-318.

Cribb, T.H., Bray, R.A., Olson, P.D. & Littlewood, D.T.J. 2003. Life cycle evolution in the Digenea: a new perspective from phylogeny. *Advances in Parasitology*, 54(1): 197-254.

D'orbigny, A.D. 1834–1847, Mollusques, in C.P. Bertrand (ed.), Voyage dans l'Amerique Meridionale (Le Bresil, La Republique Orientale de L'Uruguay, La Republique Argentine, La Patagonie, La Republique du Chili, La Republique de Bolivia, La Republique du Perou), execute pendant les annees 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833: Chez Ve. Levrault, Paris, Livraison 82, p. 489-528.

Defeo, O. & de Alava, A. 1995. Effects of human activities on long-term trends in sandy beach populations: the wedge clam *Donax hanleyanus* in Uruguay. *Marine Ecology Progress Series*, 123: 73-82.

Delgado, E. & Defeo, O. 2007. Tisular and population level responses to habitat harshness in sandy beaches: the reproductive strategy of *Donax hanleyanus*. *Marine Biology*, 152(4): 919-927.

Dillenburg, S.R. & Barboza, E.G. 2014. The strike-fed sandy coast of Southern Brazil. *Geological Society, London, Special Publications*, 388(1): 333-352.

Dillenburg, S.R., Roy, P.S., Cowell, P.J. & Tomazelli, L.J. 2000. Influence of antecedent topography on coastal evolution as tested by the shoreface translation-barrier model (STM). *Journal of Coastal Research*, 16: 71-81.

Dillenburg, S.R., Hesp, P.A., Dillenburg, S.R., Barboza, E.G., Tomazelli, L.J., Ayup-Zouain, R.N. & Clerot, L.C. 2009. The holocene coastal barriers of Rio Grande do Sul.

In: Dillenburg, S.R. & Hesp, P.A. (Eds.). *Geology and geomorphology of Holocene coastal barriers of Brazil*, Berlin, p. 53-91.

Farrar, L., Graves, E., Petsios, E., Portell, R.W., Grun, T.B., Kowalewski, M. & Tyler, C.L. 2020. Characterization of traces of predation and parasitism on fossil echinoids. *Palaios*, 35(5): 215-227.

Galaktionov, K.V. 2007. A description of the parthenogenetic metacercaria and cercaria of *Cercaria falsicingulae* I larva nov. (Digenea: Gymnophallidae) from the snails *Falsicingula* spp. (Gastropoda), with speculation on an unusual life-cycle. *Systematic Parasitology*, 68(2): 137-146.

Gianuca, N.M. 1985. *The ecology of a sandy beach in Southern Brazil*. 330 p. Tese de Doutorado, University of Southampton.

Gil, G.M. & Thomé, J.W. 2004. Proporção sexual e comprimento de concha na primeira maturação sexual em *Donax hanleyanus* Philippi (Bivalvia, Donacidae) no Rio Grande do Sul, Brasil. *Revista Brasileira de Zoologia,* 21(2): 345-350.

Herrmann, M., Carstensen, D., Fischer, S., Laudien, J., Penchaszadeh, P.E. & Arntz, W.E. 2009. Population structure, growth, and production of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) from Northern Argentinean beaches. *Journal of Shellfish Research*, 28(3): 511-526.

Hill-Spanik, K.M., Sams, C., Connors, V.A., Bricker, T. & de Buron, I. 2021. Molecular data reshape our understanding of the life cycles of three digeneans (Monorchiidae and Gymnophallidae) infecting the bivalve, *Donax variabilis*: it’s just a facultative host. *Parasite*, 28.

Holland, S.M. 2019. Estimation, not significance. *Paleobiology*, 45(1): 1-6.

Hudson, P.J. & Dobson, A.P. 1995. Macroparasites: observed patterns in naturally fluctuating animal populations. *Ecology of Infectious Diseases in Natural Populations*, 5: 144-176.

Huntley, J.W. 2007. Towards establishing a modern baseline for paleopathology: trace-producing parasites in a bivalve host. *Journal of Shellfish Research*, 26(1): 253-259.

Huntley, J.W. & Scarponi, D. 2012. Evolutionary and ecological implications of trematode parasitism of modern and fossil northern Adriatic bivalves. *Paleobiology*, 38(1): 40-51.

Huntley, J.W. & Scarponi, D. 2015. Geographic variation of parasitic and predatory traces on mollusks in the northern Adriatic Sea, Italy: implications for the stratigraphic paleobiology of biotic interactions. *Paleobiology*, 41(1): 134-153.

Huntley, J.W. & Scarponi, D. 2021. Parasitism and host behavior in the context of a changing environment: The Holocene record of the commercially important bivalve *Chamelea gallina*, northern Italy. *PLoS ONE*, 16(4): e0247790.

Huntley, J.W. & De Baets, K. 2015. Trace fossil evidence of trematode—bivalve parasite—host interactions in deep time. *In*: Rollinson, D., Stothard, R. (Eds.). *Advances in Parasitology*. Academic Press, p. 201-231.

Huntley, J.W. & Kowalewski, M. 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. *Proceedings of the National Academy of Sciences*, 104(38): 15006-15010.

Huntley, J.W., Fürsich, F.T., Alberti, M., Hethke, M. & Liu, C. 2014. A complete Holocene record of trematode–bivalve infection and implications for the response of parasitism to climate change. *Proceedings of the National Academy of Sciences*, 111(51): 18150-18155.

Ituarte, C., Cremonte, F. & Scarano, A. 2009. Tissue reaction of *Tagelus plebeius* (Bivalvia: Psammobiidae) against larval digeneans in mixohaline habitats connected to the south-western Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 89(3): 569-577.

Ituarte, C., Cremonte, F. & Zelaya, D.G. 2005. Parasite-mediated shell alterations in Recent and Holocene sub-Antarctic bivalves: the parasite as modeler of host reaction. *Invertebrate Biology*, 124(3): 220-229.

Ituarte, C.F., Cremonte, F. & Deferrari, G. 2001. Mantle-shell complex reactions elicited by digenean metacercariae in *Gaimardia trapesina* (Bivalvia: Gaimardiidae) from the Southwestern Atlantic Ocean and Magellan Strait. *Diseases of Aquatic Organisms*, 48(1): 47-56.

Johnson, P.T. & Hoverman, J.T. 2014. Heterogeneous hosts: how variation in host size, behaviour and immunity affects parasite aggregation. *Journal of Animal Ecology*, 83(5): 1103-1112.

Klompmaker, A.A., Kelley, P.H., Chattopadhyay, D., Clements, J.C., Huntley, J.W. & Kowalewski, M. 2019. Predation in the marine fossil record: studies, data, recognition, environmental factors, and behavior. *Earth-Science Reviews*, 194: 472-520.

Komsta, L. & Novomestky, F. 2022. moments: Moments, Cumulants, Skewness, Kurtosis and Related Tests. R package version 0.14.1. https://CRAN.R-project.org/package=moments

Köpen, W. 1948. *Climatologia: con un estudio de los climas de la tierra*. México, Fondo de Cultura Econômica, 479 p.

Kosnik, M.A., Jablonski, D., Lockwood, R. & Novack-Gottshall, P.M. 2006. Quantifying molluscan body size in evolutionary and ecological analyses: maximizing the return on data-collection efforts. *Palaios*, 21(6): 588-597.

Lauckner, G. 1983. Diseases of Mollusca: Bivalvia. *In:* O. Kinne. (Ed.). *Diseases of Marine Animals Introduction. Bivalvia to Scaphopoda*. Biologische Anstalt Helgoland, Hamburg, p. 477–961.

Legendre, P. 2018. Lmodel2: Model II Regression. R package version 1.7-3. https://CRAN.R-project.org/package=lmodel2

Lightfoot, J. 1786. A Catalogue of the Portland Museum, lately the property of the Dutchess Dowager of Portland, deceased; which will be sold by auction. London, Skinner & Co., 194p.

Lima, S.F., Almeida, L.E. & Toldo Jr., E. 2001. Estimativa da Capacidade de Transporte Longitudinal de Sedimentos a partir de Dados de Ondas para a Costa do Rio Grande do Sul. *Pesquisas em Geociências*, 28: 99-107.

Linhares, B.D.A., Bordin, J., Nunes, G.T. & Ott, P.H. 2021. Breeding biology of the American Oystercatcher *Haematopus palliatus* on a key site for conservation in southern Brazil. *Ornithology Research*, 29(1): 16-21.

Linnaeus, C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 824p.

Littlewood, D.T.J. & Donovan, S.K. 2003. Feature: fossil parasites: a case of identity. *Geology Today*, 19(4): 136-142.

Lopes, R.P., Oliveira, L.C., Figueiredo, A.M.G., Kinoshita, A., Baffa, O. & Buchmann, F.S. 2010. ESR dating of Pleistocene mammal teeth and its implications for the biostratigraphy and geological evolution of the coastal plain, Rio Grande do Sul, southern Brazil. *Quaternary International*, 212(2): 213-222.

Lopes, R.P., Kinoshita, A., Baffa, O., Figueiredo, A.M.G., Dillenburg, S.R., Schultz, C.L. & Pereira, J.C. 2014. ESR dating of Pleistocene mammals and marine shells from the coastal plain of Rio Grande do Sul state, southern Brazil. *Quaternary International*, 352: 124-134.

Morales-Castilla, I., Matias, M.G., Gravel, D., & Araújo, M.B. 2015. Inferring biotic interactions from proxies. *Trends in Ecology & Evolution*, 30(6): 347-356.

Marcogliese, D.J. 2004. Parasites: small players with crucial roles in the ecological theater. *EcoHealth*, 1(2): 151-164.

Marcogliese, D.J. 2005. Parasites of the superorganism: are they indicators of ecosystem health? *International Journal for Parasitology*, 35(7): 705-716.

Marcogliese, D.J. 2008. The impact of climate change on the parasites and infectious diseases of aquatic animals. *Revue Scientifique et Technique*, 27(2): 467-484.

Marcogliese, D.J. 2016. The distribution and abundance of parasites in aquatic ecosystems in a changing climate: more than just temperature. *Integrative and Comparative Biology*, 56(4): 611-619.

Marcomini, S.C., Penchaszadeh, P., Lopez, R.A. & Luzzatto, D. 2002. Beach morphodynamics and clam (*Donax hanleyanus*) densities in Buenos Aires, Argentina. *Journal of Coastal Research*, 18: 601-611.

Marini, K., Spotorno, P., Diniz, D. & Dentzien-Dias, P. 2022. Ecological interactions on shells of *Mactra isabelleana* d'Orbigny, 1846 (Mollusca: Bivalvia) from southern Brazil: first record of a unique host–parasite interaction. *Aquatic Ecology*, 56(4): 1205-1216.

Martinho, C.T., Dillenburg, S.R. & Hesp, P. 2009. Wave energy and longshore sediment transport gradients controlling barrier evolution in Rio Grande do Sul, Brazil. *Journal of Coastal Research*, 25(2): 285-293.

Martinho, C.T., Hesp, P.A. & Dillenburg, S.R. 2010. Morphological and temporal variations of transgressive dunefields of the northern and mid-littoral Rio Grande do Sul coast, Southern Brazil. *Geomorphology*, 117(1-2): 14-32.

Mawe, J. 1823. *The Linnaean system of conchology, describing the orders, genera and species of shells, arranged into divisions and families*. London, 207 p.

Montenegro, D., Romero, M.S. & González, M.T. 2021. Morphological and molecular characterization of larval digenean trematodes (Parvatrema: Gymnophallidae) and their pathological effects on the clam *Leukoma thaca* (= *Protothaca thaca*) (Bivalvia: Veneridae) (Molina, 1782) from northern Chile. *Parasitology International*, 80: 102238.

Mouritsen, K.N. & Poulin, R. 2002. Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology*, 124(7): 101-117.

Mouritsen, K.N. & Poulin, R. 2005. Parasites boosts biodiversity and changes animal community structure by trait-mediated indirect effects. *Oikos*, 108(2): 344-350.

Philippi, R.A. 1847. Versuch einer systematischen Eintheilung des Geschlechtes Trochus. *Zeitschrift für Malakozoologie*, p.17-26.

Pimpão, D.M. 2004. *Moluscos bivalves da plataforma externa e talude superior ao largo de Rio Grande*. Porto Alegra, 190 p. Dissertação – Instituto de Biociências, Universidade Federal do Rio Grande do Sul.

Poulin, R. 2010. Parasite manipulation of host behavior, an update and frequently asked questions. *In:* Brockmann, H.J. (Ed.). *Advances in the Study of Behavior*. Burlington, Academic Press, p. 151-186

R CORE TEAM. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2022. Disponível em: https://www.R-project.org/.

Raffel, T.R., Lloyd-Smith, J.O., Sessions, S.K., Hudson, P.J. & Rohr, J.R. 2011. Does the early frog catch the worm? Disentangling potential drivers of a parasite age–intensity relationship in tadpoles. *Oecologia*, 165: 1031-1042.

Reeve, L.A. 1854. Monograph of the genus Mesodesma. *Conchologia Iconica, or,illustrations of the shells of molluscous animals*. London, Reeve & Co. Pls 1-4.

Rios, E.C. 2009. *Compendium of Brazilian sea shells*. Rio Grande, Evangraf, p. 676.

Risoli, M.C., Defeo, O., Yusseppone, M.S., Piola, A.R., Clara, M.L. & Lomovasky, B.J. 2022. Disentangling patterns in population parameters of the wedge clam *Donax hanleyanus* from sandy beaches of Argentina: The role of environmental variability. *Marine Environmental Research*, 174: 105564.

Rodrigues, S.C., Simões, M.G., Kowalewski, M., Petti, M.A., Nonato, E.F., Martinez, S. & Del Rio, C.J. 2008. Biotic interaction between spionid polychaetes and bouchardiid brachiopods: Paleoecological, taphonomic and evolutionary implications. *Acta Palaeontologica Polonica*, 53(4): 657-668.

Rogers, R.R., Curry Rogers, K.A., Bagley, B.C., Goodin, J.J., Hartman, J.H., Thole, J.T. & Zatoń, M. 2018. Pushing the record of trematode parasitism of bivalves upstream and back to the Cretaceous. *Geology*, 46(5): 431-434.

Rosa, M.L.C.C. 2012. *Geomorfologia, Estratigrafia de Sequências e Potencial de Preservação dos Sistemas Laguna-Barreira do Quaternário Costeiro do Rio Grande do Sul*. Porto Alegre, 251 p. Tese, Programa de Pós-graduação em Geociências, Instituto de Geociências, Universidade Federal do Rio Grande do Sul.

