UNIVERSIDADE FEDERAL DO CEARÁ
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MARIANY OLIVEIRA ARRUDA

BORING ACTIVITY OF THE SPONGE *Cliothosa delitrix* (PANG, 1973) (CLIONAIDAE, CLIONAIDA) IN THERMORESISTANT CORALS AND THE STATE OF THE ART OF THE ORDER CLIONAIDA IN CEARÁ

FORTALEZA
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Dissertação de mestrado apresentada ao Programa de Pós-Graduação em Ciências Marinhas Tropicais da Universidade Federal do Ceará, como requisito parcial à obtenção do título de Mestra em Ciências Marinhas Tropicais. Área de concentração: Ciência, Tecnologia e Gestão Costeira e Oceânica.

Orientador: Prof. Dr. Marcelo de Oliveira Soares.
Coorientadora: Prof.ª Dra. Sula Salani Mota.

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que não desistiram no meio do caminho.

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“O mar é tudo. Ele cobre sete décimos do globo terrestre. Seu sopro é puro e saudável. É um deserto imenso, onde o homem jamais está sozinho, pois sente a vida se movimentando por todos os lados". (Júlio Verne, 1870, p. 37).”

RESUMO

Cliothosa delitrix, esponja bioerosiva da família Clionaidae, destaca-se nos recifes por sua elevada taxa de bioerosão em colônias de corais, especialmente sob condições de estresse ambiental. Esse comportamento a torna uma competidora eficiente, pois esponjas bioerosivas erodem o substrato calcário e limitam o crescimento recifal. Esse processo pode estar se intensificando em função das mudanças climáticas globais, contribuindo para o agravamento da degradação dos recifes de corais. Nesse contexto, este estudo se alinha ao Objetivo de Desenvolvimento Sustentável (ODS) 14, que visa a conservação e o uso sustentável dos oceanos. O objetivo geral deste trabalho foi conduzir o primeiro estudo ecológico sobre os estágios de desenvolvimento de *C. delitrix* e sua ocupação em colônias do coral resistente *Siderastrea stellata*, comparando indivíduos branqueados e saudáveis no Parque Estadual Marinho da Pedra da Risca do Meio (PEMPRIM), além de registrar e descrever espécimes da ordem Clionaida ao longo da costa do Atlântico Sudoeste Equatorial (Ceará). Coletamos os espécimes através de busca ativa em recifes entremarés ao longo da costa do Ceará e com mergulho autônomo no PEMPRIM (entre 15 e 30 m de profundidade). Após a coleta, os organismos foram conservados em álcool 80% e identificados no laboratório, a partir da confecção de lâminas de espículas e de esqueleto das esponjas. Para o estudo ecológico de *C.delitrix*, coletamos os dados entre março e julho de 2024 (durante o quarto evento global de branqueamento de corais). Fizemos fotoquadrados de 50 x 50 cm², ao longo de transectos lineares de 20 m, gerando um total de 40 imagens por local de mergulho. Além disso, quantificamos cada *C. delitrix* e os seus estágios de desenvolvimento, em seguida, estimamos a sua área de ocupação (cm²) nos corais medindo sua área (cm²). Os resultados indicam a presença da esponja *C. delitrix* perfurando colônias de corais saudáveis e branqueadas. Das 347 colônias de coral contabilizadas, ~52% apresentaram branqueamento, enquanto 48% não mostraram sinais desse fenômeno. Entre as colônias de coral branqueadas, 37,99% foram perfuradas pela esponja, enquanto apenas 2,98% das colônias não branqueadas apresentaram essa bioerosão, sugerindo maior vulnerabilidade à colonização por *C. delitrix* após estresse térmico e branqueamento em massa de corais. Ademais, não houve correlação significativa entre a perfuração da esponja e a profundidade, o que indica adaptação a diferentes profundidades e que a disponibilidade de corais e sua condição de estresse (ou seja, branqueamento) são as variáveis mais importantes no processo de bioerosão. Complementarmente, identificamos 5 espécies de Clionaida na costa do Ceará onde registramos pela primeira vez para o Atlântico Sudoeste Equatorial as espécies *Cliothosa delitrix* e *Cliona* *carteri* (Clionaidae), *Spirastrella hartmani* (Spirastrellidae), além de *Placospongia giseleae* (Placospongiidae) e confirmamos a presença do complexo de espécies *Cliona celata* (Clionaidae). Com isso, ampliamos o conhecimento taxonômico sobre esponjas nessa região tropical e caracterizamos a ocupação espacial de indivíduos de *C. delitrix*, seus estágios de desenvolvimento e uma possível preferência em colônias branqueadas no coral maciço *Siderastrea stellata*..A dissertação será apresentada em dois capítulos: o primeiro sobre a atividade perfuradora da esponja *Cliothosa delitrix* e o segundo sobre o estado da arte da ordem Clionaida no Ceará.

Palavras-chave: bioerosão; taxonomia; conservação.

ABSTRACT

Cliothosa delitrix, a bioeroding demosponge of the family Clionaidae, stands out on reefs due to its high bioerosion rates in coral colonies, particularly under environmental stress conditions. This behavior makes it an efficient competitor in these environments, as bioeroding sponges erode the calcareous substrate. This process may be intensifying as a result of global climate change, contributing to the ongoing degradation of coral reefs. In this context, this study aligns with Sustainable Development Goal (SDG) 14, which aims to conserve and sustainably use the oceans. The general objective of this study was to conduct the first ecological investigation of the developmental stages of *C. delitrix* and its occupation of colonies of the stress-tolerant coral *Siderastrea stellata*, comparing bleached and healthy individuals at the Pedra da Risca do Meio Marine State Park (PEMPRIM), as well as to record and describe species of the order Clionaida along the Southwestern Equatorial Atlantic coast (Ceará, Brazil). Specimens were collected through active intertidal searches and scuba diving along the Ceará coast and at PEMPRIM (15–30 m depth). After collection, organisms were preserved in 80% ethanol and identified in the laboratory based on spicule and skeletal preparations. Ecological data on *C. delitrix* were collected between March and July 2024, during the fourth global coral bleaching event. We obtained 50 × 50 cm photoquadrats along 20 m linear transects, yielding a total of 40 images per dive site. Each individual and its developmental stage were quantified, and occupied area (cm^2) on coral colonies was estimated. Results indicate the presence of *C. delitrix* boring into both healthy and bleached coral colonies. Of the 347 coral colonies surveyed, ~52% were bleached and 48% showed no signs of bleaching. Among bleached colonies, 37.99% were bored by the sponge, whereas only 2.98% of non-bleached colonies showed bioerosion, suggesting greater vulnerability to *C. delitrix* colonization following thermal stress and mass bleaching events. No significant correlation was found between sponge boring and depth, indicating adaptation across depth ranges and highlighting coral availability and stress condition (i.e., bleaching) as the most important drivers of bioerosion. Additionally, five species of Clionaida were identified along the Ceará coast, including the first records for the Southwestern Equatorial Atlantic of *Cliothosa delitrix* and *Cliona carteri* (Clionaidae), *Spirastrella hartmani* (Spirastrellidae), and *Placospongia giseleae* (Placospongiidae), and confirmation of the *Cliona celata* species complex. These findings expand regional taxonomic knowledge and characterize the spatial occupation, developmental stages, and possible preference of *C. delitrix* for the massive coral *Siderastrea stellata* with higher boring rates in bleached colonies. The dissertation will be presented in two chapters: the first on the boring activity of the sponge *Cliothosa delitrix*, and the second on the state of the art of the order Clionaida in Ceará.

Keywords: bioerosion; taxonomy; conservation.

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1 INTRODUÇÃO GERAL

As esponjas (Filo Porifera) se destacam por serem componentes essenciais de ecossistemas, desempenhando importante papel na estruturação e no funcionamento dos ambientes marinhos e dulcícolas, desde zonas tropicais, como no Caribe (Diaz; Rützler, 2001) até áreas mais frias, como na Antártica (Mitchell et al., 2020). Entre elas, as esponjas (processo de erosão biológica) são as principais responsáveis pela bioerosão em recifes rasos e de águas quentes em escala global, contribuindo com aproximadamente dois terços (⅔) desse processo (Shönberg, Fang; Carballo, 2017).

Após dois séculos de investigação, sabe-se que os clionídeos são endolíticos e escavam galerias dentro do substrato por meio da combinação de processos químicos e mecânicos, os quais foram investigados por meio de análises da ultraestrutura celular e de micro-sensores de troca iônica (Pomponi, 1980; Hatch, 1980; Shönberg, 2008). Esse modo de vida desempenha um papel central na remodelação dos recifes e na geração de microhabitats bentônicos, além de contribuir para a reciclagem do carbonato de cálcio no ambiente marinho.

Quando nos referimos às esponjas bioerosivas clássicas, estamos tratando principalmente de espécies pertencentes à ordem Clionaida, especialmente à família Clionaidae d'Orbigny, 1851, que reúne os perfuradores mais eficientes de substratos calcários . Outras famílias também integram essa ordem, como **Spirastrellidae** Ridley & Dendy, 1886, **Placospongiidae** Gray, 1867, e **Acanthochaetetidae** Fischer, 1970 (fóssil), mas não são reconhecidas como compostas por perfuradores clássicos (Hooper & van Soest, 2002; Morrow & Cárdenas, 2015; de Voogd *et al.*, 2025).

Grande parte do conhecimento atual sobre a ecologia e a diversidade de Clionaida deriva de estudos conduzidos no Grande Caribe, particularmente envolvendo os gêneros *Cliona* Grant, 1826 e *Cliothosa* Topsent, 1905. Nessas regiões, essas esponjas tornaram-se significativamente mais abundantes nas últimas décadas, em associação ao aumento da temperatura da água, à eutrofização costeira e à maior disponibilidade de substrato carbonático, resultante da mortalidade coralínea (Chaves-Fonnegra, 2011, 2014).