Rosa, M.L.C.D.C., Barboza, E.G., Abreu, V.D.S., Tomazelli, L.J. & Dillenburg, S.R. 2017. High-Frequency Sequences in the Quaternary of Pelotas Basin (coastal plain): a record of degradational stacking as a function of longer-term base-level fall. *Brazilian Journal of Geology*, 47: 183-207.

Ruiz, G.M. & Lindberg, D.R. 1989. A fossil record for trematodes: extent and potential uses. *Lethaia*, 22(4): 431-438p.

Scarponi, D., Azzarone, M., Kowalewski, M. & Huntley, J.W. 2017. Surges in trematode prevalence linked to centennial-scale flooding events in the Adriatic. *Scientific Reports*, 7(1): 5732.

Shaw, D.J. & Dobson, A.P. 1995. Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review. *Parasitology*, 111(S1): S111-S133.

Shaw, D.J., Grenfell, B.T & Dobson, A.P. 1998. Patterns of macroparasite aggregation in wildlife host populations. *Parasitology*, 117: 597-610.

Schmitt, W.L. 1935. Crustacea Macrura and Anomura of Porto Rico and the Virgin Islands. *Scientific survey of Porto Rico and the Virgin Islands*, 15(2): 125-227.

Smith, R.J. 2009. Use and misuse of the reduced major axis for line-fitting. American *Journal of Physical Anthropology*, 140: 476-486.

Stanley, S.M. 2008. Predation defeats competition on the seafloor. *Paleobiology*, 34(1): 1-21.

Studer, A., Thieltges, D.W. & Poulin, R. 2010. Parasites and global warming: net effects of temperature on an intertidal host–parasite system. *Marine Ecology Progress Series*, 415: 11-22.

Thompson, G.A. & Sánchez De Bock, M.F. 2009. Influence of beach morphodynamics on the bivalve *Donax hanleyanus* and *Mesodesma mactroides* populations in Argentina. *Marine Ecology*, 30(2): 198-211.

Todd, J.A. & Harper, E.M. 2011. Stereotypic boring behaviour inferred from the earliest known octopod feeding traces: Early Eocene, southern England. *Lethaia*, 44(2): 214-222.

Toldo Jr, E, Almeida, L., Nicolodi, J. L., Absalonsen, L. & Gruber, N. 2006. O controle da deriva litorânea no desenvolvimento do campo de dunas e da antepraia no litoral médio do Rio Grande do Sul. *Pesquisas em Geociências*, 33: 35-42.

Tomazelli, L. & Villwock J. 1992. Considerações sobre o ambiente praial e a deriva litorânea de sedimentos ao longo do litoral norte do Rio Grande do Sul, Brasil. *Pesquisas em Geociências*, 19(1): 3-12.

Tomazelli, L.J. & Villwock, J.A. 2000. O cenozóico costeiro do rio grande do sul. *In*: Holz, M; Ros, L.F. (Eds.). *Geologia do Rio Grande do Sul*, p. 375-406.

Tomazelli, L.J. & Villwock, J.A. 2005. Mapeamento geológico de planícies costeiras: o exemplo da costa do Rio Grande do Sul. *Gravel*, 3(1): 110-115.

Tomazelli, L.J. & Dillenburg, S.R. 2007. Sedimentary facies and stratigraphy of a last interglacial coastal barrier in south Brazil. *Marine Geology*, 244(1-4): 33-45.

Tomazelli, L.J., Dillenburg, S.R. & Villwock, J.A. 2000. Late Quaternary geological history of Rio Grande do Sul coastal plain, southern Brazil. *Brazilian Journal of Geology*, 30: 474-476

Tomazelli L. J., Villwock, J.A., Dillenburg, S.R, Bachi, F.A. & Dehnhardt, B.A. 1998. Significance of present-day coastal erosion and marine transgression, Rio Grande do Sul, Southern Brazil. *Anais da Academia Brasileira de Ciências,* 70: 221-229.

Travessas, F.A., Dillenburg, S.R. & Clerot, L.C.P. 2005. Estratigrafia e evolução da barreira holocênica do Rio Grande do Sul no trecho Tramandaí-Cidreira. *Boletim Paranaense de Geociências*, 57.

Van Valen, L.M. 1973. A new evolutionary law. *Evolutionary Theory*, 10: 71-74.

Vazquez, N.N., Ituarte, C., Navone, G.T. & Cremonte, F. 2006. Parasites of the stout razor clam *Tagelus plebeius* (Psammobiidae) from the southwestern Atlantic Ocean. *Journal of Shellfish Research*, 25(3): 877-886.

Vermeij, G.J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, 3: 245-258.

Villwock, J.A. & Tomazelli, L.J. 2007. Planície Costeira do Rio Grande do Sul: gênese e paisagem atual. *Regiões da Lagoa do Casamento e dos Butiazais de Tapes, Planície Costeira do Rio Grande do Sul*, 20.

Wiggers, F. 2003. *Moluscos gastrópodes da plataforma continental externa e talude continental ao largo da laguna dos Patos-Rio Grande do Sul, Brasil*. Porto Alegre, 128 p. Dissertação – Instituto de Biociências, Universidade Federal do Rio Grande do Sul.

Wilson, K., Bjørnstad, O.N., Dobson, A.P., Merler, S., Poglayen, G., Randolph, S.E., Read, A.F. & Skorping, A. 2002. Heterogeneities in macroparasite infections: patterns and processes. In: Hudson, P.J., Rizzoli, A., Grenfell, B.T., Heesterbeek, H. & Dobson, A.P. (Eds.). *The Ecology of Wildlife Diseases*. Oxford University Press, Oxford, p. 6-44.

Zuschin, M., Stachowitsch, M. & Stanton Jr, R.J. 2003. Patterns and processes of shell fragmentation in modern and ancient marine environments. *Earth-Science Reviews*, 63(1-2): 33-82.

5 ARTIGO SUBMETIDO

The power of location: prevalence of traces of parasites in marine mollusks reflects the spatial mixing within coast sectors with different stratigraphic scenarios

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Abstract —Traces of parasitism found in fossil records are considered rare. Digenetic trematodes are of particular interest in this context. Understanding the dynamics of this interaction is essential, as it may be linked to global patterns of sea level rise and temperature change. This study evaluated the prevalence of traces of parasitism preserved in mollusk shells collected from coastal regions with recent and ongoing retrogradational and progradational patterns on the north coast of Rio Grande do Sul, Brazil. It investigated the relationship between host body size and parasite abundance, and the distribution of parasite traces within the valves of the host organism. By analyzing the traces of trematode parasites found only in the valves of the bivalve mollusk *Donax hanleyanus*, we determined that the prevalence and abundance of parasites was higher in hosts with larger body sizes and, therefore, older ages, and that the extra pallial environment is the preferred location for parasite settlement. We observed a strong pattern of aggregation among hosts and a lack of selectivity for specific shells (left or right), which supports the use of parasite traces as a proxy for studies in the fossil record. The overall prevalence (0.599) was found to be high, but no clear relationship was established with the dominant sediment stacking pattern. This suggests that, at a local scale, autogenic factors overlap with stratigraphic variations in relative sea level. The findings highlight the need for continued research for a deeper understanding of parasitism patterns in the fossil record.

Keywords: Stratigraphic paleobiology, Trematoda, South America.

INTRODUCTION

Ecological interactions that involve competition, such as parasitism and predation, are fundamental drivers of ecosystem dynamics throughout the history of life on Earth (e.g., Van Valen 1973; Vermeij 1977). Both of these interactions are evolutionary phenomena. However, while predation results in the death of the prey, parasitism involves the utilization of the host, which may or may not result in the host's death (Clarke 1954; Baumiller and Gahn 2002).

Previous research has demonstrated that ecological interactions preserved in the fossil record play a key role in both escalation theory (Vermeij 1977) and the Red Queen hypothesis (Van Valen 1973). Historically, most studies in this field have focused on prey–predator interactions (e.g., Kelley et al. 2003; Huntley and Kowalewski 2007; Stanley 2008; Klompmaker et al. 2017, 2019), likely due to their greater preservation potential in the fossil record (Farrar et al. 2020). However, more recent studies have shifted their focus to host–parasite interactions, primarily through the examination of small marks, blisters, and sheets on the shells of bivalve mollusks (e.g., Huntley 2007; Huntley and Scarponi 2012, 2015; Marini et al. 2022) and brachiopods (Rodrigues et al. 2008).

Parasitism can have a wide range of effects on populations, including feminization, reduced fertility, disease, extinction events, speciation, and increased evolutionary rates (Littlewood and Donovan 2003). Previous research has demonstrated that parasites can significantly influence the structure and functioning of marine invertebrate communities, particularly in unconsolidated sediment environments (e.g., Mouritsen and Poulin 2005; Hudson et al. 2006). Additionally, parasites can impact certain abilities of their hosts, such as mobility, which can lead to changes in host species abundance and interactions (Mouritsen and Poulin 2005). The influence of climatic conditions on the maintenance of these interactions is also noteworthy, as it can affect the transmission of parasites between populations, disrupting the way these interactions occur and leading to epidemics and increasing the risk of host extinction (Hudson et al. 2006; Tjendra et al. 2020). For instance, some studies have found that temperature increases caused by climate change can interfere with the life cycle of parasites, such as trematodes, particularly in their infectious stages (e.g., Mouritsen and Poulin 2005; Studer et al. 2010; Díaz-Morales et al. 2022).

Trematode parasites, particularly those in the subclass Digenea, have a complex life cycle in which the first intermediate host, typically a gastropod, gives rise to cercariae that infect the second host, in this case, a bivalve (Ruiz and Lindberg 1989; Cribb et al. 2003; Pinto and Melo 2013). The cycle is completed when the metacercariae-infected host is consumed by the definitive host, commonly a bird or mammal (Swennen 1969; Cribb et al. 2003; Littlewood and Donovan 2003). As metacercariae, they infest the extra-pallial region of the valves of bivalves, causing geochemical changes that often leave behind preservable traces, allowing the study of host–parasite interactions in the sedimentary record (Huntley and Scarponi 2015, 2021; Leung 2017). This is a promising area of research as studies on body fossils of parasites are relatively uncommon and have been limited to sites of exceptional fossil preservation (*Konservate-Lagerstätten*) (e.g., Maas et al. 2006).

Ruiz and Lindberg (1989) were the first to describe trematodes in bivalves in the fossil record, suggesting that interactions with these parasites can provide paleo-environmental and evolutionary information about their hosts. Since then, similar studies have been conducted on brachiopods, where the interaction occurs with polychaete parasites (Spionidae) (Rodrigues et al. 2008), and in mollusks (e.g., Huntley and Scarponi 2012; Marini et al. 2022). More recent studies have also analyzed the association between prevalence values and stratigraphic events correlated with moments of maximum flooding caused by climate change, which may indicate a possible future scenario, if the ongoing changes in the "Anthropocene" continue at this intensity (e.g., Huntley 2007; Huntley et al. 2014; Huntley and Scarponi 2015, 2021; Scarponi et al. 2017).

As previously mentioned, recent studies on traces of parasitism in the fossil record have primarily focused on mollusks, particularly bivalves, in the Northern Hemisphere (e.g., Huntley and Scarponi 2015, 2021; Scarponi et al. 2017), except for Marini et al. (2022). Despite an increase in research on these interactions, they are still considered rare, despite their significant importance to society. This study aimed to add to the understanding of these interactions. To do this, we studied coastal sectors in southern

Brazil that currently and in the recent past (Holocene) have both retrogradational and progradational behavior, and we analyzed traces that could indicate the presence of host–parasite interactions between bivalve mollusks and trematode parasites in these sectors. We analyzed and quantified the types of traces and their location in the valves, as well as the body size of the host, seeking to relate this data with prevalence values and how they influence the host's behavior. Our results demonstrated that these interactions are present in the Southern Hemisphere. Still, we were not able to establish a distinct relationship between the prevalence of parasitism and the predominant stacking pattern when compared to previous studies. However, this work emphasizes the need for more integrated studies and a closer examination of these interactions.

MATERIALS AND METHODS

Study Area

The study area was located on the north coast of Rio Grande do Sul, Brazil, and covered the municipalities of Torres in the north and Palmares do Sul in the south (Fig. 1). This area is part of the northern sector of the coastal plain of Rio Grande do Sul (CPRS). The CPRS is located on the onshore portion of the Pelotas Basin and contains primarily sediment from the land, dating back to the Lower Cretaceous period. The area has one of the most complete records of Quaternary sedimentation, which can be observed in the most recent portion of the coastal plain (Tomazelli 2000).

The study area was located within the Laguna-Barrier System IV, the most recent of a complex sedimentary structure of coastal barriers and back barriers formed in response to changes in relative sea level during the Late Quaternary (Tomazelli et al. 2000). System IV formed during the Holocene, between 7.8–7.2 ka, during the final stages of the Post-Glacial Marine Transgression, reaching its transgressive peak at 5.6 ka with sea level 1–4 meters above current levels (Angulo et al. 2006; Dillenburg et al. 2009; Dillenburg et al. 2013). This system occupies the entire current coast, resulting in two projections toward the basin and two indentations toward the mainland (Villwock and Tomazelli 2007; Dillenburg et al. 2009; Dillenburg and Barboza 2014; Rosa et al. 2017).

According to Dillenburg et al. (2000), the Holocene coastal barriers in Rio Grande do Sul display progradational and retrogradational stacking patterns. This study area has two sections. The first section is between the cities of Imbé and Torres, and it has a slightly concave coastline, with the greatest progradation occurring in Balneário de Curumim (Dillenburg et al. 2000, 2009). The second sector covers the area from Tramandaí to Palmares do Sul, where the coastline is slightly convex toward the basin (Dillenburg et al. 2009). At the Jardim do Éden beach, south of Tramandaí, outcrops of lagoon muds are found, indicating that the transgression occurred due to a negative sediment balance (Travessas et al. 2005). Similarly, the municipality of Cidreira is exposed to stronger waves and has a high rate of retrogradation (Dillenburg et al. 2000; Travessas et al. 2005). This sector has a predominantly retrogradational pattern and eroding coastline (Esteves et al. 2006; Martinho et al. 2008).

Data Collection and Analysis

Samples were collected from 16 different locations between the municipalities of Imbé and Torres in southern Brazil, which is referred to as the "north area" and has a predominantly progradational coastline (as shown in Fig. 1). Additionally, samples were collected from 11 locations between the municipalities of Tramandaí and Balneário Dunas Altas, in Palmares do Sul, which is referred to as the "south area" and has a predominantly retrogradational coastline (as shown in Fig. 1). Sampling was done every 5 km by using a 1 square meter quadrant to collect all mollusks present on the surface (up to 1 cm deep) of the beach. The collected samples were stored in pots. In the laboratory, the samples were cleaned, placed on trays to dry, and then re-stored in pots with the collection location marked.