Em alguns recifes caribenhos, esse aumento tem promovido um desequilíbrio entre os processos de acreção e erosão, comprometendo a manutenção estrutural (*reef budget* ou balanço carbonático) dos recifes (Kennedy et al., 2013).

Diante dessa problemática atual, elas passaram a ser incluídas em projetos de biomonitoramento e em estudos de modelagem ambiental. Isso ocorre porque sua crescente abundância em corais resistentes ao estresse térmico demonstra que podem atuar como bioindicadoras sensíveis das mudanças climáticas e da perda de resiliência estrutural dos ecossistemas coralíneos, tornando necessário estudá-las para investigar, a longo prazo, sua relação com a saúde dos recifes (Callahan, 2005; Kennedy et al., 2013).

Do ponto de vista ecológico, *Cliothosa delitrix* destaca-se como uma das principais esponjas bioerosivas do Atlântico Ocidental, apresentando altas taxas de perfuração e forte associação com corais termorresistentes, como *Siderastrea stellata* Verrill, 1868 (Chaves-Fonnegra; Zea, 2011; Chaves-Fonnegra, 2014). A ocupação desses corais por *C. delitrix*, especialmente após eventos de branqueamento, pode acelerar a perda estrutural dos recifes e comprometer sua recuperação, funcionando como um organismo-chave na transição de recifes construtores para recifes erosivos (Carbalo et al., 2013; Chaves-Fonnegra, 2014) (Figura 1).

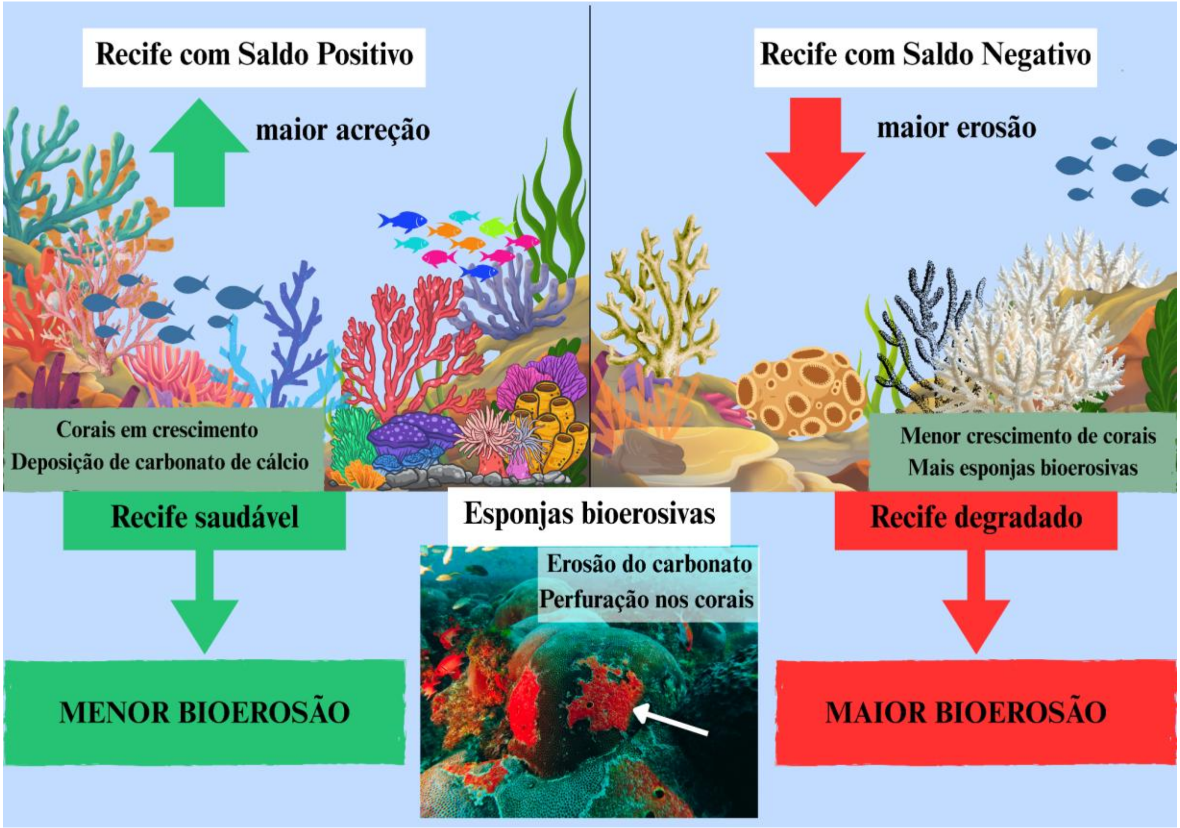

Figura 1. Esquema ilustrando recifes com balanço positivo e negativo, destacando o papel das esponjas bioerosivas no equilíbrio entre acreção e erosão. (elaborado pela autora)

Apesar dos avanços no Caribe, o conhecimento sobre a ordem Clionaida no Atlântico Sul, região com elevada biodiversidade e importantes funções ecológicas (Banha, 2025), ainda é marcado por lacunas taxonômicas. No Brasil, as esponjas ocorrem desde a foz do rio Amazonas até o Rio Grande do Sul, incluindo ilhas oceânicas (Muricy et al., 2011; Moura et al., 2016). Embora cerca de 25 espécies de esponjas bioerosivas já tenham sido registradas no país, o conhecimento permanece limitado, tornando essa região uma das menos documentadas globalmente para esse grupo, especialmente quando comparada ao Caribe, onde já foram registradas cerca de 62 espécies bioerosivas (Shönberg; Fang; Carballo, 2017).

Apesar de diversas questões taxonômicas em aberto, algumas revisões importantes já foram propostas, refletindo a complexidade da sistemática do grupo. Entre elas, destacam-se: (a) a realocação de *Cliothosa delitrix*, anteriormente incluída no gênero *Cliona*; e (b) a sinonimização de espécies anteriormente separadas com base na distribuição geográfica e em traços ecológicos, como *Cliona laticavicola* e *Cliothosa delitrix*, agora consideradas a mesma espécie com base em evidências genéticas e morfológicas. Nesse processo, *C. delitrix* foi mantida como o nome válido, enquanto *C. laticavicola* passou a ser interpretada como um estágio ontogenético inicial e um ecofenótipo da mesma espécie. Tais mudanças reforçam a importância de investimentos contínuos em taxonomia, sistemática e genética para o aprofundamento do conhecimento sobre esse grupo (Shönberg, Fang; Carballo, 2017; Chaves-Fonnegra et al., 2017).

Considerando a escassez de estudos no Atlântico Sul, a intensificação de ondas de calor marinhas (Duarte et al., 2020; Soares et al., 2022) e eventos globais de branqueamento coralíneo cada vez mais frequentes, como o registrado em quarto evento global de 2024 (Reimer et al., 2024), torna-se essencial a ampliação de estudos, na região. Essas condições ambientais tendem a favorecer a expansão de esponjas bioerosivas (Chaves-Fonnegra et al., 2011, 2014), tornando urgente sua inclusão em programas de monitoramento e gestão ambiental, tanto para prever a trajetória futura dos recifes com corais quanto para subsidiar estratégias de conservação e mitigação dos impactos da bioerosão (Shönberg; Fang; Carballo, 2017; Spady et al., 2026).

Com base no que foi explicitado acima, esta dissertação tem como principais objetivos: (I) Elucidar a distribuição de *C. delitrix* em toda a extensão batimétrica do recife estudado; (II) Caracterizar os padrões de ocupação de *C. delitrix* em colônias de *S. stellata* em estado branqueado e saudável e os seus estágios de desenvolvimento; (III) Avaliar potenciais diferenças na ocupação de esponjas entre colônias de corais branqueados e não branqueados; (IV) Estabelecer parâmetros de base para futuro biomonitoramento de esponjas escavadoras, especialmente à luz da aceleração das mudanças climáticas globais; (V) Identificar as espécies de esponjas da ordem Clionaida do estado do Ceará; (VI) Descrever os novos registros cearenses.

Por fim, fornecemos novos registros de esponjas da ordem Clionaida e sua atualização taxonômica e geográfica para o estado do Ceará (Atlântico Sudoeste Equatorial), além do primeiro estudo ecológico de *C. delitrix* perfurando corais branqueados durante o quarto evento global de branqueamento que ocorreu no ano de 2024, contribuindo para o avanço da taxonomia, do conhecimento sobre a dinâmica bioerosiva e da resiliência estrutural dos recifes do oceano Atlântico Sul. Para esse fim, estruturamos a dissertação de mestrado em dois capítulos em língua inglesa para fins de publicação breve em revista internacional com fator de impacto, visando auxiliar no processo de internacionalização da pós-graduação.

ESTRUTURA DA DISSERTAÇÃO

CHAPTER 1 - Stress-Tolerant Coral Faces Bioerosion: Sponge Colonization Under Mass Bleaching

Objetivo Geral

Investigar o desenvolvimento da esponja bioerosiva *Cliothosa delitrix* e a sua ocupação no coral resistente *Siderastrea stellata* no Atlântico Sudoeste Equatorial (Parque Estadual Marinho Pedra da Risca do Meio, Ceará, Brasil).

Objetivos específicos

- Elucidar a distribuição de *C. delitrix* em relação a profundidade de diferentes recifes;
- Caracterizar os padrões de ocupação de *C. delitrix* em colônias de *S. stellata* em estado branqueado e saudável e os seus estágios de desenvolvimento;
- Avaliar potenciais diferenças na ocupação de esponjas entre colônias de corais branqueados e não branqueados;
- Estabelecer parâmetros de base para futuro biomonitoramento de esponjas escavadoras, especialmente à luz da aceleração das mudanças climáticas globais.

Hipóteses

A taxa de ocupação de *C. delitrix* varia significativamente de acordo com a profundidade do recife e seu processo de bioerosão é maior em corais branqueados do que em corais saudáveis.

CHAPTER 2 – Order Clionaida, 1851 (Demospongiae: Clionaida) from Equatorial Southwestern Atlantic coast (Ceará State, Brazil)

Objetivo Geral

Registrar e fornecer a descrição taxonômica das espécies das esponjas da ordem Clionaida no litoral do Atlântico Sudoeste Equatorial (Ceará, Brasil), bem como sua distribuição geográfica.

Objetivos específicos

- Identificar as espécies de esponjas da ordem Clionaida no litoral do Atlântico Sudoeste Equatorial (do Ceará);
- Descrever os novos registros para essa região equatorial.

Hipóteses

Novos registros de esponjas da ordem Clionaida são possíveis devido à escassez de estudos e à dificuldade taxonômica de identificação dessas espécies.

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CHAPTER 01 - Stress-Tolerant Coral Faces Bioerosion: Sponge Colonization Under Mass Bleaching

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ABSTRACT

Global climate change has accelerated ocean warming, increasing thermal stress events that cause mass coral bleaching. In contrast, some tolerant organisms, such as certain sponge species, thrive under these novel ocean conditions. Despite their ecological importance, bioeroding sponges remain understudied in tropical reef systems. Here, we report the presence and ecological patterns of the coral-excavating sponge *Cliothosa delitrix* on Southwestern Atlantic reefs during the Fourth Global Coral Bleaching Event (2024). The sponge was found on six different low-latitude reef sites between 15 to 30 meters depth, colonizing both healthy and bleached colonies of the dominant, stress-tolerant coral *Siderastrea stellata*. Of the 347 coral colonies, ~ 52% showed bleaching, while 48 % showed no signs of this phenomenon. Bioerosion by *C. delitrix* was dramatically higher in bleached coral colonies, with an incidence approximately 13-fold greater compared to unbleached colonies (~38% vs. ~3%, respectively). This suggests the increased vulnerability of thermally stressed corals to sponge colonization. Sponge coverage was positively correlated with *S. stellata* available substrate (r = 0.93), and the abundance of small sponge individuals (< 5 cm^2) suggests high post-bleaching recruitment. Furthermore, there was no significant correlation (r = 0.17) between sponge perforation and depth, which indicates adaptation to different reef depths and that the availability of corals and their bleaching are the most important variables. This novel report of sponges colonizing key and bleached coral builders underscores the potential for opportunistic expansion of thermally resistant bioeroders under ongoing global climate change, even in reefs dominated by resilient coral species.

Keywords: *Cliothosa delitrix; Siderastrea stellata;* Coral bleaching; Coral-excavating sponge; Brazilian coral reefs.

1 INTRODUCTION

The increase in ocean temperatures due to global climate change has intensified the frequency and severity of mass coral bleaching events, substantially impacting tropical reef ecosystems (Carballo et al. 2013; Reimer et al. 2024; Vercelloni et al. 2020). As these bleaching events weaken coral health (e.g.: susceptibility to diseases, mortality), more heat-resistant species, such as bioeroding sponges, can opportunistically proliferate (Bell et al. 2008; Santos et al. 2023), further threatening coral resilience, carbonate growth, and their reef persistence. Although generally more tolerant, sponges may also experience stress due to increasing ocean temperatures (McMurray et al. 2011; Marlow et al. 2018; Whalan 2018).

Bioeroding sponges are highly effective competitors on coral reefs, as they erode and modify the carbonate substrate they are associated with, often making corals more fragile and reducing their resistance to wave impact (Hein and Risk 1975; Schönberg et al. 1997; Callahan 2005; Chaves-Fonnegra and Zea 2011). Although coral-excavating sponge processes are common, there is still no consensus on their ecological interactions. Various authors describe it in different ways, such as spatial competition (Acker and Risk 1985; Rützler 2002), epizoism (Antonius and Ballesteros 1998), infestation (Glynn 1997) or asymmetric space competition (López-Victoria 2003; Chaves-Fonnegra and Zea 2011).

In addition, these excavating sponges play an important role in the reef budget (Rützler 2002; De Bakker et al. 2024) and in the carbonate cycle (Schönberg et al. 2017). Although they contribute to reef erosion, they also generate biogenic sediments that help form and maintain the reef structure, facilitating the settlement of new larvae and organisms (De Bakker et al. 2024). Thus, they have a direct influence on the resilience of coral reef ecosystems, especially under increasing environmental stress linked to global climate change, including marine heatwaves, eutrophication and ocean acidification (Webb et al. 2017; Chaves-Fonnegra et al. 2018).

Excavating sponges belong to four orders of demosponges: Clionaida (Family Clionaidae - *Cliona, Cliothosa, Cervicornia, Spheciospongia* and other genera); Tetractinellida (Family Thoosidae - *Thoosa, Alectona*); Haplosclerida (Family Akaidae - *Aka*) and Poecilosclerida (Family Acarnidae - *Paracornulum, Zyzzya*) (Rützler 2002; De Voogd et al. 2025). Among the species of bioeroding sponges, some belonging to *Cliothosa* have dominated both living and dead coral reef communities, along with *Cliona* spp (Risk et al. 1995; Cruz-Barraza et al. 2011). These sponges can notoriously modify the carbonate structure of reef-building corals, leaving them more vulnerable to stressful situations (Chaves-fonnegra and Zea 2011).

The sponge *Cliothosa delitrix* is a bright orange, encrusting, burrowing sponge without symbiotic zooxanthellae (Pang 1973). This species has been shown to be a strong competitor for space and with significant growth on tropical reefs, especially due to climate change (Aguillera-Pérez 2024). In the Caribbean, this species has been quite damaging during the drilling process, leading some coral species to death, such as *Siderastrea siderea, Montastraea cavernosa, Diploria strigosa* and *Porites astreoides* (Chaves-Fonnegra and Zea 2011). Due to ongoing global warming and marine heatwaves, studies are needed to assess the presence and rate of occupancy of *C. delitrix* in bleached and healthy coral colonies. Connected to the Caribbean reefs but quite different, the extreme and marginal Southwestern Atlantic reefs are located off the coast of Brazil and are more than 4,000 km long (Costa et al. 2024). Their unique conditions include both particular environmental features (e.g., moderate turbidity and high sedimentation) and ecological/evolutionary aspects such as the high rate of endemism, low coral taxonomic and functional richness (around 20 species, and the occurrence of stress-tolerant corals such as the dominant *S. stellata* (Leão et al. 2003; Bleuel et al. 2024).

In South Atlantic reefs, *C. delitrix* remains a poorly studied species, despite some regional contributions (Muricy et al. 2008; Amaral et al. 2010; De Moraes et al. 2019; Praxedes et al. 2024). However, its role as a bioeroder, particularly its occupancy rates, developmental stages, or substrate preferences regarding healthy versus bleached coral colonies, remains largely unexplored. This knowledge gap becomes especially critical given the increasing frequency and severity of coral bleaching events associated with global climate change (Sully 2019; Vercelloni et al. 2020). As bleaching transitions from episodic disturbance to a recurrent driver of reef dynamics, understanding how opportunistic species like *C. delitrix* exploit these stressed conditions is essential to predict future shifts in reef community structure and resilience. In this context, the present study investigated the colonization of the excavating sponge *C. delitrix* on colonies of the coral *S. stellata* in the reefs of Pedra da Risca do Meio Marine State Park (PEMPRIM), with the following objectives: (I) elucidate the distribution of *C.delitrix* throughout the bathymetric range of the reef studied; (II) characterize the occupancy patterns of *C. delitrix* on *S. stellata* colonies; (III) identify the developmental stages of the excavating sponge *C. delitrix*; (IV) assess potential differences in sponge occupancy between bleached and unbleached coral colonies; and (V) establish baseline parameters for future biomonitoring of excavating sponges, especially in light of accelerating global climate change.

This study contributes to advancing the understanding of *C. delitrix* ecology and highlights the importance of continuous monitoring in Marine Protected Areas, particularly under ongoing increases in thermal stress affecting marginal and extreme reefs in the South Atlantic.

2 MATERIAL AND METHODS

2.1 Study site

The equatorial shelf margin, which includes the northernmost Brazilian reefs, is the least studied region of the Southwest Atlantic coast (Leão et al. 2016; Soares et al. 2019). Despite the shortage of studies, this low-latitude area serves as a natural laboratory for studies of the reef ecosystem and current global change impacts, such as coral bleaching, providing valuable information about extreme and marginal reefs (Soares et al. 2019).

The research was conducted in The Pedra da Risca do Meio Marine State Park (PEMPRIM), a Marine Protected Area (MPA) and subunit of the South Atlantic Reef system (Costa et al. 2024). The PEMPRIM is located about 18 km off the coast of Fortaleza, covering approximately 33.2 km², and is the only fully submerged MPA in the state of Ceará (Soares et al. 2011, 2016). The park consists of sandstone reefs at depths ranging from ~15 to ~ 30 meters, with a seabed supporting a benthic community of calcareous and filamentous algae, sponges, ascidians, and reef-building corals such as *S. stellata* (Campos et al. 2003; Lima-Filho 2006; Salani et al. 2006; Soares et al. 2016; Costa et al. 2024) (Fig. 1).

Oceanographic conditions are suboptimal for coral growth, characterized by intense trade winds, oligotrophic waters, moderate turbidity and sea surface temperature ranging from 26° to 30° C (Soares et al. 2016, 2019; Costa et al. 2024). The moderate water turbidity is driven by persistent trade winds and coastal currents that keep particles suspended in the water column (Costa et al. 2024).