The mollusk specimens collected were identified to the most specific taxonomic level possible, using local literature references (Wiggers 2003; Pimpão 2004; Rios 2009). The maximum length (L) and height (H) of each valve were measured in millimeters using a digital caliper with an accuracy of up to 0.1 mm. From these measurements, the body size of each specimen was estimated using the geometric mean method (Kosnik et al. 2006). Body size was calculated only for valves with less than 10% fragmentation (Zuschin et al. 2003).

Each specimen was examined under a stereomicroscope (10x magnification) for the presence of potential interaction traces by observing geochemical changes caused by parasites, which are interpreted as a defense mechanism (Ituarte et al. 2001; Ituarte et al. 2005). Two main types of parasites commonly leave their traces preserved in the shells of bivalve mollusks: i) trematode parasites, which are known to produce pits, pearls, and igloo-blisters traces (Huntley and Scarponi 2012; Roger et al. 2018); and ii) some polychaetes that produce tube-shaped and U-shaped traces, and may also present structures called mud-blisters on the inner part of the shell (Blake and Evans 1973; Ruiz and Lindberg 1989; Rodrigues et al. 2008).

A thorough examination for traces was conducted on both the internal and external surfaces of the valves. Each specimen was classified based on the presence or absence of traces, as well as the type of trace found, its location on the valve (interior of the pallial line, pallial sinus, scars of the adductor muscles, or on the margins of the valve), and when identified, the traces were quantified (Cremonte and Ituarte 2003; Huntley and Scarponi 2012, 2021). In order to confirm the origin of the characteristics, our set of specimens was compared to specimens of *Chamelea gallina* (Linnaeus, 1758) from previous studies in the Mediterranean Sea (e.g., Scarponi et al. 2017; Huntley and Scarponi 2021).

Numerical Analyses

The prevalence of infestation was calculated by dividing the number of infested individuals by the total number of specimens (for each sector of the coast and per sample) (Huntley and Scarponi 2012). A 95% confidence interval was calculated per sample using the "*prop.test*" function of the basic R (R Core Team 2022). The abundance of trematode traces was calculated as the total number of pits in a valve, while the mean abundance was calculated as the total number of traces in a sample divided by the total number of individuals (including individuals without traces) (Huntley and Scarponi 2021). To ensure that only individuals were counted, the number of organisms was estimated as the number of closed valves plus the number of disarticulated valves that were most frequent: right or left.

Size measurements (length and height) were previously compared with body size (Kosnik et al. 2006) using a reduced major axis (RMA) regression, which takes into account potential errors in both axes (Smith 2009). These measurement errors can be visually identified as outliers in the graph prior to other numerical analyses. Body size was chosen as it is a more general measure that can be compared with other taxonomic groups (e.g., Smith et al. 2016) due to the ubiquity of the parasites. The RMA analysis was performed using the "lmodel2" package with 9,999 permutations (Legendre 2018).

A potential selectivity of parasite prevalence in relation to host size was investigated through a parametric comparison of the distribution of mean body sizes. A t-test was conducted between individuals with preserved traces and those without preserved traces. Since the t-test is sensitive to sample size (Holland 2019), before conducting the test, the sample with the largest relative n was resampled to the smallest sample size without replacement.

The prevalence of parasitism was evaluated between the two sectors using the non-parametric Mann–Whitney–Wilcoxon test, which was preceded by an arcsine transformation to minimize extreme values in the distribution (Huntley and Scarponi 2015). Both parametric (t-test) and non-parametric (Mann–Whitney–Wilcoxon) tests were conducted for each coastal sector (progradational or retrogradational) to determine if this pattern was specific to a particular stratigraphical pattern. Correlations between variables were calculated using the "*cor.test*" function. Skewness was calculated using the "*skewness*" function from the "moments" package (Komsta and Novomestky 2022). The variation of traces between shell sectors was assessed using the Kruskal–Wallis rank sum test. All numerical analyses and graphs were generated in the R language (R Core Team 2022).

RESULTS

A total of 754 mollusk shells were collected, comprised of 22 species (Table 1), from 27 samples (Table 2). Among the sectors, the retrogradational sector had the highest species diversity, with 17 species, while the progradational sector had 11 species (Table 1). As for the frequency of species, in both sectors, *D. hanleyanus* had the highest relative frequency (Table 1). Specimens of this species were the only ones that exhibited traces of parasitism, limited to trematodes. No traces associated with polychaetes were found. The traces found in *D. hanleyanus*, as described by Huntley and De Baets (2015), had an oval shape, sometimes circular, with thin raised edges, referred to as pits; this type of trace implies that the host was still alive during the interaction and trying to isolate the parasite (Fig. 2).

Out of the total shells of *D. hanleyanus*, there were 384 right valves and 188 left valves, with 52 valves being articulated. This means that our sample universe consisted of at least 436 individuals (219 in the progradational sector and 217 in the retrogradational sector). Of these, 261 exhibited traces of parasitism, while 175 did not. There was no preference for parasitism traces in relation to valves (Mann–Whitney test, $p = 0.233$). The overall prevalence of parasitism in individuals of *D. hanleyanus* was 0.599, with values varying between samples, with the highest value being 0.800 and the lowest being 0.238 (Table 2). The overall prevalence for the predominantly progradational sector was 0.639, while for the predominantly retrogradational sector it was 0.540. The prevalence between sectors yielded threshold results that did not allow us to reject the null hypothesis (Mann–Whitney test after arcsine transformation, $p = 0.083$). The mean abundance of traces per sample ranged from 0.250 to 8.375 (Table 2).

The body size of *D. hanleyanus* specimens was positively correlated with valve length (Fig. 3A; r = 0.995). Most specimens were similar in size to adults of the species (93.1%; > 15 mm in length) (Defeo and Alava 1995), while few were juveniles (Fig. 3B). No recruit specimens were identified in our samples.

The mean body size for infested individuals was 16.45 mm, while for non-infested individuals it was 15.71 mm. Body size among individuals with traces compared to those without traces showed results that rejected the null hypothesis ($t = -2.788$, $df = 310.51$, $p = 0.006$). Similarly, when we compared the mean body size of infested and non-infested individuals between the retrogradational and progradational sectors, we found that the results were statistically significant only for the progradational sector ($t = -3.763$, $df = 151.89$, $p = 0.0002$; retrogradational, $t = -0.027$, $df = 199.66$, $p = 0.978$) (Fig. 4).

The number of trematode traces appeared to be increasing, although the change was almost undetectable when considering body size (r = 0.010, *p* = 0.8655; Fig. 5A). However, there was a decrease in the number of traces in individuals with a body size of 20 mm or more (Fig. 5A). The distribution of traces was skewed to the right (g1 = 1.091; Fig. 5B). When looking at the samples (n = 25), there was a positive correlation between the variance ($\log_{10}$) and the mean abundance ($\log_{10}$) (r = 0.959), with a slope of 2.029 (Fig. 6).

We observed a different distribution of trematode traces across the interior of the shells. The extrapallial space had the highest concentration of traces (70%), followed by the sector that outlines the pallial sinus posteriorly (25.5%), the margin of the shell (3.4%), and the posterior (0.8%) and anterior adductor muscles (0.3%) (Fig. 7B). Our findings indicated that the number of traces across the different areas of the shell was not equal, thus rejecting the null hypothesis (Kruskal–Wallis, $p < 0.001$). However, there were no significant differences between the sectors (Kruskal–Wallis, $p > 0.05$).

DISCUSSION

The trace pattern identified in this study is often associated with digenetic trematodes of the family Gymnophallidae (Huntley and De Baets 2015; Fig. 2). There have been several cases of trematode parasite infections reported in bivalves of the Donacidae family (e.g., Ansell 1983; Lauckner 1983; Hill-Spanik et al. 2021). The presence of traces exclusively in *D. hanleyanus* valves may suggest a potential specificity, as suggested by Huntley and Scarponi (2012). Donacidae species typically inhabit intertidal zones of dissipative beaches, burying themselves up to 5 cm into the sediment (Herrmann et al. 2009) and are a major energy source for higher trophic levels (Gianuca 1985). In these coastal areas, prey (invertebrates) and both local and migratory seabirds (predators) are sympatric (Neves and Bemvenuti 2006; Müller and Barros 2013). This prey–predator convergence completes the parasite cycle when a bird consumes the intermediate host (e.g., a bivalve). In our study area, for example, *D. hanleyanus* is one of the main sources of food for resident seabirds such as the American oystercatcher (*Haematopus palliatus* (Temminck, 1820)) (Linhares et al. 2021). Infected organisms are often manipulated in some way by the parasites for them to complete their life cycle (Poulin 2010). The encystment of the parasite in the feet of the bivalves can cause this manipulation. However, the Gymnophallidae family is known to target the extrapallial space of its hosts (Lauckner 1983). However, the underlying mechanism of this manipulation remains a topic of ongoing research. The presence of specific traces in a single species may indicate that this selective strategy is not random. For example, organisms infested with *Tagelus plebeius* ([Lightfoot], 1786) may be more susceptible to predation by *H. palliatus* (Addino et al. 2010). Moreover, the co-occurrence of *D. hanleyanus* and *T. plebeius* is inversely proportional, which may indicate interspecific competition between them (Defeo and Alava 1995), even though both are recognized hosts (Defeo and Alava 1995). However, it is worth noting that while predation by seabirds completes the life cycle of trematodes, it can also lead to a negative preservation bias of infested specimens due to the increased fragmentation of these shells by birds (e.g., Cadée 1989, 1994, 1995; Zuschin et al. 2003).

The absolute prevalence values obtained in our study were slightly higher than those reported in the Adriatic Sea (Scarponi et al. 2017; Huntley and Scarponi 2021). The north sector of our study area, predominantly progradational, exhibited slightly higher values. However, not statistically significant compared to the south sector, which is predominantly retrogradational (Fig. 8). Our findings do not demonstrate a clear association between sediment stacking pattern and prevalence, as previously observed in studies of the Adriatic coast (Scarponi et al. 2017; Huntley and Scarponi 2021).

The Po Delta in the northern Adriatic Sea is dominated by waves and has a high sedimentary input from the rivers in the Po River basin (Correggiari et al. 2005; Stefani and Vincenzi 2005; Amorosi et al. 2019). In contrast, the coast of Rio Grande do Sul has a sandy coast that is also dominated by waves but has a reduced sedimentary input (Tomazelli et al. 1998; Dillenburg et al. 2009). This area has a hydrographic system with rivers, but the sediment discharge is blocked by the lagoon-barrier system (Tomazelli 1998). Thus, littoral drift and the existing topography are autogenic determinant factors in the sediment balance along the coast (Dillenburg et al. 2000). Most of the swells that hit the coast of Rio Grande do Sul have a north-northeast origin, but those that come from the south, though less frequent, can transport more than 30% of the sediment in a northeast direction, allowing for the littoral drift in that direction

(Tomazelli and Villwock 1992; Lima et al. 2001; Toldo et al. 2006) (Fig. 8). The RS coastline has projections associated with a convex shoreline, which leads to higher wave energy, resulting in erosion and a retrogradational barrier. On the other hand, the embayment is associated with a concave shoreline, where the waves reach the shore with less energy, leading to a progradational barrier (Dillenburg et al. 2000; Martinho et al. 2010; Dillenburg and Barboza 2014; Rosa et al. 2017) (Fig. 8). Martinho et al. (2009) observed that the amount of sediment transported along a coastline was greater where the coast was convex than where it was concave. Dillenburg et al. (2000) also noted that the study area had both progradational and retrogradational stacking patterns, as well as transitional sectors with agradational behavior. We can infer that the shape of the coast and the littoral drift are significant factors in understanding the prevalence values found, since the littoral drift can transport sediment and bioclastic material from retrogradational to progradational sectors, in agreement with the prevailing direction of drift toward the northeast. The Holocene coastal barrier in Rio Grande do Sul has been greatly impacted by the combined effect of coastal drift and the pre-existing topography over the last 5,000 years, with the drift being particularly influential when sea level changes slowed down (Dillenburg et al. 2000; Martinho et al. 2009; Dillenburg and Barboza 2014). Additionally, some sections of the sector have been found to be still actively prograding (Esteves et al. 2006). Recent research did not identify any alterations to the sedimentary record due to the increase in sea level caused by global warming (Barboza et al. 2021).

When considering the entire sample of individuals, those that were infested tended to be larger than those that were not. The progradational sector, even when the results were marginal, showed a clear selectivity in terms of the size of the infested individuals. It is known that age and size go hand in hand, so older and larger individuals are more likely to accumulate parasites than younger, smaller ones (Ituarte et al. 2009; Huntley and Scarponi 2012, 2021). Additionally, the same process that makes hosts more vulnerable to predators also increases their susceptibility to cercariae, as larger individuals have higher filtration rates, thus raising the potential for infestation.

We found that, while the number of traces increased with body size, from 20 mm onward the trend reversed. Hudson and Dobson (1995) observed a relationship between host age and parasite intensity that produces distinct patterns. Among these patterns, one demonstrates a decrease in the number of parasites as the age of the hosts increases, which is likely due to the death of the host, the acquisition of immunity, or some predisposition to infestation (Hudson and Dobson 1995; Wilson et al. 2002; Raffel et al. 2011). It was evident that there was no preference between left and right valves. This is supported by Huntley's (2007) interpretation, which suggests that there is no evidence of one valve being more advantageous than the other from the same organism. This further reinforces the notion that valves can be used to study interactions by traces in fossil records. Moreover, the non-discriminatory nature of valves is a useful tool for fossils or sub-fossils, as it allows us to assume that an infected valve is representative of a preserved infected organism (Huntley 2007; Huntley and Scarponi 2012).

Our analyses of the distribution of the traces revealed a pattern of aggregation of the parasites. This aggregation is evidenced when a large proportion of individuals have a small number of parasites, while a small number of individuals have a large number of parasites (Shaw and Dobson 1995; Shaw et al. 1998). The degree of aggregation can be measured by the variance ratio to the mean, with values greater than one indicating aggregation (Wilson et al. 2002). Similar to Huntley and Scarponi (2021), we used the mean abundance, which is the number of traces found in each individual valve. As our data were collected from various locations and a substantial number of samples, we applied a linear regression model with logarithmic transformation to calculate the slope between the mean abundance and the variance (Shaw and Dobson 1995; Wilson et al. 2002; Johnson and Hoverman 2014). The resulting slope value was relatively high (Fig. 6) when compared to other studies of aggregation (e.g., Johnson and Hoverman 2014; Huntley and Scarponi 2021). The aggregation of parasites is caused by a variety of heterogeneous factors, including host gender, age, body condition, and genetics (Wilson et al. 2002). Seasonality and the period in which the host is exposed to the parasite also contribute to this aggregation (Wilson et al. 2002; Raffel et al. 2011). High levels of aggregation can lead to increased mortality rates, whereas moderate levels are optimal for selection (Shaw and Dobson 1995; Poulin 2007). The degree of aggregation found in our study may also provide insight into population structure, as strongly aggregated parasites can act as regulators of population growth and exert some control over population stability (Anderson and May 1978; Adler and Kretzschmar 1992). Additionally, the distribution of parasites among hosts can reveal the dynamics of coevolutionary processes, including the defense mechanisms developed by hosts (Morand and Krasnov 2008). It is important to note that our data on parasite abundance were based on the presence or absence of preserved traces (e.g., Huntley and Scarponi 2021).

Our data demonstrated a selection as to where the parasite settled. By analyzing the traces, we found that 70% of the parasites of the Gymnophallidae family tended to prefer to colonize the extrapallial environment when metacercariae. This preference was also found by Ituarte et al. (2005) in Holocene valves of *Cyamiomactra* sp. with traces in the extrapallial space corresponding to the family Gymnophallidae. In cases of high infestation or in older individuals, metacercariae can also be found in the vicinity of the pallial sinus, as reported by Lauckner (1983) and Ituarte et al. (2009). Our data also corresponded to the areas mentioned by these authors, where the pallial sinus area had a preference of 25.5%. *Tagelus plebeius* individuals that are older and heavily infested with Gymnophallids can develop blisters and orange-brown pigmentation in the pallial sinus, as reported by Ituarte et al. (2009). However, Laucker (1983) reported that the metacercariae of the *Gymnophalluus strigatus* preferentially colonize the extrapallial environment of valves of the Donacidae family in the Mediterranean Sea and the European Atlantic. The way in which the host responds may vary according to the species and even the place where the parasite is established, although there are similarities between the types of induced reaction (Ituarte et al. 2001; Cremonte and Ituarte 2003; Ituarte et al. 2005; Vázquez et al. 2006). According to Ituarte et al. (2005), understanding the different responses induced by gymnophallids can provide insight into the evolutionary history of the host–parasite interaction.

CONCLUSION

Traces of metacercariae of the Gymnophallidae family were found exclusively in valves of *Donax hanleyanus* along the retrogradational, and progradational sectors of the coast of Rio Grande do Sul, southern Brazil, suggesting a specific host preference by trematode parasites. This is the first time that these traces have been observed on the Brazilian coast. A relatively higher parasite prevalence was observed in the progradational sector compared to the retrogradational sector, which differs from previous research findings. Previous research has shown that time-averaging does not significantly impact the prevalence rate of the parasite (e.g., Huntley and Scarponi 2012, 2015). However, our findings indicated that local factors such as the predominant shoreline behavior and sedimentary processes may play a significant role in determining the spatial distribution of the parasite, potentially confusing any patterns of prevalence related to the predominant shoreline behavior and its associated fossil record. Nevertheless, further research into the local characteristics of this region is needed to understand better how the parasite–host interaction behaves along the resulting sedimentary record in this region.

Trematodes prefer larger hosts, as infested individuals tend to be larger than non-infested ones, up to a maximum size of 20 mm, beyond which trace abundance decreases significantly. However, they do not prefer either the right or left valve. The distribution of traces indicates a high degree of aggregation of parasites among their hosts. This non-selectivity of valves and the aggregation of traces suggest that the use of traces could be a reliable indicator of interactions in the fossil record. The extrapallial space of the valve appears to be the location where the highest number of traces are concentrated, as has been observed in modern bivalves. However, it is important to note that taphonomic biases may affect the degree of preservation of traces on parasitized valves, although they do not appear to have a major impact.

Therefore, the fossil record can provide us with invaluable information regarding the response of parasites to climate change as well as to environmental changes related to relative variations in sea level. This information can be used to develop measures for the conservation and preservation of ecosystem services that are essential for society in light of the potential consequences of ongoing global warming. In conclusion, the results presented and discussed in this paper further emphasize the importance of conducting quantitative studies on the parasitism–host interaction, as they can provide a wealth of information that can be used to make predictions in a changing global environment.

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DECLARATION OF COMPETING INTERESTS

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data is available from the Dryad digital repository.

LITERATURE CITED

Addino, M., B. J. Lomovasky, F. Cremonte, and O. Iribarne. 2010. Infection by gymnophallid metacercariae enhances predation mortality of SW Atlantic stout razor clam *Tagelus plebeius*. Journal of Sea Research 63:102–107.

Adler, F. R., and M. Kretzschmar. 1992. Aggregation and stability in parasite—host models. Parasitology 104:199–205.

Amorosi, A., G. Barbieri, L. Bruno, B. Campo, T. M. Drexler, W. Hong, and K. M. Bohacs. 2019. Three-fold nature of coastal progradation during the Holocene eustatic highstand, Po Plain, Italy–close correspondence of stratal character with distribution patterns. Sedimentology 66:029–3052.

Anderson, R. M., and R. M. May. 1978. Regulation and stability of host-parasite population interactions: I. Regulatory processes. The Journal of Animal Ecology 47:219–247.

Angulo, R. J., G. C. Lessa, and M. C. de Souza. 2006. A critical review of mid-to late-Holocene sea-level fluctuations on the eastern Brazilian coastline. Quaternary Science Reviews 25:486–506.

Ansell, A. D. 1983. The biology of the genus *Donax*. Pp. 607–635 *in* A. McLachlan and T. Erasmus, eds. Sandy Beaches as Ecosystems. Developments in Hydrobiology. Springer, Dordrecht.

Baets, K. D., J. W. Huntley, A. A. Klompmaker, J. D. Schiffbauer, and A. D. Muscente. 2021. The fossil record of parasitism: its extent and taphonomic constraints. Pp. 1–50. *in* K. D. Baets and J. W. Huntley, eds. The Evolution and Fossil Record of Parasitism. Springer, Cham.

Barboza, E. G., S. R. Dillenburg, M. N. Ritter, R. J. Angulo, A. B. da Silva, M. L. C. D. C. Rosa, F. Caron, and M. C. de Souza. 2021. Holocene Sea-Level Changes in Southern Brazil Based on High-Resolution Radar Stratigraphy. Geosciences 11:326

Baumiller, T. K., and F. J. Gahn. 2002. Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid-crinoid interaction. The Paleontological Society Papers 8:195–210.

Blake J., and J.Evans. 1973. Polydora and related genera (Polychaeta: Spionidae) as borers in mollusk shells and other calcareous substrates. Veliger 15:235–249.

Cadée, G. C. 1989. Size-selective transport of shells by birds and its palaeoecological implications. Palaeontology 32:429–437.

Cadée, G. C. 1994. Eider, shelduck, and other predators, the main producers of shell fragments in the Wadden Sea. Palaeontology 37:181–202.

Cadée, G. C. 1995. Birds as producers of shell fragments in the Wadden Sea, in particular the role of the Herring gull. Geobios 18:77–85.

Clarke, G. L. 1954. Elements of Ecology. John Wiley, New York, p. 534.

Correggiari, A., A. Cattaneo, and F. Trincardi. 2005. The modern Po Delta system: lobe switching and asymmetric prodelta growth. Marine Geology 222:49–74.

Cremonte, F. 2004. Life cycle and geographic distribution of the gymnophallid *Bartolius pierrei* (Digenea) on the Patagonian coast, Argentina. Journal of Natural History 38:1591–1604.

Cremonte, F., and C. F. Ituarte. 2003. Pathologies elicited by the gymnophallid metacercariae of *Bartolius pierrei* in the clam *Darina solenoides*. Journal of the Marine Biological Association of the United Kingdom 83:311–318.

Cribb, T. H., R. A. Bray, P. D. Olson, and D. T. J. Littlewood. 2003. Life cycle evolution in the Digenea: a new perspective from phylogeny. Advances in Parasitology 54:197–254.

Defeo, O., and A. de Alava. 1995. Effects of human activities on long-term trends in sandy beach populations: the wedge clam *Donax hanleyanus* in Uruguay. Marine Ecology Progress Series 123:73–82.

Díaz-Morales, D. M., C. Bommarito, J. Vajedsamiei, D. S. Grabner, G. Rilov, M. Wahl, and B. Sures. 2022. Heat sensitivity of first host and cercariae may restrict parasite transmission in a warming sea. Scientific Reports 12:1174.

Dillenburg, S. R., and E. G. Barboza. 2014. The strike-fed sandy coast of Southern Brazil. Geological Society, London, Special Publications 388:333–352.

Dillenburg, S. R., P. S. Roy, P. J. Cowell, and L. J. Tomazelli. 2000. Influence of antecedent topography on coastal evolution as tested by the shoreface translation-barrier model (STM). Journal of Coastal Research 16:71–81.

Dillenburg, S. R., E. G. Barboza, L. J. Tomazelli, R. N. Ayup-Zouain, P. A. Hesp, and L. C. Clerot. 2009. The Holocene Coastal Barriers of Rio Grande do Sul. Pp. 53–91 *in* S. R. Dillenburg and P. A. Hesp, eds. Geology and Geomorphology of Holocene Coastal Barriers of Brazil. Springer, Berlin, Heidelberg.

Dillenburg, S. R., E. G. Barboza, L.J. Tomazelli, M. L. C. D. C. Rosa, and G. S. Maciel, G. S. 2013. Aeolian deposition and barrier stratigraphy of the transition region between a regressive and a transgressive barrier: an example from Southern Brazil. Journal of Coastal Research 65:464–469.

Dobson, A. P., and P. J. Hudson. 1995. Microparasites: observed patterns in wild animal populations. Pp. 58–89 *in* B. Grenfell and A. Dobson, eds. Ecology of Infectious Diseases in Natural Populations. Cambridge University Press.

Esteves, L. S., J. J. Williams, and S. R. Dillenburg. 2006. Seasonal and interannual influences on the patterns of shoreline changes in Rio Grande do Sul, southern Brazil. Journal of coastal research 22:1076–1093.

Farrar, L., E. Graves, E. Petsios, R. W. Portell, T. B. Grun, M. Kowalewski, and C. L. Tyler. 2020. Characterization of traces of predation and parasitism on fossil echinoids. Palaios 35:215–227.

Gianuca, N. M. 1985. The ecology of a sandy beach in Southern Brazil. Doctoral dissertation, University of Southampton. 330 p.

Herrmann, M., D. Carstensen, S. Fischer, J. Laudien, P. E. Penchaszadeh, and W. E. Arntz. 2009. Population structure, growth, and production of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) from Northern Argentinean beaches. Journal of Shellfish Research 28:511–526.

Hill-Spanik, K. M., C. Sams, V. A. Connors, T. Bricker, and I de Buron. 2021. Molecular data reshape our understanding of the life cycles of three digeneans (Monorchiidae and Gymnophallidae) infecting the bivalve, *Donax variabilis*: it’s just a facultative host!. Parasite 28:34.

Holland, S. M. 2019. Estimation, not significance. Paleobiology 45:1–6.

Hudson, P. J., A. P. Dobson, and K. D. Lafferty. 2006. Is a healthy ecosystem one that is rich in parasites?. Trends in Ecology & Evolution 21:381–385.

Huntley, J. W. 2007. Towards establishing a modern baseline for paleopathology: trace-producing parasites in a bivalve host. Journal of Shellfish Research 26:253–259.

Huntley, J. W., and D. Scarponi. 2012. Evolutionary and ecological implications of trematode parasitism of modern and fossil northern Adriatic bivalves. Paleobiology 38:40–51.

Huntley, J. W. and D. Scarponi. 2015. Geographic variation of parasitic and predatory traces on mollusks in the northern Adriatic Sea, Italy: implications for the stratigraphic paleobiology of biotic interactions. Paleobiology 41:134–153.

Huntley, J. W., and D. Scarponi. 2021. Parasitism and host behavior in the context of a changing environment: The Holocene record of the commercially important bivalve *Chamelea gallina*, northern Italy. PloS one 16:e0247790.

Huntley, J. W., and K. De Baets. 2015. Trace fossil evidence of trematode–bivalve parasite–host interactions in deep time. Advances in Parasitology 90:201–231.

Huntley, J. W., and M. Kowalewski. 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. Proceedings of the National Academy of Sciences 38:15006–15010.

Huntley, J. W., F. T. Fürsich, M. Alberti, M. Hethke, A. C. Liu. 2014. A complete Holocene record of trematode–bivalve infection and implications for the response of parasitism to climate change. Proceedings of the National Academy of Sciences 111:18150–18155.

Ituarte, C. F., F. Cremonte, and A. Scarano. 2009. Tissue reaction of *Tagelus plebeius* (Bivalvia: Psammobiidae) against larval digeneans in mixohaline habitats connected to the south-western Atlantic. Journal of the Marine Biological Association of the United Kingdom 89:569–577.

Ituarte, C. F., F. Cremonte, and D. G. Zelaya. 2005. Parasite-mediated shell alterations in Recent and Holocene sub-Antarctic bivalves: the parasite as modeler of host reaction. Invertebrate Biology 124:220–229.

Ituarte, C. F., F. Cremonte, and G. Deferrari. 2001. Mantle-shell complex reactions elicited by digenean metacercariae in *Gaimardia trapesina* (Bivalvia: Gaimardiidae) from the Southwestern Atlantic Ocean and Magellan Strait. Diseases of Aquatic Organisms 48:47–56.

Johnson, P. T., and J. T. Hoverman. 2014. Heterogeneous hosts: how variation in host size, behaviour and immunity affects parasite aggregation. Journal of Animal Ecology 83:1103–1112.

Kelley, P. H., and T. A. Hansen. 2003. The fossil record of drilling predation on bivalves and gastropods. Pp.119–139. *in* P. H. Kelley, M. Kowalewski, and T. A. Hansen, eds Predator–Prey Interactions in the Fossil Record. Topics in Geobiology. Springer, Boston, MA.

Klompmaker, A. A., M. Kowalewski, J. W. Huntley, and S. Finnegan. 2017. Increase in predator-prey size ratios throughout the Phanerozoic history of marine ecosystems. Science 356:1178–1180.