Due to the turbidity and resuspension of sediments present in the environment, coral richness is low in these extreme and marginal turbid reefs (see definition in Schoepf et al. 2023). The dominant coral species that occurs in the area is the scleractinian *S. stellata* (> 90% of coral colonies), as well as the less abundant *Montastraea cavernosa* and *Mussismilia hispida* (Soares et al. 2016, 2019; Costa et al. 2024).

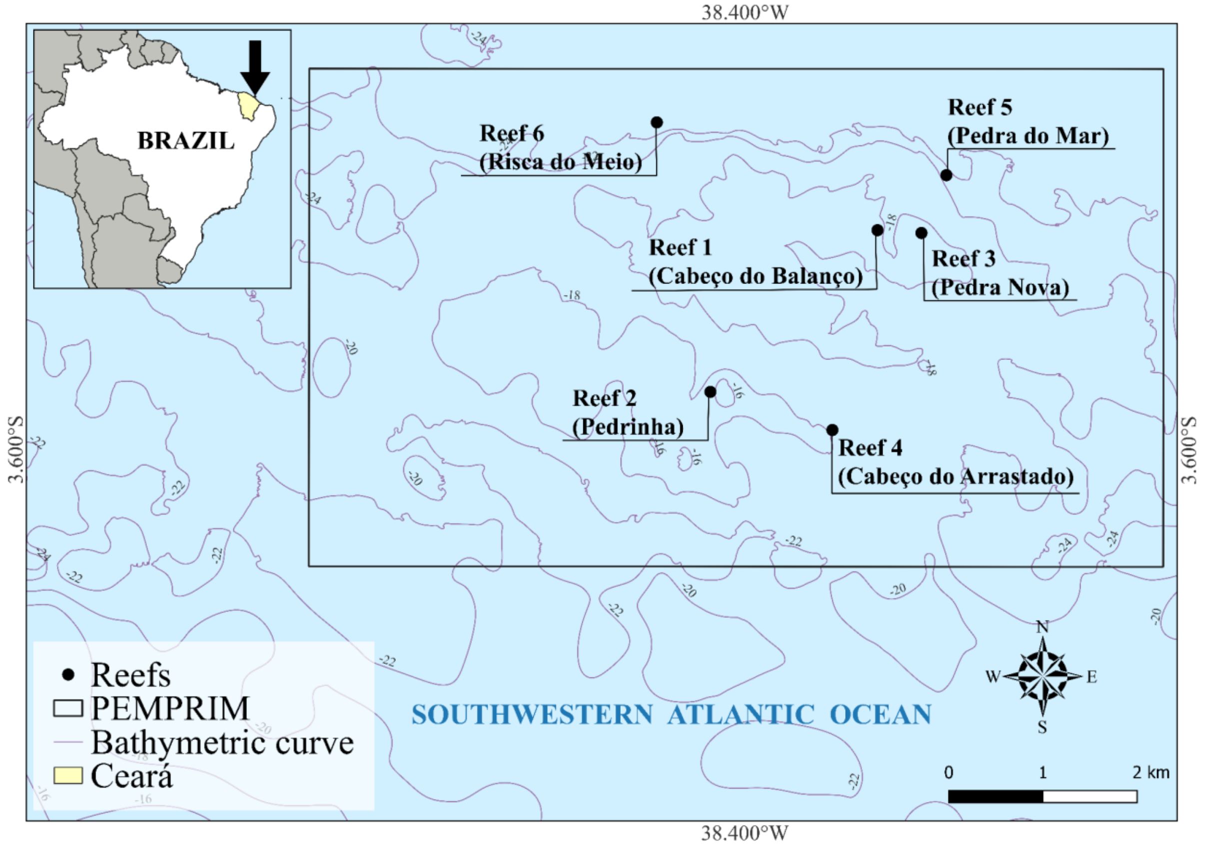

Fig. 1 Geographic location and bathymetry of the study area within the Pedra da Risca do Meio Marine State Park (PEMPRIM), a Marine Protected Area (MPA) located off the coast of Ceará, Brazil, in the Southwestern Tropical Atlantic. The map highlights the six reef sites (Reefs 1–6) surveyed during the study, distributed across a depth gradient ranging from 15 to 30 meters

2.2. Sampling data

Data collection was conducted between March and July 2024 during the fourth Global Coral Bleaching event, when Degree Heating Weeks (DHW) values reached up to 20.67 °C-weeks (Fig. 2c), indicating prolonged thermal stress conditions across the study region, at reef sites with depths ranging from 15–30 meters. At each reef site, photoquadrats of 50 x 50 cm^2 were taken side by side, along 20 m linear transects, generating a total of 40 images per dive site.

The images were analyzed to record the presence of the sponge *C. delitrix* piercing healthy and bleached *S. stellata* coral colonies. We quantified each *C. delitrix* and categorized them according to their stages of development: i) alpha (endolithic-papillate, the oscular and ostial papillae superficially pierce the substrate) and ii) beta (mainly endolithic or epilithicfouling, the sponge acquires a fouling growth and its papillae fuse together) (Schönberg et al. 2017), which still allowed visualization of the healthy or bleached coral substrate. Colonies of *S. stellata* were counted and classified into two categories: i) healthy and ii) bleached according to the literature (Soares et al. 2019; Lucas et al. 2023). Afterwards, we estimated the area of occupation (cm^2) of sponges on corals by measuring their area (cm^2) using the Image J Software (Schneider et al. 2012).

Finally, a bibliographic survey was carried out to investigate more precisely the worldwide distribution of *C. delitrix* and its association with reef-building corals. To do this, two bibliographic databases were used: "Google scholar" and "Web of Science", using the keywords: "*Cliothosa delitrix* (Pang 1973); "*Cliona delitrix* (Pang 1973)"; "*Cliothosa delitrix* AND Brazil"; "*Cliona delitrix* AND Brazil"; "*Cliothosa delitrix* AND corals"; "*Cliona delitrix* AND corals"; "*Cliona delitrix* AND *Siderastrea stellata*"; *Cliothosa delitrix* AND *Siderastrea stellata*". In addition to these digital platforms, we also used the World Porifera DataBase (De Voogd et al. 2025) to confirm the sponge species distribution.

2.3. Taxonomy: corals and sponges

The sponge species *C. delitrix* (Pang 1973) was identified by its bright orange color and prominent papillae. Two specimens with the characteristics mentioned above were collected by scuba diving. The identification slides of the spicules were mounted in the laboratory so that their measurements could be taken and compared with the taxonomic bibliography available for the excavating sponge species (Pang 1973; Muricy et al. 2008; Moraes 2011).

To confirm the coral species *S. stellata* Verril, 1868, we used morphological descriptions available for the group (Milne and Haime 1857; Menezes et al. 2014). Voucher specimens (LIMCEPOR414; LIMCEPOR413) were deposited in the Porifera collection of the Laboratório de Invertebrados Marinhos do Ceará, located at the Universidade Federal do Ceará (UFC).

2.4. Data analysis

To estimate the difference in the probability of *S. stellat*a colonies being perforated by *C. delitri*x depending on their bleaching status, we fitted a Bayesian generalised linear model with a Bernoulli distribution and a logit link, using the brms package in R (Bürkner 2017). The binary response variable indicated whether a given colony was eroded (1) or not (0), and bleaching condition ("Bleached" or "Healthy") was included as a fixed effect. The model was run with three chains of 6000 iterations, a warm-up of 1000, and thinning of 3. We assessed model convergence via trace plots, Rhat values (≈1.00), and effective sample size. Posterior estimates were summarised as marginal predicted probabilities with 95% highest posterior density (HPD) intervals, extracted via emmeans. In parallel, Pearson's correlation analysis was employed to investigate the linear relationship between depth and the area occupied by *C. delitrix*, as well as between the area of *S. stellata* and the area colonized by *C. delitrix.* Individuals of the latter species were categorized into size classes based on the ranges proposed by López-Victoria and Zea (2005), namely: 0–5 cm² (small), 6–15 cm² (medium), 16–45 cm² (large) and greater than 45 cm² (very large). Correlation analyses and graphical representations were conducted using R software (R Core Team 2024), and maps were generated using QGIS software (QGIS Development Team 2024).

3 RESULTS

3.1 Records and Geographical distribution of excavating-sponge *Cliothosa delitrix*

For the first time, we document the occurrence of *Cliothosa delitrix* across six low-latitude reef sites (~3.6°S) within the Pedra da Risca do Meio Marine State (PEMPRIM), at depths ranging from 15 to 30 meters during the fourth Global Coral Bleaching event (Fig.2a, b, c). Based on these records, we update the species' known distribution in the Southwestern Atlantic, which had previously been limited in Brazil to the states of Rio Grande do Norte (4°53'00,0 - 4°57'31" °S), Pernambuco (8º03'28" ºS), and Bahia (15° – 17°S) (Fig 3a, b). We highlight its presence in the PEMPRIM, off the coast of Ceará, located in the Southwest Equatorial Atlantic (Fig. 3c). This study also represents the first baseline assessment in Brazil to investigate the occupancy rates of *C. delitrix* on bleached and healthy colonies of the stress-tolerant coral *S. stellata*.