Klompmaker, A. A., P. H. Kelley, D. Chattopadhyay, J. C. Clements, J. W. Huntley, and M. Kowalewski. 2019. Predation in the marine fossil record: studies, data, recognition, environmental factors, and behavior. Earth-Science Reviews 194:472–520.

Komsta, L., and Novomestky, F. 2022. moments: Moments, Cumulants, Skewness, Kurtosis and Related Tests. R package version 0.14.1. https://CRAN.R-project.org/package=moments

Kosnik, M. A., D. Jablonski, R. Lockwood, and P. M. Novack-Gottshall. 2006. Quantifying molluscan body size in evolutionary and ecological analyses: maximizing the return on data-collection efforts. Palaios 21:588–597.

Lauckner, G. 1983. Diseases of Mollusca: Bivalvia. Pp. 477–961 *in* O. Kinne, ed. Diseases of Marine Animals Introduction. Bivalvia to Scaphopoda. Biologische Anstalt Helgoland, Hamburg.

Legendre, P. 2018. lmodel2: Model II Regression. R package version 1.7-3. https://CRAN.R-project.org/package=lmodel2

Leung, T. L. 2017. Fossils of parasites: what can the fossil record tell us about the evolution of parasitism?. Biological Reviews 92:410–430.

Lima, S. F., L. E. Almeida, and E. Toldo Jr. 2001. Estimativa da Capacidade de Transporte Longitudinal de Sedimentos a partir de Dados de Ondas para a Costa do Rio Grande do Sul. Pesquisas Em Geociências 28:99–107.

Linhares, B. D. A., J. Bordin, G. T. Nunes, and P. H. Ott. 2021. Breeding biology of the American Oystercatcher *Haematopus palliatus* on a key site for conservation in southern Brazil. Ornithology Research 29:16–21.

Littlewood, D. T. J., and S. K. Donovan. 2003. Feature: fossil parasites: a case of identity. Geology Today 19:136–142.

Maas, A., A. Braun, X. P. Dong, P. C. Donoghue, K. J. Müller, E. Olempska, and D. Waloszek. 2006. The ‘Orsten’–more than a Cambrian Konservat-Lagerstätte yielding exceptional preservation. Palaeoworld 15:266–282.

Marini, K., P. Spotorno, D. Diniz, and P. Dentzien-Dias. 2022. Ecological interactions on shells of *Mactra isabelleana* d'Orbigny, 1846 (Mollusca: Bivalvia) from southern Brazil: first record of a unique host–parasite interaction. Aquatic Ecology 56:1205–1216.

Martinho C. T., S. R. Dillenburg, and P. A. Hesp. 2008. Mid to Late Holocene evolution of transgressive dunefields from Rio Grande do Sul coast, southern Brazil. Marine Geology 256:49–64.

Martinho C. T., S. R. Dillenburg, and P. A. Hesp. 2009. Wave energy & longshore sediment transport gradients controlling barrier evolution in Rio Grande do Sul, Brazil. Journal of Coastal Research 25:285–293.

Martinho C. T., P. A. Hesp, and S. R. Dillenburg. 2010. Morphological & temporal variations of transgressive dunefields of the northern e mid-littoral Rio Grande do Sul coast, Southern Brazil. Geomorphology 117:14–32.

Morand, S., and B. Krasnov. 2008. Why apply ecological laws to epidemiology?. Trends in parasitology 24:304–309.

Mouritsen, K. N., and R. Poulin. 2005. Parasites boosts biodiversity and changes animal community structure by trait-mediated indirect effects. Oikos 108:344–350.

Mouritsen, K. N., S. McKechnie, E. Meenken, J. L. Toynbee, and R Poulin. 2003. Spatial heterogeneity in parasite loads in the New Zealand cockle: the importance of host condition and density. Journal of the Marine Biological Association of the United Kingdom 83:307–310.

Müller, A., and M. P. de Barros. 2013. Diversidade e abundância de aves costeiras em um trecho do litoral norte do Rio Grande do Sul, Brasil. Biotemas 26:163–175.

Neves, F. M., and C. E. Bemvenuti. 2006. Spatial distribution of macrobenthic fauna on three sandy beaches from northern Rio Grande do Sul, southern Brazil. Brazilian Journal of Oceanography 54:135–145.

Pimpão, D. M. 2004. Moluscos bivalves da plataforma externa e talude superior ao largo de Rio Grande, Rio Grande do Sul, Brasil. Master dissertation, Universidade Federal do Rio Grande do Sul. 190 p.

Pinto, H. A., and de A. L. Melo. 2013. Larvas de trematódeos em moluscos do Brasil: panorama e perspectivas após um século de estudos. Journal of Tropical Pathology 42.

Poulin, R. 2007. Are there general laws in parasite ecology?. Parasitology 134:763–776.

Poulin, R. 2010 Parasite manipulation of host behavior, an update and frequently asked questions. Pp. 151–186 *in* H. J. Brockmann, ed. Advances in the Study of Behavior. Academic Press, Burlington.

R Core Team. R. 2022. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Raffel, T. R., J. O. Lloyd-Smith, S. K. Sessions, P. J. Hudson, and J. R. Rohr. 2011. Does the early frog catch the worm? Disentangling potential drivers of a parasite age–intensity relationship in tadpoles. Oecologia 165:1031–1042.

Rios, E. D. C. 2009. Compendium of Brazilian sea shells. Editora Evangraf, Porto Alegre, 668 p.

Rodrigues, S. C., M. G. Simões, M. Kowalewski, M. A. Petti, E. F. Nonato, S. Martinez, and C. J. Del Rio. 2008. Biotic interaction between spionid polychaetes and bouchardiid brachiopods: Paleoecological, taphonomic and evolutionary implications. Acta Palaeontologica Polonica 53:657–668.

Rogers, R. R., K. A. Curry Rogers, B. C. Bagley, J. J. Goodin, J. H. Hartman, J. T. Thole, and M. Zatoń. 2018. Pushing the record of trematode parasitism of bivalves upstream and back to the Cretaceous. Geology 46:431–434.

Rosa, M. L. C. D. C., E. G. Barboza, V. D. S. Abreu, L. J. Tomazelli, and S. R. Dillenburg. 2017. High-Frequency Sequences in the Quaternary of Pelotas Basin (coastal plain): a record of degradational stacking as a function of longer-term base-level fall. Brazilian Journal of Geology 47:183–207.

Ruiz, G. M., and D. R. Lindberg. 1989. A fossil record for trematodes: extent and potential uses. Lethaia 22:431–438.

Scarponi, D., M. Azzarone, M. Kowalewski, and J. W. Huntley. (2017). Surges in trematode prevalence linked to centennial-scale flooding events in the Adriatic. Scientific Reports 7:5732.

Shaw, D. J., B. T. Grenfell, and A. P. Dobson. 1998. Patterns of macroparasite aggregation in wildlife host populations. Parasitology 117:597–610.

Smith, R. J. 2009. Use and misuse of the reduced major axis for line-fitting. American Journal of Physical Anthropology 140:476–486.

Smith, F. A., J. L. Payne, N. A. Heim, A. B. Meghan, S. Finnegan, M. Kowalewski, S. K. Lyons, C. R. McClain, D. W. McShea, P. M. Novack-Gottshall, P. S. Anich, and S. C. Wang. 2016. Body size evolution across the Geozoic. Annual Review of Earth and Planetary Sciences 44:523–55.

Stanley, S. M. 2008. Predation defeats competition on the seafloor. Paleobiology 34:1–21.

Stefani, M., and S. Vincenzi. 2005. The interplay of eustasy, climate and human activity in the late Quaternary depositional evolution and sedimentary architecture of the Po Delta system. Marine Geology 222:19–48.

Studer, A., D. W. Thieltges, and R. Poulin. 2010. Parasites and global warming: net effects of temperature on an intertidal host–parasite system. Marine Ecology Progress Series 415:11–22.

Swennen, C. 1969. Crawling-tracks of trematode infected *Macoma balthica* (L.). Netherlands Journal of Sea Research 4:376–379.

Thieltges, D. W., and K. Reise. 2007. Spatial heterogeneity in parasite infections at different spatial scales in an intertidal bivalve. Oecologia 150:569–581.

Tjendra Y., A. F. Al Mana, A. P. Espejo, Y. Akgun, N. C. Millan, C. Gomez-Fernandez, and C. Cray. 2020. Predicting Disease Severity and Outcome in COVID-19 Patients: A Review of Multiple Biomarkers. Arch Pathol Lab Med. 144:1465–1474.

Toldo Jr, E, L. Almeida, J. L. Nicolodi, L. Absalonsen, and N. Gruber. 2006. O controle da deriva litorânea no desenvolvimento do campo de dunas e da antepraia no litoral médio do Rio Grande do Sul. Pesquisas em Geociências 33:35–42.

Tomazelli L. J., J. A. Villwock, E. L. Loss, and E. A. Denhardt. 1982. Caracterização de um depósito praial pleistocênico na Província Costeira do Rio Grande do Sul. Pp. 1514–1523 *in* 32º Congresso Brasileiro de Geologia, Salvador, Anais.

Tomazelli, L. J., S. R. Dillenburg, and J. A. Villwock. 2000. Late Quaternary geological history of Rio Grande do Sul coastal plain, southern Brazil. Brazilian Journal of Geology 30:474–476.

Tomazelli L. J., J. A. Villwock, S. R. Dillenburg, F. A. Bachi, and B. A. Dehnhardt. 1998. Significance of present-day coastal erosion and marine transgression, Rio Grande do Sul, Southern Brazil. Anais da Academia Brasileira de Ciências 70:221–229.

Travessas F.A., S. R. Dillenburg, and L. C. P. Clerot. 2005. Estratigrafia e evolução da barreira holocênica do Rio Grande do Sul no trecho Tramandaí-Cidreira. Boletim Paranaense de Geociências 53:57–73.

Van Valen, L. 1973. A new evolutionary law. Evolutionary Theory 1:1–30.

Vázquez, N. N., C. F. Ituarte, G. T. Navone, and F. Cremonte. 2006. Parasites of the stout razor clam *Tagelus plebeius* (Psammobiidae) from the southwestern Atlantic Ocean. Journal of Shellfish Research 25:877–886.

Vermeij, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. Paleobiology 3:245–258.

Villwock, J. A., and L. J. Tomazelli. 2007. Planície Costeira do Rio Grande do Sul: gênese e paisagem atual. Biodiversidade. Regiões da Lagoa do Casamento e dos Butiazais de Tapes, Planície Costeira do Rio Grande do Sul. Brasília: Ministério do Meio Ambiente/SBF.

Wiggers, F. 2003. Moluscos gastrópodes da plataforma continental externa e talude continental ao largo da laguna dos Patos-Rio Grande do Sul, Brasil.

Wilson, K.O. N. Bjornstad, A. P. Dobson, S. Merler, G. Poglayen, S. E. Randolph, A. F. Read, and A. Skorping. 2002. Heterogeneities in macroparasite infections: patterns and proceeds. Pp. 6–44 *in* P. J. Hudson, A. Rizzoli, B. T. Grenfell, H. Heesterbeek, and A. P. Dobson, eds. The Ecology of Wildlife Diseases. Oxford University Press, Oxford.

Zuschin, M., M. Stachowitsch, and R. J. Stanton Jr. 2003. Patterns and processes of shell fragmentation in modern and ancient marine environments. Earth-Science Reviews 63:3–82.

FIGURE CAPTION

Figure 1 - Study area in southern Brazil. A, Schematic map showing the study area. B, Location of collected samples. The circles on the map represent the sample number and their location. Due to the scale of the image and proximity between samples, the circle representing sample number 1 for both sectors is shared. Created using Basemap – ArcMap

Figure 2 - Valve of *Donax hanleyanus* with traces of trematodes. A, Overview of trace location. B, Emphasis on the various traces induced by trematodes indicated by the arrows. Scale: 5 mm.

Figure 3 - Body size distribution of shells of *Donax hanleyanus*. A, Correlation between body size and valve length. B, Histogram of body size of individuals classified as juveniles and adults.

Figure 4 - Body size distribution (mm) between infested and non-infested individuals by coastline behavior.

Figure 5 - A, Number of trematode traces per valve of *Donax hanleyanus* in relation to body size (mm). B, Frequency distribution of *Donax hanleyanus* valves based on the number of trematode traces per valve (abundance).

Figure 6 - Analysis of mean pit abundance and variance of pit abundance at the sample level. The dotted line indicates the best linear model. Samples with a 1:1 ratio should show an equal distribution of trematode traces in shells.

Figure 7 - Right valve of the bivalve mollusk *Donax hanleyanus*. A, Demarcating the location of the traces according to the morphology of the valve: 1 and 4 = adductor muscle scars; 2 = pallial sinus; 3 = extrapallial space; 5 = valve margin. B, Demarcations including the frequency of traces for each location.

Figure 8 - The local (autogenic) characteristics of the study area, such as the direction and rate of longitudinal sediment transport, and their relationship to the prevalence of

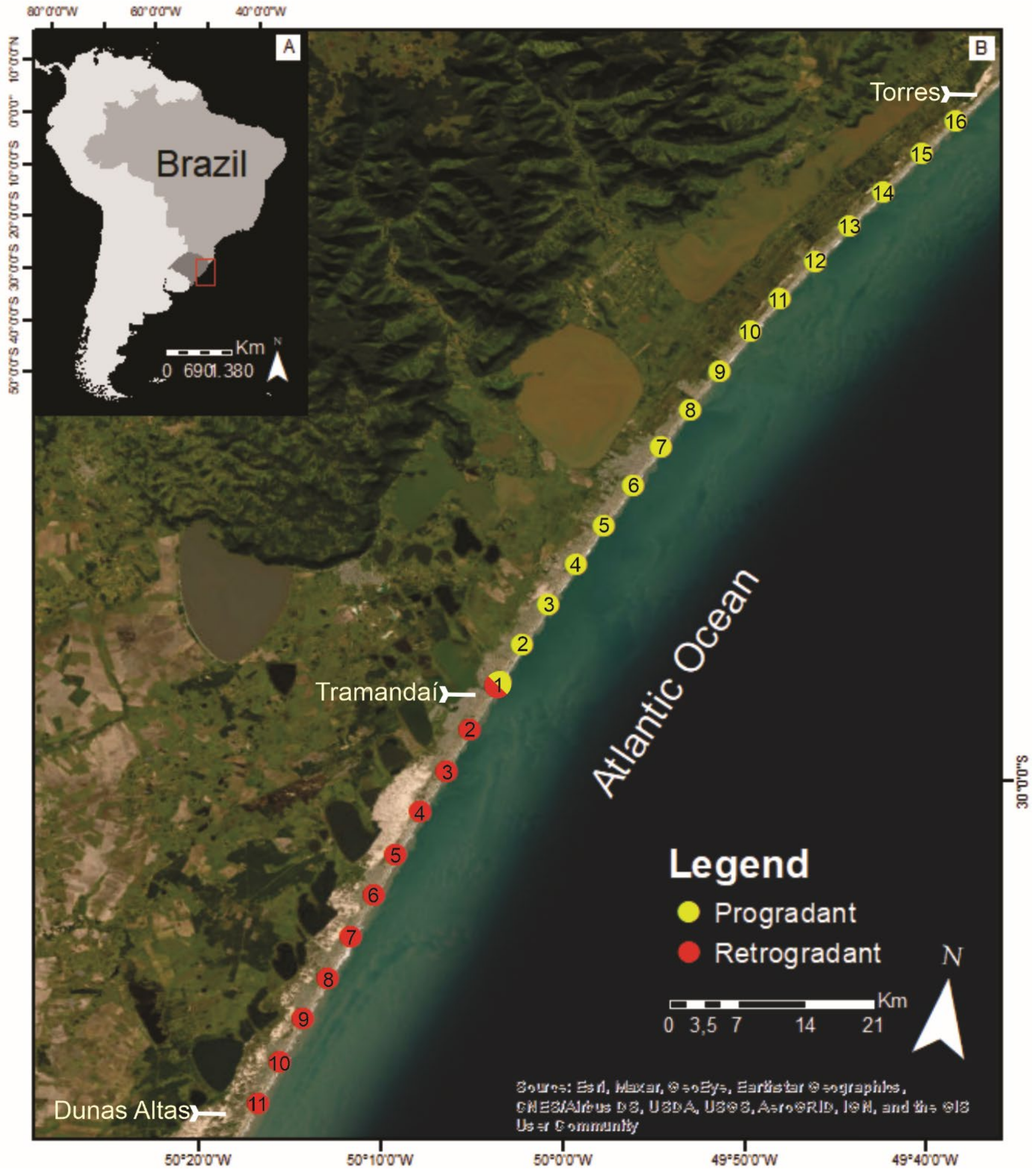
parasitism (as seen in Fig. 1) were also considered. Capital letters (B, C, D, and E) represent the types of barrier described by Dillenburg et al. (2000). Arrows present in the DLT line indicate the predominant direction of longitudinal sediment transport (modified from Lima et al. 2001). The low, medium, and high LST classification corresponds to the longitudinal sediment transport values (modified from Martinho et al. 2009). PR represents the prevalence of parasitism in the predominantly progradational and retrogradational sectors, respectively.

TABLE CAPTION

Table 1 - Species identified and their relative frequency (Fr) for the sectors.

Table 2 - Numerical summary of parasitism traces found in *Donax hanleyanus* by sample. n whole indicates the total number of shells per sample. n pits is the number of shells with at least one parasitism trace. Sum pits represents the total number of pits in all shells. Mean abundance is the sum pits divided by n whole.

Figure 1



Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 2

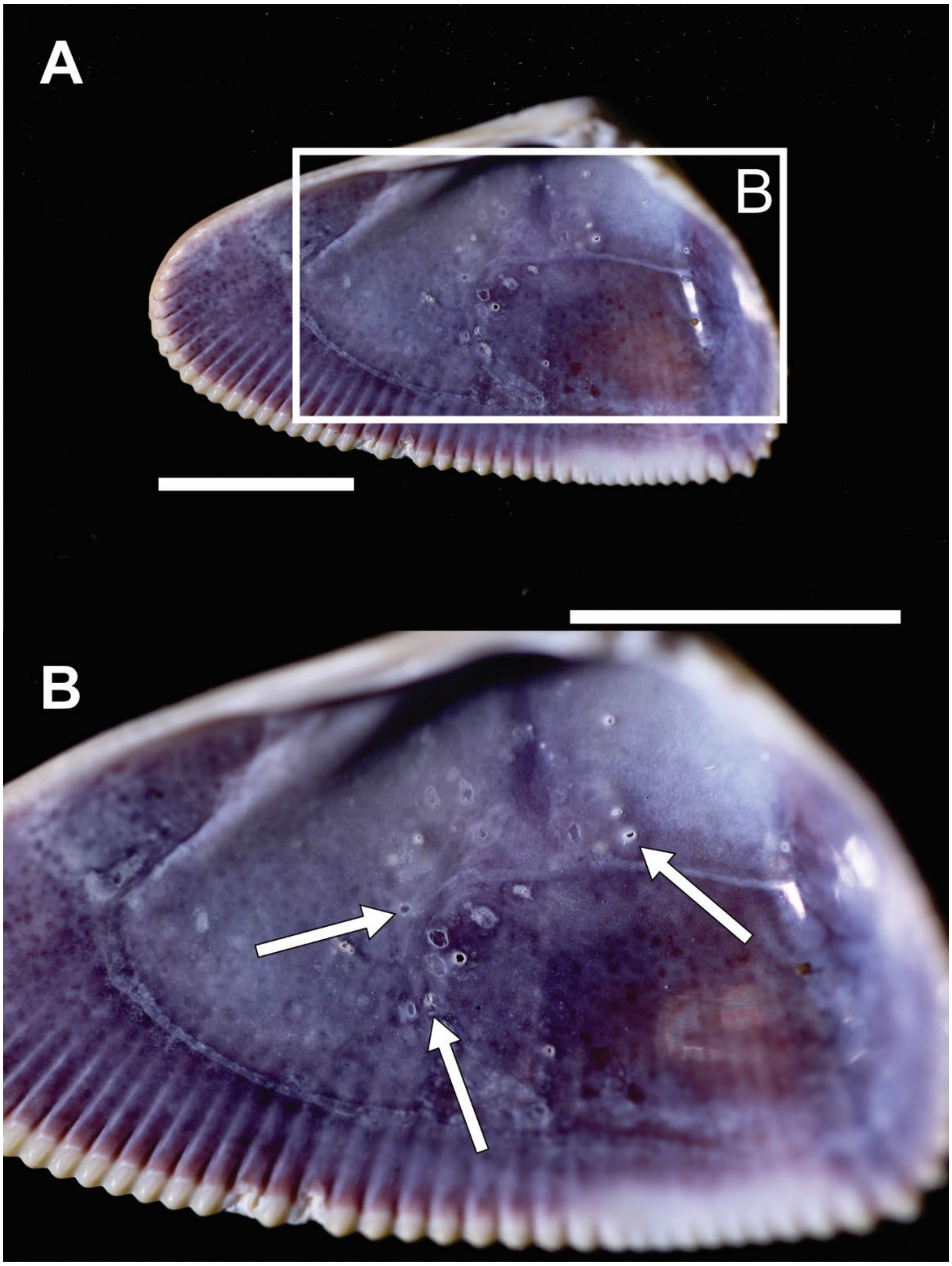


Figure 3

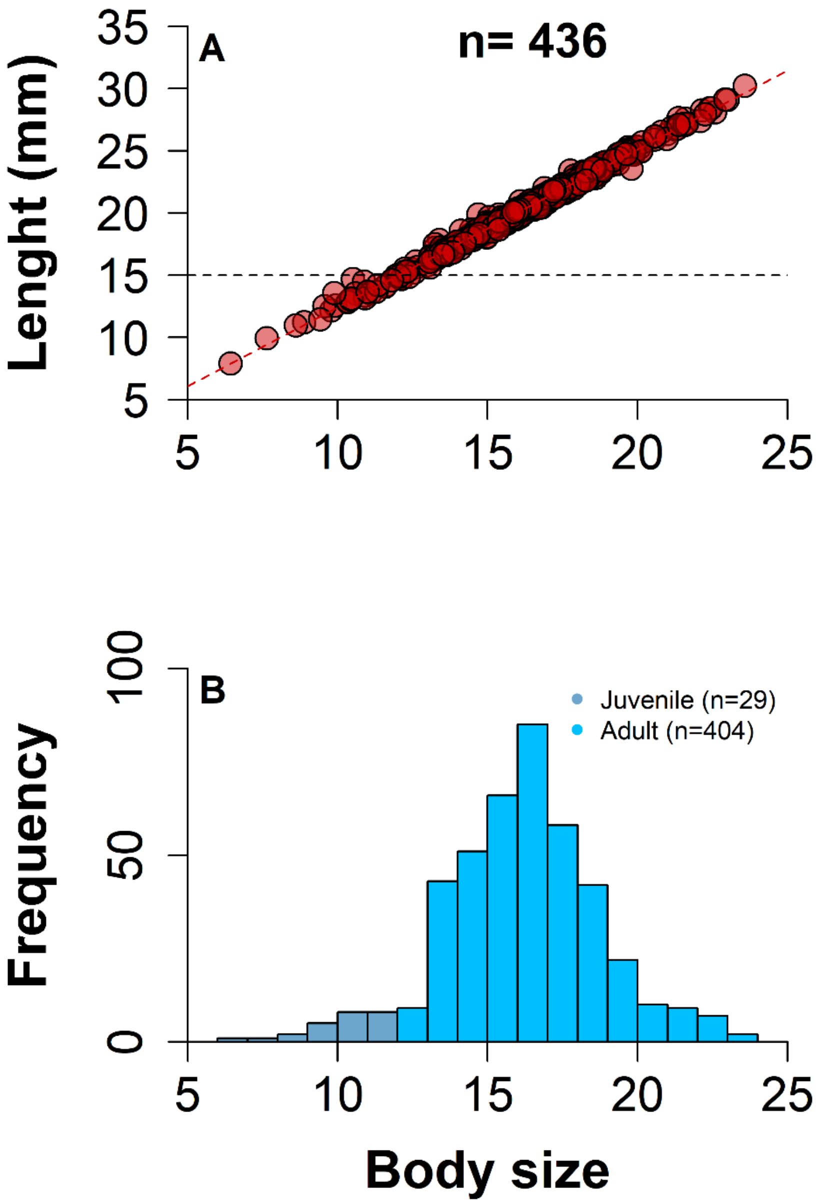

A
n= 436
Lenght (mm)
35
30
25
20
15
10
5
5
10
15
20
25
B
Juvenile (n=29)
Adult (n=404)
Frequency
100
50
0
5
10
15
20
25
Body size

Figure 4

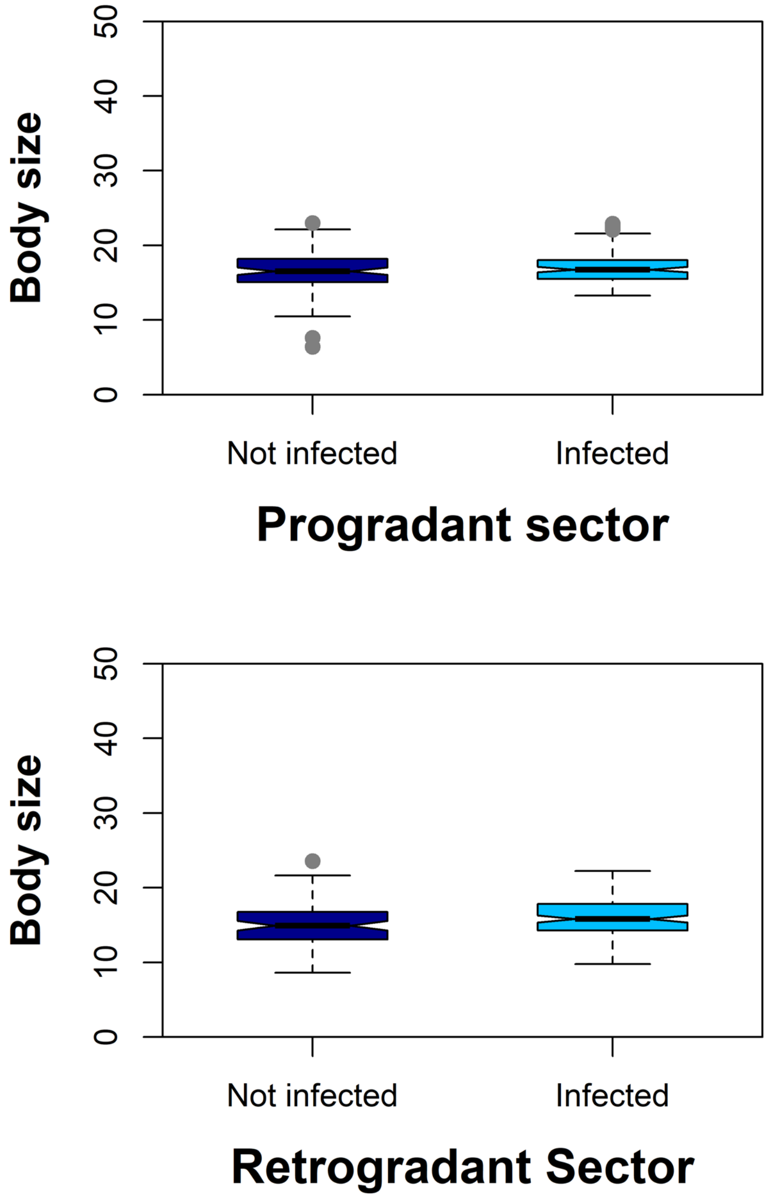

Body size
0
10
20
30
40
50
Not infected
Infected
Progradant sector
Body size
0
10
20
30
40
50
Not infected
Infected
Retrogradant Sector