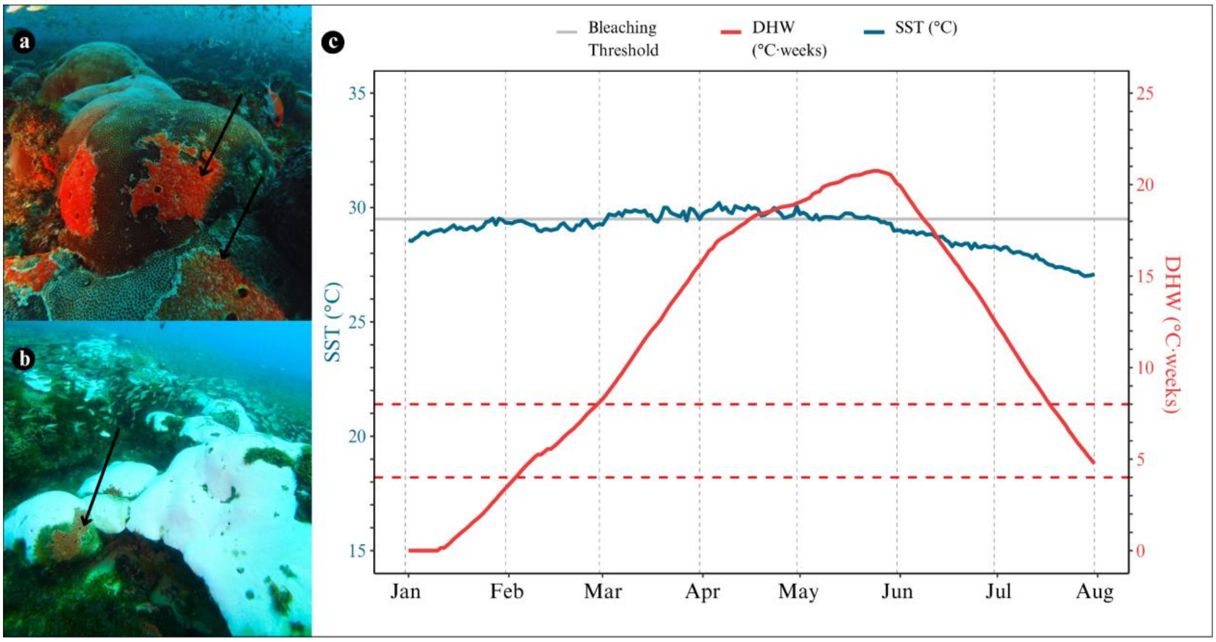

Fig. 2 In situ images showing the excavating sponges *Cliothosa delitrix* drilling colonies of the stress-tolerant coral *Siderastrea stellata* (black arrow) (a, b) Sea Surface Temperature (SST) and Degree Heating Weeks (DHW) values during the five-months study period (c). Dashed lines represent the 4 and 8 DHWs, and the grey line indicates the bleaching threshold, defined as 1°C above the Averaged Maximum Monthly Mean (MMM)

Fig. 3 Global distribution of *Cliothosa delitrix* (Pang, 1973). (a) Known worldwide records (red dots, left panel); (b) previously reported records from the Southwest Atlantic (red dots, right panel); and (c) new records from the six reefs of the Marine Protected Area off the coast of Ceará, Brazil, in the Southwest Equatorial Atlantic (black dots, bottom panel)

3.2 Developmental stages of *Cliothosa delitrix* and colonization in the stress-tolerant coral *Siderastrea stellata*

A total of 73 specimens of *C. delitrix* were recorded, 22% of which were in the alpha stage of development and 78% in the beta stage (Fig. 4a). Only two specimens were seen in the gamma stage, but it was not possible to see the substrate they were associated with, as the sponge typically dominates the entire colonized surface at this stage. Therefore, these data were excluded from our analysis. Of the 347 *Siderastrea stellata* colonies surveyed, 51.6% (n = 179) exhibited bleaching, while 48.4% (n = 168) remained unbleached (Fig. 4b). Erosion by *Cliothosa delitrix* was recorded in 68 of the bleached colonies, compared to only 5 cases among unbleached colonies, indicating a strong association between bleaching and sponge colonization. This pattern was supported by a Bayesian Bernoulli model, which estimated the probability of erosion to be 38.0% (95% HPD: 31.2–45.2%) in bleached colonies and 2.9% (95% HPD: 0.8–5.6%) in healthy ones (Fig. 4c). The model indicated a more than 13-fold increase in erosion probability associated with bleaching, highlighting thermal stress as a key driver of sponge-induced bioerosion in this system, indicating a sharp increase in vulnerability to sponge colonization under thermal stress.

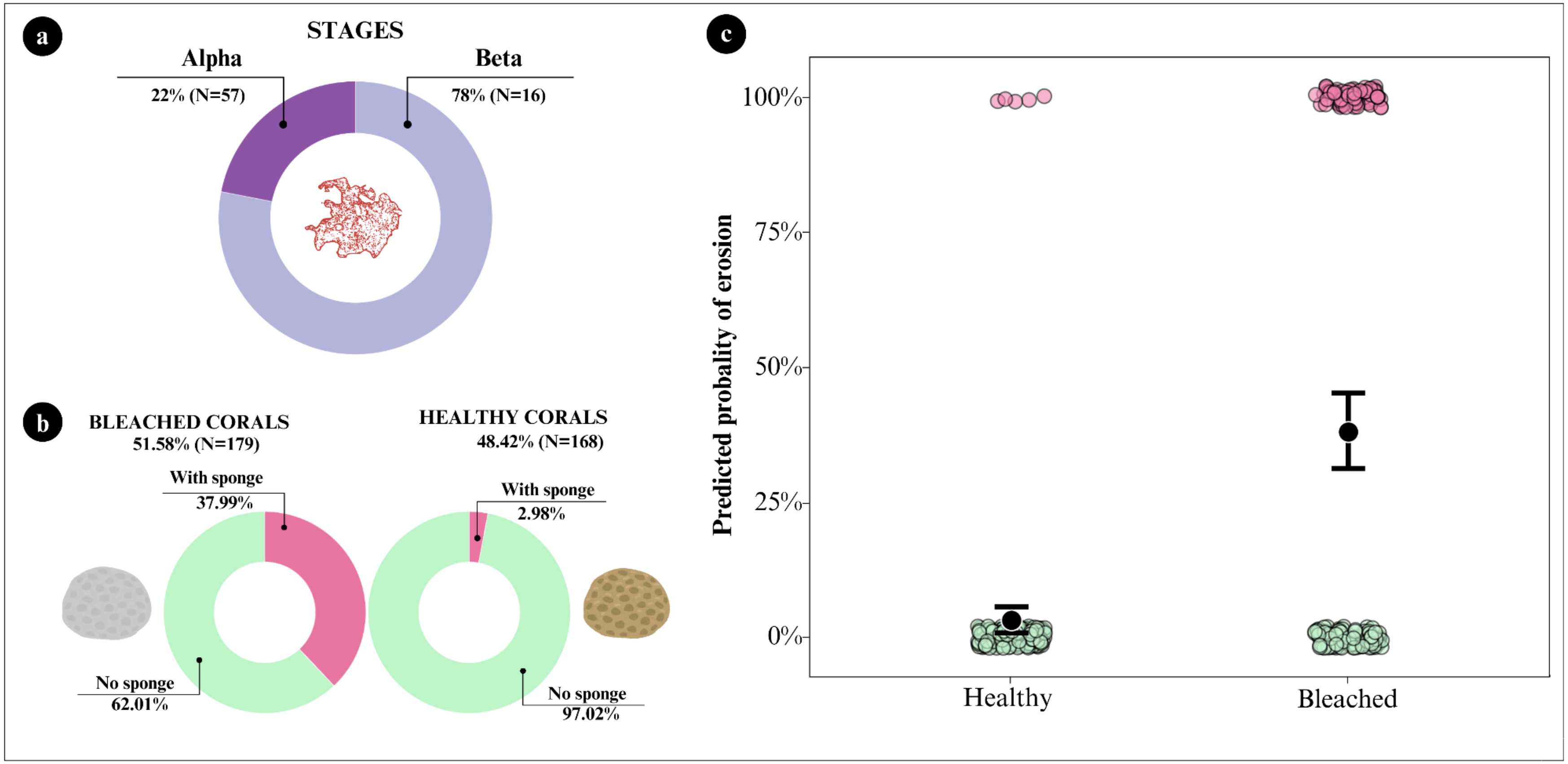

Fig. 4 Development stages of *Cliothosa delitrix* (a). Influence of bleaching on the occupation of *C. delitrix* in *Siderastrea stellata* (b) and (c) Predicted erosion probabilities by *Cliothosa delitrix* in *Siderastrea stellata* colonies under different bleaching conditions. Black points represent estimated marginal means from a Bayesian Bernoulli model, with vertical bars indicating the 95% high posterior density intervals (HPD). Jittered coloured points correspond to observed binary data (0 = not eroded, 1 = eroded)

3.3 Size frequency distribution

The size distribution of burrowing sponges at different reef sites reveals a clear predominance of smaller individuals (Fig. 5a). Sponges smaller than 5cm² had the highest relative proportions in most of the sites, except for the Reef 5 (Pedra do Mar). Medium-sized sponges (6–15 cm²) were recorded at Reefs 1 (Cabeço do Balanço), 2 (Pedrinha), 4 (Arrastado), and 5 (Pedra do Mar), but were absent from Reefs 3 (Pedrinha) and 6 (Pedra da Risca). Larger sponges (16–45 cm²) were more common at Reefs 1, 2, 3, 4, and 6, with Reef 5 being the only site where individuals of this size class were not observed. The largest sponges, those over 45 cm², were most abundant at Reefs 4, 5 and 6, while no individuals of this size were recorded at Reefs 2 and 3 (Fig.5a).

At Reef 1 (Cabeço do Balanço) and Reef 4 (Arrastado), the “0–5 cm²” class represents more than half of the composition, with 65.51% and 61.11% respectively, indicating communities highly dominated by smaller individuals (Fig. 5a). Reef 3 (Pedra Nova) also follows this pattern: 66.6% of the individuals recorded belonged to the smallest class, while the other 33.3% were in the “16–45 cm²” class. No individuals were recorded in the “6–15 cm²” or “>45 cm²” classes at this site, reinforcing the predominance of smaller sizes.

The intermediate ranges, such as “6–15 cm²” and “16–45 cm²”, appear in a more balanced way at some sites, such as reefs 2 (Pedrinha), 3 (Pedra Nova) and 5 (Pedra do Mar), but with less representation in relation to the smaller range. On the other hand, the “>45 cm²” class, corresponding to the largest individuals, was not very expressive or was absent from most of the reef sites, which may reflect low natural occurrence or environmental conditions that hamper the development of larger sponges. In general, the data indicates an asymmetrical size structure, with small organisms dominating and a progressive reduction in relative frequency as sponge size increases, a population pattern that is repeated in most of the reef sites evaluated. This denotes expressive recruitment and marked mortality following the sponge’s natural life cycle.

3.4. Correlation of the area of occupation of *Cliothosa delitrix* by depth and available reef substrate, in each site evaluated

In our baseline study, the largest presence of *C. delitrix* occurred at depths between 15 and 20 meters (n=62) (Fig. 5b), but the rate of sponge perforation showed no significant correlation with depth ($r^2 = 0.03$, $p = 0.13$) (Fig. 5c). The area of occupation of *C. delitrix* on the reefs of the marine park had a very strong positive correlation with the available substrate of *S. stellata* ($r^2 = 0.87$, $p < 0.001$) (Fig. 5d).

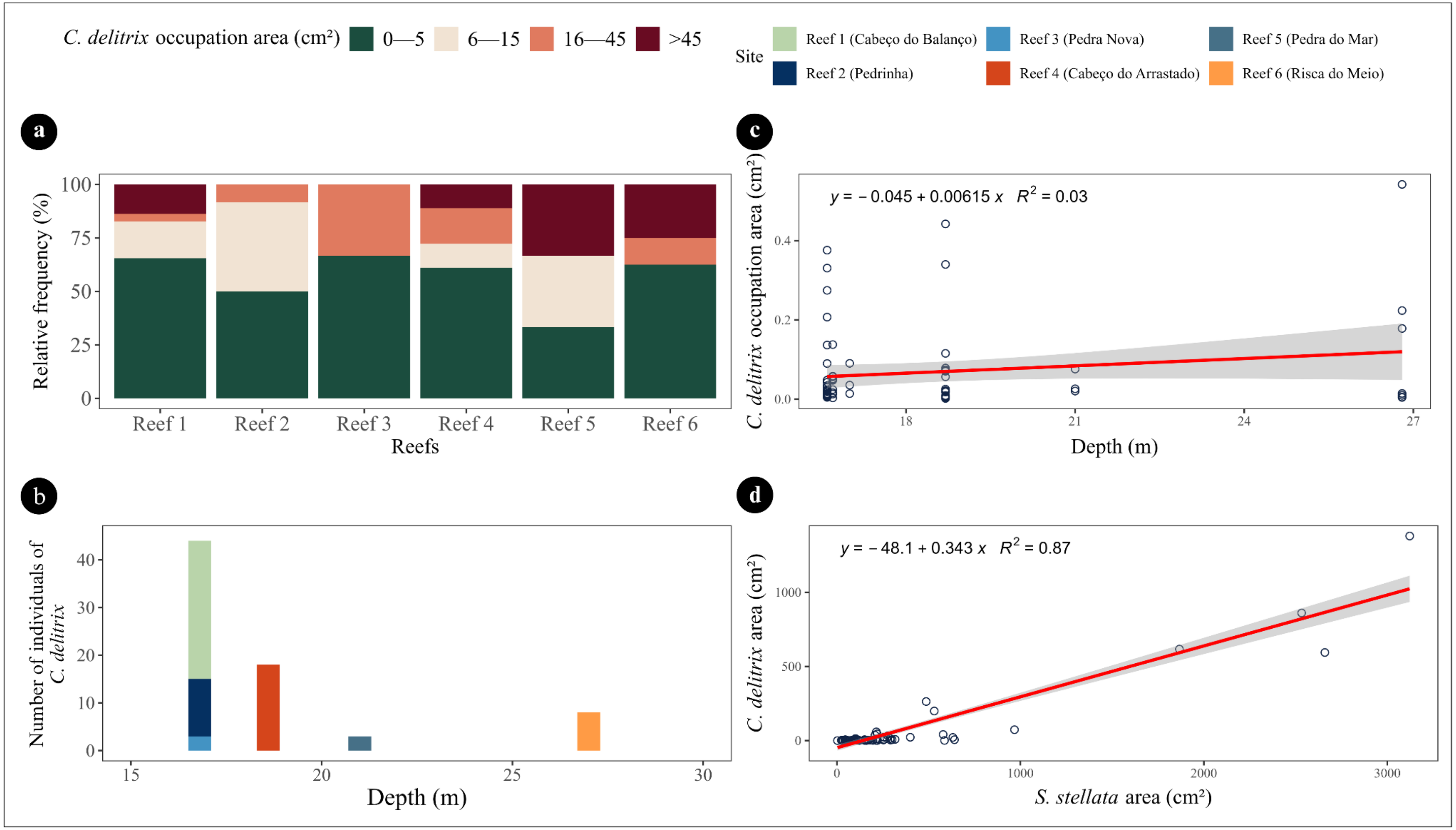

Fig. 5 Size-frequency distribution for the *Cliothosa delitrix* in different low-latitude reefs (Equatorial SW Atlantic) (a). Size is the area in cm^2. Size intervals are small (0–5 cm²), mid-size (6–15 cm²), large (16–45 cm²) and very large (>45 cm²). Reef 1: Cabeço do Balanço; Reef 2: Pedrinha; Reef 3: Pedra Nova; Reef 4: Arrastado; Reef 5: Pedra do Mar; Reef 6: Pedra da Risca. Number of individuals of *C. delitrix* at different depths on reefs of Pedra da Risca do Meio MPA (b); (c) dispersion of data between area of occupation by *C. delitrix* and depth, with fitted linear regression line (r = 0.179, p = 0.13) and (d) dispersion of the data between the area occupied by *C. delitrix* and the available area of *Siderastrea stellata*, with adjusted linear regression line (r = 0.935, p < 0.001).

4. DISCUSSION

Coral reefs worldwide are increasingly shaped by recurring thermal stress events, which weaken coral health and disrupt reef-building processes (Morais et al. 2022; Cornwall et al. 2021). While the effects of bleaching on coral mortality are well documented (Hughes et al. 2018; Morais et al. 2021), the ecological consequences of this stress in terms of opportunistic colonization by bioeroders remain less understood. We found the coral-excavating sponge *Cliothosa delitrix* on six different low-latitude reefs at 15 to 30 meters depth, marking the first documented occurrence of this species in the Equatorial Southwestern Atlantic. The sponges are colonizing both healthy and bleached colonies of the dominant, stress-tolerant coral *Siderastrea stellata*. Of the 347 coral colonies, ~ 52% showed bleaching, while 48 % showed no signs of this phenomenon. Among the bleached coral colonies, 37.99% were perforated by the sponge, while only 2.98% of the unbleached colonies showed this bioerosion, suggesting increased vulnerability to *C. delitrix* colonization following thermal stress and mass coral bleaching. Moreover, sponge coverage is positively correlated with available S. stellata substrate ($r^2 = 0.9387$), and the abundance of small sponge individuals (< 5 cm^2) suggests high post-bleaching recruitment. Furthermore, there was no significant correlation ($r = 0.17$) between sponge perforation and depth, which indicates adaptation to different reef depths and that the availability of corals and their stress condition (i.e., bleaching) are the most important variables. Our novel report of sponges colonizing key and bleached coral builders underscores the potential for opportunistic expansion of thermally resistant bioeroders under ongoing global climate change, even in extreme and marginal reefs dominated by resilient coral species.

4.1. Sponge records and depth distributions

Cliothosa delitrix (Pang 1973) is one of the most widely studied excavating sponges in the Greater Caribbean (Pang 1973; Rose and Risk 1985; Chaves-Fonnegra and Zea 2005, 2007, 2011, 2015) (Kobuk 1989; Lehnert 1998; Halperin et al. 2016) (Fig. 3a) (see other papers in Table S1 and S2). Outside of these regions mentioned above, few studies have been carried out on this species, such as the one carried out in the tropical South Atlantic region (Fig. 3b) (Table S2).

Twenty-four studies mention *C. delitrix* in their text, but only five of them were carried out in Brazilian marginal coral reefs, in the southwest Atlantic region (Muricy et al. 2008; Amaral et al. 2010; Moraes et al. 2019; Bettcher et al. 2023; Praxedes et al. 2024) (see papers in table S2). Records of this sponge occurred on intertidal sandstone reefs during low tide (Bettcher et al. 2023; Praxedes et al. 2024) and on offshore reefs with depths of up to 23 meters (Amaral et al. 2010; Moraes et al. 2019). Some of these records were made in Marine Protected Areas, such as Abrolhos Bank (the richest SW Atlantic coral reef), where *C. delitrix* was the second most abundant species found (Moraes et al. 2019) and Parque Marinho da Coroa Alta (Bettcher et al. 2023), both located in the state of Bahia (Brazil).

The occurrence of *C. delitrix* in marine protected areas is worrying, as this species is among the most destructive of Caribbean coral reefs, due to its high bioerosion capacity and rapid reproduction at temperatures above 25ºC (Rützler 2002; Chaves-Fonnegra 2014). In recent decades, their abundance has increased significantly, driven mainly by global climate change and human activities that impact tropical reef environments (Chaves-Fonnegra 2011, 2014; Morris et al. 2022).

Another important result concerns the presence of *C. delitrix* at depths between 15 and 30 meters (n = 62) (Fig. 5b) and its associated bioerosion rate. Surprisingly, no significant correlation was found between sponge colonization and depth ($r^2 = 0.03$, $p = 0.13$; Fig. 5c). It is important to note that there is a substantial body of literature supporting the idea that depth positively influences sponge abundance and diversity, primarily because suspended particulate and dissolved organic matter are more plentiful at greater depths, providing a richer trophic subsidy for filter-feeding organisms (MacGeachy and Stearn 1976; Lesser 2006; Lesser and Slattery 2018; Morais 2024). However, this pattern was not observed for *C. delitrix* in the present study, suggesting that the species is capable of successful settlement and bioerosion across the full range of reef depths surveyed.

The finds presented in this study suggest that, even in shallower environments, *C. delitrix* finds favourable ecological conditions for its colonization and the drilling rate does not seem to be directly related to depth, since they occur from the intertidal zone (Bettcher et al. 2023; Praxedes et al. 2024) to deeper regions (Pang 1973; Pérez et al. 2017; Moraes et al. 2019). Furthermore, our records between 25 and 30 m depth represent the deepest known occurrence of *C. delitrix* in Southwestern Atlantic coral reefs.

In this sense, this confirms the broad environmental tolerance of *C. delitrix* (Carballo et al. 2013), a species able to colonize reefs in different depth strata, which indicates that its ecological success is not directly related to the depth of the reefs in the South Atlantic. This characteristic may be associated with its ability to bore into varied calcareous substrates, its independence from photosynthetic energy sources and its physiological resilience in the face of stressful conditions, such as rising temperatures and coral bleaching (Chaves-Fonnegra and

Zea et al. 2011; Chaves-Fonnegra et al. 2015; Carballo et al. 2013). This ecological flexibility allows *C. delitrix* to settle not only in healthy coral colonies but also in bleached or dead hosts—a pattern confirmed in this study by the markedly higher colonization rates observed in bleached colonies. This ability to exploit compromised corals significantly expands its potential area of occupation and may enhance its persistence under future climate-driven disturbances (Chadwick and Morrow 2011).

4.2. Developmental stages and sponge sizes

Sponges of the Clionaidae family have five stages of development: alpha, beta, gamma and delta, the latter recently described (Schönberg et al. 2017). In this study, we mainly found the initial alpha and beta stages (Fig. 4a), which provides an important baseline for future monitoring.

After two centuries of research, it is known that bioerosive sponges are endolithic and excavate galleries within the substrate through a combination of chemical and mechanical processes, which have been investigated through analysis of cell ultrastructure and ion exchange microsensors (Pomponi 1976, 1980; Hatch 1980; Schönberg 2008). The chemical process is mediated by specialized cells aided by the enzymes anhydrase and phosphatase, as well as a corrosive chemical agent that dissolves calcium carbonate. The mechanical process occurs through the action of spicules, which scrape and deteriorate the substrate, removing fragments in combination with the chemical factors (Hancock 1849, 1867). Despite these advances, this is the first ecological investigation of *Cliothosa delitrix* on South Atlantic reefs at these depths (down to 30 m) evaluating developmental stages as well as occupancy rates in healthy and bleached colonies.

The higher proportion of small individuals found compared to the larger ones (Fig. 5a) may be related to high recruitment rates, possibly successful after the bleaching of *S. stellata* colonies. This phenomenon highlights the susceptibility to colonization in recently exposed substrates following intense climate change events (López-Victoria and Zea 2005). However, according to the same authors, it is potentially misleading to essay estimations of sponge recruitment and growth patterns based solely on size frequency, since the size of these organisms is not necessarily associated with their age. Therefore, in order to understand the recruitment pattern of *C. delitrix* in the marine park, long-term monitoring is necessary, identifying when individuals start colonizing and for how long they remain. In addition, it is essential to investigate whether other factors, apart from the availability of clean substrate, influence the permanence and growth of these sponges on coral heads.

4.3. Sponge occupancy during mass coral bleaching

Previous studies show that *C. delitrix* tends to colonize living or recently dead corals, especially those with more open and labyrinthine skeletal structures, which favor its propagation (López-Victoria and Zea 2005; Chaves-Fonnegra and Zea 2011). In addition, the low presence of competitors, such as algae, can facilitate the development of sponge larvae on these substrates (López-Victoria and Zea 2005; Chaves- Fonnegra and Zea 2011). In new, clean substrates, this sponge is capable of killing coral tissue when it reaches approximately 2 cm of perforation, even before it occupies all the available structure. However, its bioerosion process is slower compared to other zooxanthellate bioerosive sponges of the Clionaidae family, since *C. delitrix* seems to require more energy to make deeper excavations (Chaves-Fonnegra and Zea 2011).

Cliothosa delitrix can excavate approximately 10–12 cm of the coral structure, due to its high mechanical and chemical etching capacity, resulting in the formation of white areas around its periphery, indicative of the death of the coral tissue (Pang 1973). It shows a preference for massive corals (Ward-Paige et al. 2005) belonging to *Montastraea*, *Siderastrea*, *Diploria*, *Colpophyllia* and *Porites*, possibly due to the larger substrate area available and protection from currents and predators (see table S1). On the other hand, it is rarely associated with foliaceous or branching corals (Chaves-Fonnegra and Zea 2011). Our results reinforce this aspect detected in the Caribbean of preference for massive corals, as we detected it mainly in the species *S. stellata* (Fig. 2a, b). An important aspect is that the impacts of *C. delitrix* on Brazilian reefs may be greater than in the Caribbean, given the low coral cover and high dominance of a few species (functional redundancy) of reefs in the South Atlantic. In this context, the low number of species and low benthic cover may put reef-building corals on Brazilian reefs; a component of the reef's carbonaceous architecture and growth, at greater risk from bioerosion.

In this context, there have been cases where 12 interactions between sponges and corals have occurred in just one square meter of reef, and in 80% of these, the sponges prevailed over the colonies (Suchanek et al. 1983; Vicente 1990; Chaves-Fonnegra and Zea 2011). In recent years, this process has intensified due to climate change, which directly affects corals (Goreau and Hayes 2024; Capotondi et al. 2024), making them increasingly vulnerable to colonization by bioerosive sponges, especially when they are bleached as we detected in our results on *Siderastrea stellata*.

That said, the effects of accelerating global warming translated in 2024 being considered the hottest year ever recorded, with average annual air temperatures around 1.4° C above pre-industrial levels (with a margin of uncertainty of ±0.13° C) (WMO 2025). In this scenario, the last ten years (2015–2024) correspond to the warmest decade ever documented (WMO 2025). According to the study by Destri et al. (2025), there has been a significant increase in the intensity and duration of thermal stress episodes on all South Atlantic reefs, especially in the Northeast region, where the highest mortality rates have been recorded in recent years, a figure that is probably even higher due to the scarcity of field records (Pereira et al. 2022; Destri et al. 2025).

In response to the concentration of greenhouse gases being emitted on a large scale, the warming of ocean waters also continued in 2024. The global surface temperature of the sea (TSM) and ocean heat content (OHC) above 2000 m depth reached unprecedented highs in the historical record (The OHC of 0–2000 m in 2024 exceeded that of 2023 by 16 ± 8 ZJ (1 Zetta Joules = 10^{21} Joules, with a 95% confidence interval) (Cheng et al. 2025). In addition, the two- to three-fold increase in the rate of OHC since the end of 1980 shows a trend of rapid acceleration of this warming in the world (Cheng et al. 2025).

With the intensification of the global temperature increase, the fourth global coral bleaching event was confirmed in 2023/2024 (Reimer et al. 2024). The first three global bleaching events occurred in 1997/1998, 2010 and 2020 (Reimer et al. 2024). The coral *Siderastrea stellata* severely bleached in the study area in 2010 (Soares et al. 2019) and 2020 (Lucas et al. 2023), but no studies were carried out in those years with the bioerosive sponge analyzed here. Our data indicates a higher incidence of the sponge in bleached colonies in 2023/2024, possibly due to the greater fragility of the tissue of these organisms. It is not possible to say whether the death of the colonies was also influenced by the perforation of this sponge, due to the lack of monitoring in previous years, although studies indicate that bioerosive sponges cause epidemics that can kill corals (Sullivan and Faulkner 1983; Sullivan and Faulkner 1990; Chaves-Fonnegra et al. 2008; Halperin 2016) and make it impossible for them to re-establish themselves after bleaching.

If current environmental trends are not reversed, such as increased frequency of heat waves, ocean acidification, eutrophication and large-scale bleaching, it is likely that there will be a shift in the ecological dominance in reefs (Rose and Risk 1985; Bell et al. 2018), including Brazilian marginal reefs which are already shifting to dominance by zoanthids and macroalgae (Cruz et al. 2018). Studies carried out in the Caribbean following bleaching events have revealed an increase in the abundance of bioerosive sponges from the Clionaidae family (Cortés et al. 1984; Rützler 2002).In this context, we are discussing the possibility of a phase transition in reef communities, in which the builder corals *Siderastrea stellata*, recognized for their tolerance to turbidity and sedimentation (Leão et al. 2016) but susceptible to predicted future warming (Principe et al. 2021; Martello et al. 2024) may have high rates of mortality and local disappearance considering its low coverage in the area (Costa et al. 2024). These sponges, in turn, tend to benefit from reef degradation processes because they are more resistant to stress and can access other reef organisms such as calcareous algae (Carballo et al. 2004; Carballo et al. 2013; Schönberg et al. 2017).

Given the negative effects that can be caused by *C. delitrix* on colonies of building corals, it is to be regretted that only a few studies have been carried out to test the level of competition between these organisms (Halperin 2014). An experimental study carried out by Halperin (2014) on offshore reefs located in southeast Florida, tested techniques to control the colonization of *C. delitrix* in coral colonies that were being destroyed. The experiment consisted of removing the sponges using a hammer and chisel and filling the cavities formed by the sponges' perforations in the corals with cement and epoxy. After 12 months, it was observed that the bioerosive sponges had not returned to the colonies, showing that this technique can promote the recovery of affected colonies (Halperin 2014).

In this context, it is clear how important it is to join forces to promote experiments such as the one mentioned above and increase biomonitoring of reefs in the South Atlantic region, which are often overlooked in global studies (Banha 2025). Although much less studied, these extreme and marginal reefs are home to high biodiversity and many ecological relationships that have yet to be understood and described (Banha 2025), which may be the key to understanding the recovery process of coral colonies after the bleaching process. Understanding the roles played by sponges within the reef ecosystems of the Southwest Atlantic, especially in this case, the species *C. delitrix* which demonstrates greater resistance to environmental impacts (Halperin 2014, 2016), is a way of aiding possible mitigation strategies for the recovery of corals that are being destroyed by global climate change.

In addition to the problems mentioned above, it is important to note that other environmental impacts resulting from human activities can also favor the increase of bioerosive sponges in certain regions. For example, the high availability of organic matter has been associated with the growth of these sponges on the Great Barrier Reef in Australia (Rose and Risk 1985) and in eastern India (Holmes et al. 2000). However, these factors may not be primarily responsible for influencing the colonization of *C. delitrix* on the coral reefs of Pedra da Risca do Meio, as seen on the reefs of Southeast Florida, where nutrient input does not seem to influence the increase in density of this species (Halperin 2014).

Previous studies on the Brazilian semi-arid coast indicate low nutrient levels in these environments (Barroso et al. 2022), a consequence of the arid climate and recurrent droughts, which limit the export of organic matter to the reefs (Dias et al. 2013, 2018). Added to this is the absence of upwelling (Teixeira and Machado 2013) and the presence of a permanent thermocline, which prevents the vertical mixing of nutrients in the water column (Lalli and Parsons 1997) and contributes to the oligotrophic characteristics of this reef area (Teixeira and Machado 2013).

Thus, even in oligotrophic environments such as the one studied, one of the factors that may favor *C. delitrix* is its ability to excavate corals, combined with the ability to incorporate dissolved organic carbon (DOC) as part of its diet, an advantage over other heterotrophic organisms (De Goeij et al. 2013). Studies indicate that the DOC present in tropical oceans may represent an important source of energy for bioerosive sponges, which are able to remove around 90% of total organic carbon (TOC) in the form of DOC (De Goeij et al. 2013; Mueller et al. 2017; Ribes et al. 2012). In addition, given the transformations observed on the reefs, these sponges could benefit from increased DOC production, especially in scenarios where there is a possible predominance of algae over corals, which tends to intensify the release of this compound (Mueller et al. 2017). The area studied has a high abundance of macroalgae on the different reefs (15 to 30 m) (Costa et al. 2024).

In this sense, the characteristics of this sponge are worrying from a conservation point of view, since it compromises not only shallow reefs, but also deeper areas that could act as thermal refuges in the face of climate change. In addition, its presence at multiple depths makes it difficult to establish priority areas for management and can accelerate the structural degradation of reefs, amplifying the ecological impacts on already fragile coral communities (Carballo et al. 2013; Schönberg et al. 2017).

As observed in other studies (Alvarez et al. 1990; Chaves-Fonnegra et al. 2014; Halperin 2014), there is a strong correlation between area of occupation and available substrate (Fig. 8). Of the four coral species present in the analyzed MPA, *M. cavernosa*, *M. hispida*, *Meandrina brasiliensis* and *S. stellata*, *C. delitrix* showed a preference for the latter, which is present in greater numbers (> 90% of coral colonies in the area) (Costa et al. 2024). Studies indicate its preference for massive colonies, such as *S. stellata*,(see other associations in Table S1), with a larger internal skeletal volume, which likely provide the sponge with a refuge from possible predators, as well as taking advantage of the substrate to grow in size. The preference of *C. delitrix* for massive and building corals, such as *S. stellata*, can lead to changes in the composition of reef communities on these extreme and marginal reefs (Schoepf et al. 2023), resulting in a long-term loss of cover (Chaves-Fonnegra and Zea 2007, 2011).

The number of records of *C. delitrix* is certainly still underestimated, due to the scarcity of studies and the low number of taxonomists dedicated to the fauna of the various tropical reefs in the South Atlantic. In view of this, it is essential that current research prioritizes this group of organisms in marine environment management and monitoring programs, in order to mitigate the impacts of their bioerosion and contribute to the conservation of coral reefs (Chaves-Fonnegra 2014; Schönberg and Fang 2017). An emblematic example of how poorly studied northeastern Brazilian reefs are in regard to their sponge fauna, is the recent five fold increase on the knowledge of sponge diversity (about 20 to over 100 spp) in intertidal Discovery Coast reefs (southern Bahia) reported by Bettcher et al. (2023), including seven species of clionaids.

The findings of our study highlight the importance of long-term monitoring of coral-excavating sponges in coral reefs, especially within Marine Protected Areas, in light of the rapid global warming and its consequent negative impacts on biodiversity. In this context, the need for integrated scientific efforts and expanded research on bioeroding sponges becomes evident. Understanding the ecology of these species and tracking their long-term dynamics is essential, particularly considering the high bioerosion rates attributed to sponges in many regions of the world.

This study updated the distribution of *C. delitrix* through a review of the available scientific literature, representing the first record of the species in the Equatorial Southwestern Atlantic. Moreover, this is the first study on South Atlantic reefs to characterize the developmental stages of *C. delitrix* and suggest a possible preference for the bleached massive coral S. stellata, as evidenced by a higher number of perforations compared to healthy corals.

Further studies focusing on the reproduction, nutrition, and genetics of *C. delitrix* are essential to gain a deeper understanding of its ecology and impact on South Atlantic extreme and marginal reefs. In addition, monitoring is crucial to assess the recruitment patterns of this species—before, during, and after marine heatwaves, which are becoming increasingly frequent worldwide and may significantly alter reef structure and resilience.

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Table 1. *Cliothosa delitrix* species, substrate and references

Substrate	References	Substrate	References	Substrate	References	Substrate	References
Algae		**Coral**		**Coral**		**Coral**	
Coralineous algae	4, 21	*Diploria spp.*	1	*Mycetophyllia aliciae*	1	*Siderastrea siderea*	1, 2, 3, 5, 6
Coral		*Diploria clivosa*	1	*Oculina diffusa*	1	*Siderastrea stellata**	4, 15
Acropora cervicornis	1	*Diploria labyrinthiformis*	1, 3, 5, 6	*Orbicella faveolata*	1, 2, 5	*Solenastrea bournoni*	1
Acropora palmata	2	*Diploria strigosa*	1	*Porites* sp.	13	*Stephanocoenia intersepta*	1
Agaricia agaricites	1, 3, 4	*Eusmilia fastigiata*	1	*Porites astreoides*	1, 3, 4		
Agaricia fragilis	1, 4	*Isophyllia sinuosa*	1	*Porites porites*	1	**Unspecified**	
Agaricia lamarcki	1	*Madracis decactis*	1	*Pseudodiploria clivosa*	1	coral reef area	13, 16, 17, 18, 19
Colpophyllia natans	1, 3	*Meandrina meandrites*	1	*Pseudodiploria strigosa*	3	hard bottoms/ coral reefs	20
Dendrogyra cylindrus	3	*Montastraea annularis*	7	*Scolymia spp.*	1	*R. mangle* fringe contiguous to shallow reef	13
Dichocoenia stokesii	1	*Montastraea cavernosa*	1, 3, 4, 6, 8, 9, 10, 11,12	*Siderastrea* sp.	12	beachrocks	22, 23
Favia gravida	4	*Mussismilia hispida*	4	*Siderastrea radians*	14		

*Present work, 1 – Halperin 2016; 2 – Bakker et al. 2024; 3 – Chaves-Fonnegra 2011; 4 – Moraes et al. 2019; 5 – Chaves-Fonnegra 2007; 6 – Pang 1973; 7 – Highsmith et al 1983; 8 – Aguillera-Pérez et. al 2024; 9 – Mueller 2017; 10 – Rose, 1985;11 – Buznego 1987; 12 – Pulitzer-Finali 1986; 13 – Diaz 2005; 14 – Buznego 1987; 15 – Amaral et al. 2010; 16 – Alcolado 2012; 17 – Kobluk 1989; 18 – Lehnert 1998; 19 – Vasha 2020; 20 – Pérez 2017; 21 – Muricy et al. 2008; 22 – Praxedes et al. 2024; 23 – Bettcher et al.2023

Table 2. *Cliothosa delitrix* distribution, depth and references.

Sponge species	**Region**	**Depth**	**References**
Cliothosa delitrix *(Pang 1973)*	Off Fortaleza, Ceará (Pemprim)	15-30m	This paper*
	Caribbean	Not informed	Aguillera-Pérez et al. 2024
	Rio Grande do Norte - Brazil	13-33m; intertidal zone	Muricy et al. 2008; Praxedes et al. 2024
	Mexican Caribbean	3-12m	Bakker et al. 2024
	Bahia, Brazil: Madre de Deus, Salvador, Maraú, Abrolhos; Coroa Vermelha, Coroa Alta, Marine Park; Abrolhos;	Not informed; not informed; 8-23m	Hajdu et al. 2011; Bettcher et al. 2023; Moraes et al. 2019
	Eastern Caribbean (French Antilles)	30m	Pérez 2017
	Curaçao	8m	Mueller 2017
	Southeast Florida - USA	3-21m	Halperin 2016
	Greater Caribbean: Bahamas; Florida; Belize; Panama; Curaçao	4-18m; 8-22m; 8-25m; 6-10m; 5-15m	Chaves-Fonnegra 2015
	Guadalupe,Caribbean - France (Ultramarine)	5-26m	Alcolado 2012
	SWCaribbean - Colombia	Not informed	Chaves-Fonnegra 2007; Chaves-Fonnegra 2011
	Pernambuco- Brazil	23m	Amaral et al. 2010
	Bocas del Toro - Panama	1-18m	Diaz