Figure 5

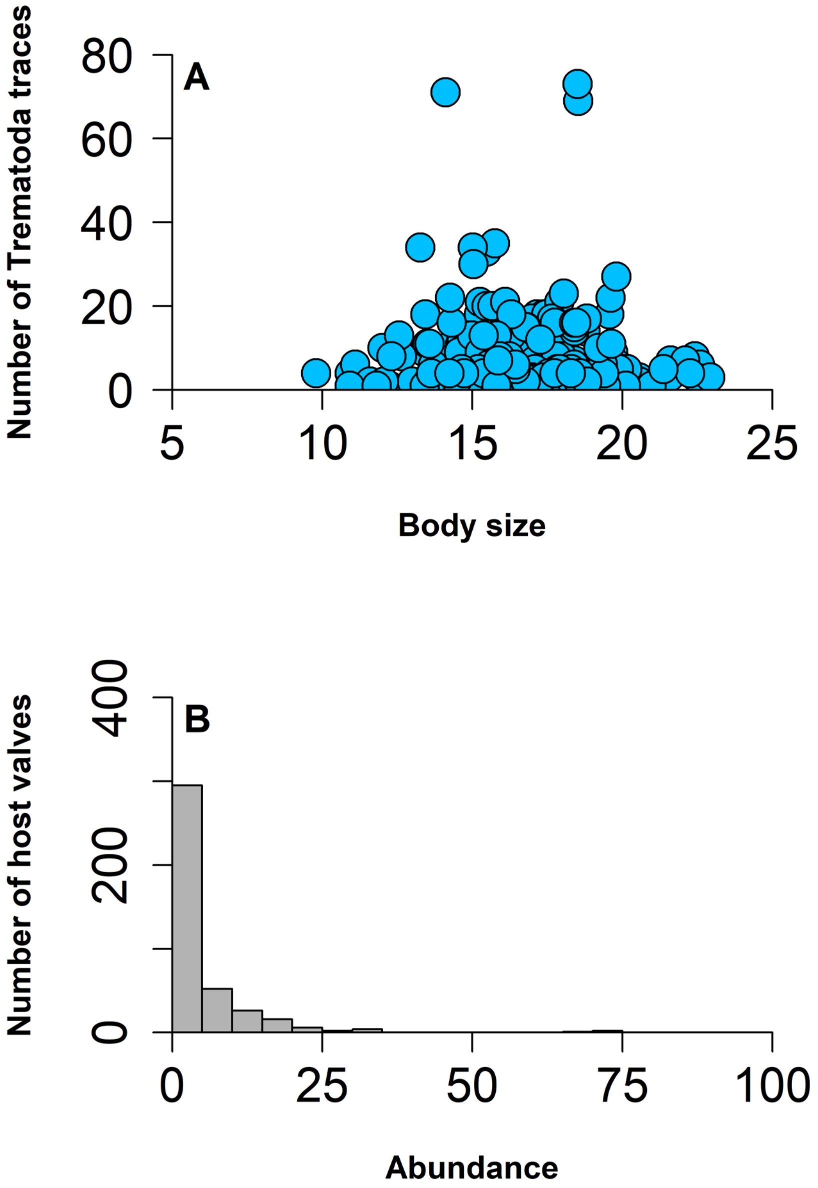

A
Number of Trematoda traces
0
20
40
60
80
5
10
15
20
25
Body size
B
Number of host valves
0
200
400
0
25
50
75
100
Abundance

Figure 6

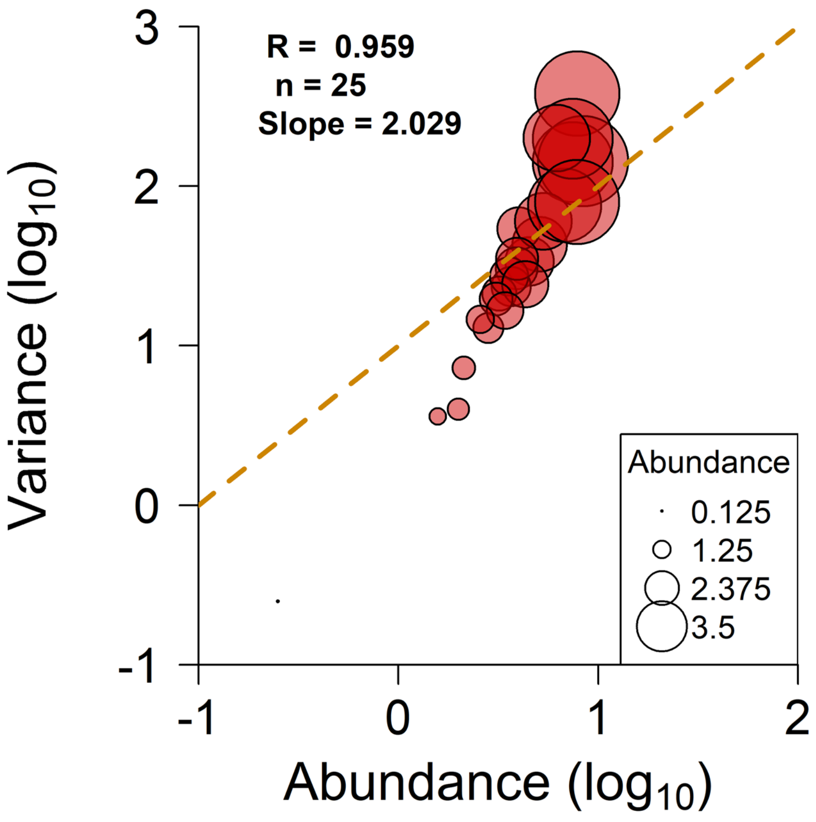

R = 0.959
n = 25
Slope = 2.029
Variance ($\log_{10}$)
Abundance ($\log_{10}$)
3
2
1
0
-1
-1
0
1
2
Abundance
0.125
1.25
2.375
3.5

Figure 7

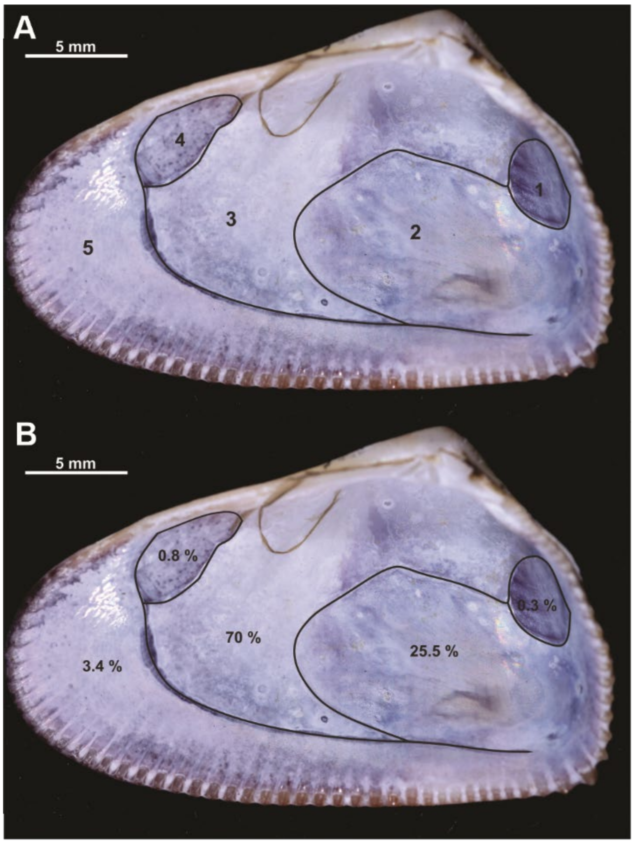
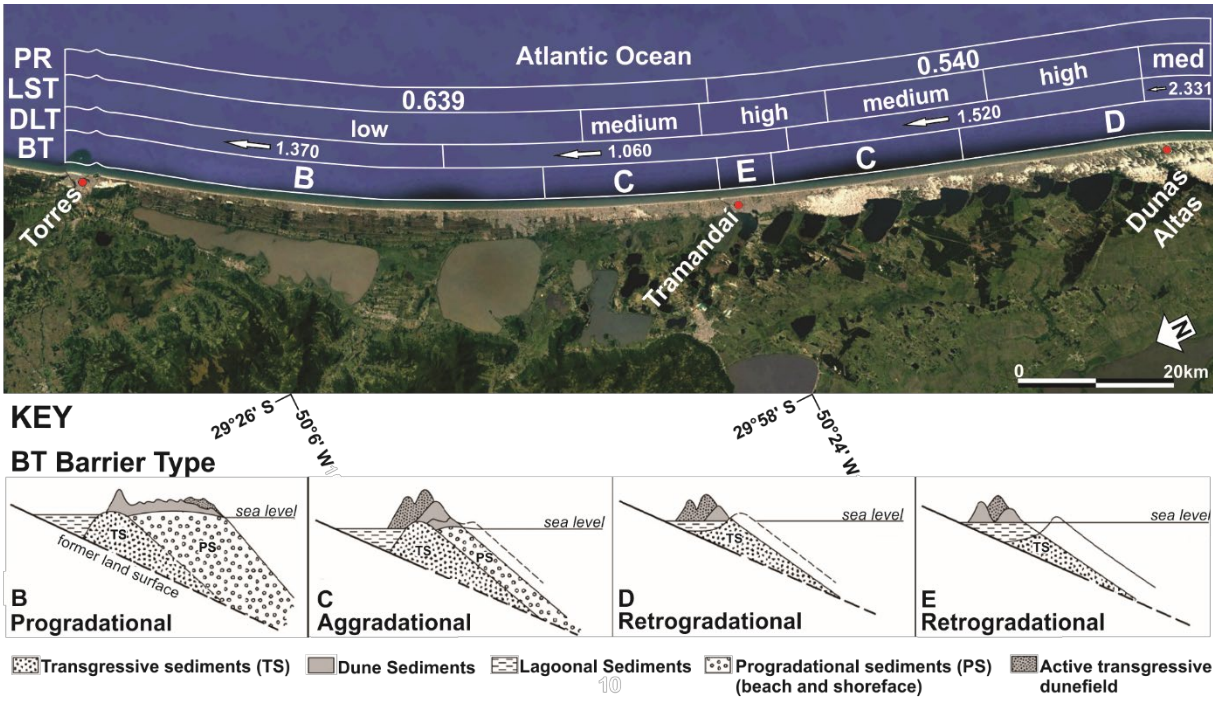


Figure 8



DLT - Resulting direction and rate net longitudinal sediment transport in 10^3 m^3/year
LST - Longshore sediments transport
PR - Prevalence
● - Locations

Table 1

Species	**Progradational - Fr (%)**	**Retrogradational - Fr (%)**
Class Gastropoda		
Tonna galea	0.0 %	0.3 %
Semicassis granulata	0.0 %	0.3 %
Buccinanops cochlidium	0.0 %	0.3 %
Pachycymbiola sp.	0.0 %	0.3 %
Olivancillaria sp.	0.0 %	0.8 %
Class Bivalvia		
Perna perna	0.0 %	0.3 %
Anadara brasiliana	0.0 %	0.3 %
Anadara chemnitzii	0.54 %	0.0 %
Lunarca ovalis	0.0 %	0.3 %
Crassostrea sp.	0.27 %	0.3 %
Divalinga quadrisulcata	0.27 %	0.0 %
Mactra isabelleana	2.45 %	8.0 %
Amarilladesma mactroides	0.82 %	3,6 %
Donax hanleyanus	94.02 %	83.7 %
Anomalocardia flexuosa	0.0 %	0.3 %
Chione cancellata	0.27 %	0.0 %
Eucallista purpurata	0.54 %	0.3 %
Pitar fulminatus	0.0 %	0.3 %
Pitar rostratus	0.27 %	0.5 %
Transennella stimpsoni	0.27 %	0.0 %
Transenpitar americana	0.0 %	0.5 %
Tivela sp.	0.27 %	0.0 %

Table 2

Sample number	Sector	n whole	n pits	Sum pits	Prevalence (CI, ± 95 %)	Mean abundance
1	retrogradational	8	4	17	0.500 (0.215 - 0.785)	2.125
2	retrogradational	16	10	69	0.625 (0.359 - 0.837)	4.313
3	retrogradational	25	13	170	0.520 (0.318 - 0.717)	6.800
4	retrogradational	25	14	186	0.560 (0.353 - 0.750)	7.440
5	retrogradational	35	17	108	0.486 (0.317 - 0.657)	3.086
6	retrogradational	27	14	76	0.556 (0.356 - 0.740)	2.815
7	retrogradational	4	1	1	0.250 (0.013 - 0.781)	0.250
8	retrogradational	29	15	180	0.621 (0.424 - 0.787)	6.207
9	retrogradational	21	11	72	0.619 (0.387 - 0.810)	3.429
10	retrogradational	21	10	54	0.524 (0.303 - 0.736)	2.571
11	retrogradational	6	4	47	0.238 (0.091 - 0.475)	7.833
1	progradational	17	12	77	0.706 (0.440 - 0.886)	4.529
3	progradational	13	7	102	0.538 (0.261 - 0.796)	7.846
4	progradational	9	6	67	0.667 (0.309 - 0.910)	7.444
5	progradational	10	8	51	0.800 (0.442 - 0.965)	5.100
6	progradational	4	2	16	0.500 (0.150 - 0.850)	4.000
7	progradational	7	4	11	0.571 (0.202 - 0.882)	1.571

8	progradational	8	6	67	0.750 (0.356 - 0.955)	8.375
9	progradational	38	27	202	0.711 (0.539 - 0.840)	5.316
10	progradational	21	12	82	0.571 (0.344 - 0.774)	3.905
11	progradational	6	4	22	0.667 (0.241 - 0.940)	3.667
12	progradational	5	2	16	0.400 (0.073 - 0.830)	3.200
14	progradational	45	31	161	0.689 (0.532 - 0.814)	3.578
15	progradational	27	16	106	0.593 (0.390 - 0.770)	3.926
16	progradational	5	3	10	0.600 (0.170 - 0.927)	2.000

ANEXO

ANEXO A – E-mail de confirmação da submissão do artigo a *Paleobiology*.

Paleobiology - Manuscript ID PAB-2023-0005

De	Paleobiology <onbehalfof@manuscriptcentral.com>
Para	<matias.ritter@ufrgs.br>
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31-Jan-2023

Dear Dr. Ritter:

Your manuscript entitled "The power of location: prevalence of traces of parasites in marine mollusks reflects the spatial mixing within coast sectors with different stratigraphic scenarios" has been successfully submitted online for consideration for publication in Paleobiology.

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Editorial Office
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APPENDIX I

Dissertation Title

"PREDOMINANCE OF PARASITE TRACES IN MARINE MOLLUSKS: NEW PARADIGMS FROM THE SOUTH AMERICAN CONTINENT"

Concentration Area: **Paleontology**

Author: **Valentina Silva dos Santos**

Supervisor: **Prof. Dr. Matias do Nascimento Ritter**

Examinator: **Prof. Dr. Daniele Scarponi**

Data: 03/07/2023

Conceito: B(GOOD)

OPINION

Evaluation of Ph.D thesis titled *PREDOMINANCE OF PARASITE TRACES IN MARINE MOLLUSKS: NEW PARADIGMS FROM THE SOUTH AMERICAN CONTINENT*

Valentina's thesis focuses on a relatively new sub-field of paleontology, which is marine paleoparasitology. It documents in a quantitative manner occurrence of trematode parasites as function of their distinctive traces left on bivalve hosts from recent coastal environments of Brazil. While discussion on host selectivity of trematodes, their distribution as a function of host age/dimension, and the most important sedimentary dynamics/processes affecting the recovered parasitic trends are well grounded. The comparison with previous studies from the N. Adriatic basin is, to me, not appropriate and should be avoided, as these N. Adriatic studies focus on different temporal, stratigraphic, and geographical scales. An in depth explanation is reported below, and my concerns and suggestions are detailed below (my text is the one reported in *italics and underlined*).

Introduction

"Trematode parasites, particularly those in the subclass Digenea, have a complex life cycle in which the first intermediate host, typically a gastropod, gives rise to cercariae that infect the second host, in this case, a bivalve"

The life cycle of digenean parasites varies a lot. The one reported is the only one, probably common, but there are others. Therefore, this entire paragraph needs to be better focused.

"a bird or mammal"

I suggest ….a bird or other vertebrate

"As previously mentioned, recent studies on traces of parasitism in the fossil record have primarily focused on mollusks, particularly bivalves, in the Northern Hemisphere

(e.g., Huntley and Scarponi 2015, 2021; Scarponi et al. 2017), except for Marini et

al.(2022).”
I suggest expanding the reference here and elsewhere. E.g., see volumes edited by De Baets and Huntley Topics in Geobiology volumes 49 and 50

Materials and Methods
Study Area
“…Late Quaternary….”
….late Quaternary, not a formalized units

“….reaching its transgressive peak at…”
…reaching maximum transgression at….

This study area has two sections. The first section is between the cities of Imbé and Torres, and it has a slightly concave coastline, with the greatest progradation occurring in Balneário de Curumim (Dillenburg et al. 2000, 2009). The second sector covers the area from Tramandaí to Palmares do Sul, where the coastline is slightly convex toward the basin (Dillenburg et al. 2009). At the Jardim do Éden beach, south of Tramandaí, outcrops of lagoon muds are found, indicating that the transgression occurred due to a negative sediment balance (Travessas et al. 2005). Similarly, the municipality of Cidreira is exposed to stronger waves and has a high rate of retrogradation (Dillenburg et al. 2000; Travessas et al. 2005). This sector has a predominantly retrogradational pattern and eroding coastline (Esteves et al. 2006; Martinho et al. 2008).
All information concerning localities reported here should also be indicated in Figure 1. Please change …that the transgression occurred … in erosion occurred.

Data Collection and Analysis

“Samples were collected from 16 different locations between the municipalities of Imbé and Torres in southern Brazil, which is referred to as the "north area" and has a predominantly progradational coastline (as shown in Fig. 1). Additionally, samples were collected from 11 locations between the municipalities of Tramandaí and Balneário Dunas Altas, in Palmares do Sul, which is referred to as the "south area" and has a predominantly retrogradational coastline (as shown in Fig. 1).”
This is a crucial point. The authors are comparing trematode dynamics within a relatively short (150km long) sector of the same system, i.e., beach barriers, that progrades and retrogrades in relation to inherited topography and related erosional dynamics. The inland sedimentary load and eustatic sea-level dynamics are the same for the entire study area sea-level, as well as probably fluvial influence regarding nutrients, water temperature, and other environmental variables. In conclusion, the candidate is evaluating variability in parasitic traces at a small-scale geographic scale within the same system (not along stratal stacking patterns that requires stratigraphic units as in Huntley and Scarponi 2012 or Scarponi et al. 2017). So the results of the Ph.D. investigation will give an overview of biotic relations strongly driven by small-scale geographic patterns influenced by local factors, such as local morphology, longshore currents strength, geomorphologic-drive wave erosion, and anthropic pressure. The candidate rightly pointed it out in the discussion chapter of her dissertation. However, comparing the results obtained here with those mentioned by the candidate (i.e., Scarponi et al., 2017; Huntley and

Scarponi, 2012, 2015) is inappropriate and should be avoided or changed (see below my explanation).
Specifically, the comparison of the spatial distribution of traces with that of Huntley and Scarponi 2015; where the nearshore environments were from two distinct domains characterized by different environmental conditions or with findings reported in Huntley and Scarponi 2012 (that evaluate predation traces within different systems tracts, multi-millennial scale units characterized by different stratal stacking patterns) and Scarponi et al. 2017 (investigates parasitic prevalence in parasequences developed over millennial-scale time spans), is not appropriate. These studies, indeed, analyze parasitic prevalence at a larger geographic scale (i.e., between different domains in Huntely and Scarponi, 2012 and here within a single domain); or at different temporal scales (fossil deposits buried in the coastal plain of the Adriatic that recorded different eustatic sea-level dynamics over the entire Holocene, i.e., Huntley and Scarponi 2012; or last eustatic sea-level rise of the last glacial-interglacial transition that originated the part of the investigated parasequences Scarponi et al., 2017). So on different time scales with respect to the findings here reported. Such evaluation requires evaluating parasitic traces in cored deposits (where the input of present-day specimens is null, see my comment below).

"…quadrant to collect all mollusks…"
Suggest to change in …mollusk remains...as the input is from dead Donax shells that are being stranded onshore by waves and not subfossil specimens.

"…to the most specific taxonomic…"
..to the lower…

"...by observing geochemical changes…"
…by following changes…

"….:i) trematode parasites, which are known to produce pits,…."
Please check or add a reference, as I'm not sure that all trematode taxa produce pits,…

"…in the Mediterranean Sea (e.g., Scarponi et al. 2017;…."
Scarponi et al., 2017 evaluate trematodes in Abra segmentum, not C. gallina,….. please change this.

Numerical Analyses

"…were conducted for each coastal sector (progradational or retrogradational) to determine if this pattern was specific to a particular stratigraphical pattern."
This is another critical point, I explain my concern here, but the author should modify it also in other parts of her dissertation. This sentence should be rephrased, as progradation or retrogradation at a small geographic scale is not equivalent to progradational or retrogradational stacking patterns that in the Adriatic studies cited developed in relation to the last glacial-interglacial transition. Most important, *Stratal*

stacking patterns describe the architecture of the sedimentary record, and not active depositional surfaces like the one investigated here. I would suggest changing it in"…were conducted for each coastal sector (progradational or retrogradational) to determine if the two investigated areas showed any statistical difference in parasitic infestation"

Results

"Among the sectors, the retrogradational sector…."
While retrogradational sector could be used, please evaluate if substituting retrogradational with concave (or iindented) and progradational with convex could be a viable option here and elsewhere in the text.

"….highest species diversity, with 17 species, while the progradational sector had 11 species (Table 1)."
Judging from table 1, the two sectors seem characterized by the same pool of species. The difference might be due to low sample intensity in both sectors, as species not present in one sector show a very low relative abundance in the other sector.

"The overall prevalence of parasitism in individuals of *D. hanleyanus* was 0.599, with…"
It is a high value. Do you have data on live-collected specimens of D. hanleyanus? If not, this could be the next step of the research. Compare dead and live traces along with radiocarbon dating of the dead shell examined.

"The mean abundance of traces per sample ranged from 0.250 to 8.375 (Table 2)."
While this info is reported in the result, it should also be discussed (along with total abundance); please check the Discussion chapter.

Discussion

"For example, organisms infested with *Tagelus plebeius* ([Lightfoot],…"
Please check; it seems unclear to me, maybe ……infested specimens of the bivalve Tagelus pelbeius...

"Our findings do not demonstrate a clear association between sediment stacking pattern and prevalence, as previously observed in studies of the Adriatic coast (Scarponi et al. 2017; Huntley and Scarponi 2021)."
Given the way of collecting samples, i.e., stranded shells I suspect that an overwhelming majority of Donax valves in both investigated sectors are coming from present-day nearshore communities from the same domain with similar environmental parameter (see comment above), the author is evaluating within-domain parasite variability and comparison with parasite infestation in an explicit sequence stratigraphic scheme (i.e., Scarponi et al., 2017; Huntley and Scarponi, 2021 should be avoided; see also comment above)

"The absolute prevalence values obtained in our study were slightly higher than those reported in the Adriatic Sea (Scarponi et al. 2017; Huntley and Scarponi

2021). The north sector of our study area, predominantly progradational, exhibited slightly higher values. However, not statistically significant compared to the south sector, which is predominantly retrogradational (Fig. 8). Our findings do not demonstrate a clear association between sediment stacking pattern and prevalence, as previously observed in studies of the Adriatic coast (Scarponi et al. 2017; Huntley and Scarponi 2021). The Po Delta in the northern Adriatic Sea is dominated by waves and has a high sedimentary input from the rivers in the Po River basin (Correggiari et al. 2005; Stefani and Vincenzi 2005; Amorosi et al. 2019). In contrast, the coast of Rio Grande do Sul has a sandy coast that is also dominated by waves but has a reduced sedimentary input (Tomazelli et al. 1998; Dillenburg et al. 2009). This area has a hydrographic system with rivers, but the sediment discharge is blocked by the lagoon-barrier system (Tomazelli 1998). Thus, littoral drift and the existing topography are autogenic determinant factors in the sediment balance along the coast (Dillenburg et al. 2000). Most of the swells that hit the coast of Rio Grande do Sul have a north-northeast origin, but those that come from the south, though less frequent, can transport more than 30% of the sediment in a northeast direction, allowing for the littoral drift in that direction (Tomazelli and Villwock 1992; Lima et al. 2001; Toldo et al. 2006) (Fig. 8). The RS coastline has projections associated with a convex shoreline, which leads to higher wave energy, resulting in erosion and a retrogradational barrier. On the other hand, the embayment is associated with a concave shoreline, where the waves reach the shore with less energy, leading to a progradational barrier (Dillenburg et al. 2000; Martinho et al. 2010; Dillenburg and Barboza 2014; Rosa et al. 2017) (Fig. 8). Martinho et al. (2009) observed that the amount of sediment transported along a coastline was greater where the coast was convex than where it was concave. Dillenburg et al. (2000) also noted that the study area had both progradational and retrogradational stacking patterns, as well as transitional sectors with agradational behavior. We can infer that the shape of the coast and the littoral drift are significant factors in understanding the prevalence values found, since the littoral drift can transport sediment and bioclastic material from retrogradational to progradational sectors, in agreement with the prevailing direction of drift toward the northeast. The Holocene coastal barrier in Rio Grande do Sul has been greatly impacted by the combined effect of coastal drift and the pre-existing topography over the last 5,000 years, with the drift being particularly influential when sea level changes slowed down (Dillenburg et al. 2000; Martinho et al. 2009; Dillenburg and Barboza 2014). Additionally, some sections of the sector have been found to be still actively prograding (Esteves et al. 2006). Recent research did not identify any alterations to the sedimentary record due to the increase in sea level caused by global warming (Barboza et al. 2021).

The authors are comparing trematode dynamics within a relatively short (150km long) sector of the same system, i.e., beach barrier, that progrades and retrogrades based on location-specific features (e.g., inherited topography and related erosional dynamics). However, the source of their study, i.e., Donax shells, mainly come from living mollusk communities in the same shallow marine environment, an upper nearshore setting in both sectors of the coast. Evaluating the degree of mixing and transportation is difficult (depending on the alongshore current carrying capacity and resistance of such shells). As for an assessment of mixing radiometric data are needed. So evaluation of parasitic traces is made within the same environment and "probably" short temporal span."

As mentioned above, the comparison reported here should be avoided.

The studies dealing with the fossiliferous succession of the Adriatic analyzed the trend of stratal stacking pattern (that is, the long-term result of larger scale relative or eustatic sea-level changes (not as here smaller scale and narrow time window). On the other hand, the one dealing with coastal taphofacies (Huntely and Scarponi 2015) investigated dead shell assemblages in two different large-scale nearshore settings characterized by other environmental variables (sedimentation nutrient, fluvial influence, etc.). For these reasons, I would not compare the findings obtained from Adriatic studies with this one. Instead, suggest erasing it and focusing on the object of this study, which is local-scale variability (see my comment above).

Signature: Daniele Scarponi
Date: 03/07/2023

Supervisor acknowledgement:

Student acknowledgement:

ANEXO I

Título da Dissertação:

“PREVALÊNCIA DE TRAÇOS DE PARASITAS EM MOLUSCOS MARINHOS: NOVOS PARADIGMAS DO CONTINENTE SUL-AMERICANO”

Área de Concentração: Paleontologia

Autora: **Valentina Silva dos Santos**

Orientador: Prof. Dr. Matias do Nascimento Ritter

Examinadora: Profa. Dra. Paula Dentzien-Dias Francischini

Data: 27/02/2023

Conceito: A

PARECER:

A dissertação aborda um tema pouco estudado com o enfoque em parasitologia na paleontologia. Sendo assim, é um estudo importante para a área. Entretanto, um conceito é abordado de forma incorreta. O uso de traço durante toda a dissertação está errado. Traço é o vestígio de uma atividade do animal. O que é chamado de traço é um crescimento anômalo na concha. Alguns autores têm usado traço, mas acredito que este erro deva ser evitado.

Na parte introdutória da dissertação, a mestranda poderia ter explorado mais o tema e ilustrado (com figuras e tabelas) melhor.

Para o artigo, acredito que deveriam de ter feito um MEV dos pits.

Considero a dissertação aprovada.

Assinatura: Data: 27/02/2023

Ciente do Orientador:

Ciente do Aluno:

ANEXO I

Título da Dissertação:

“PREVALÊNCIA DE TRAÇOS DE PARASITAS EM MOLUSCOS MARINHOS: NOVOS PARADIGMAS DO CONTINENTE SUL-AMERICANO”

Área de Concentração: Paleontologia

Autora: **Valentina Silva dos Santos**

Orientador: Prof. Dr. Matias do Nascimento Ritter

Examinador: Dr. Jorge Villegas-Martín

Data: 10/05/2023

Conceito: 9

PARECER:

O tema do projeto e nove doso e importante na área da bioerosão e pode ser de ínteres tanto para as pessoas que trabalham bioerosão, relações ecológicas, paleobiologia e paleontologia geral onde os estudos são escassos. Em geral, a linguagem e redação estão corretas, faço algumas sugestões em algumas partes, onde em minha opinião ficaria mais clara a ideia que a estudante quis expressar.A organização do texto está correta mostrando claramente a problemática a ser aborda e os objetivos principais. Em geral as figuras têm qualidade e aparecem para apoiar corretamente o texto. No entanto, sugiro adicionar citas em algumas afirmações.

, revisar no texto porque em algumas ocasiões parece dar a entender que o produtor do traço foi o icnogenero, quando este se refere a classificação icnotaxonomica. Sugiro também detalhar em algumas informações nos materiais e métodos e revisar o inglês do artigo. Outras sugestões e recomendações são adicionados sobre o pdf, que em minha opinião melhorariam o texto (ver pdf).

Assinatura: Data: 10/05/2023

Ciente do Orientador:

Ciente do Aluno: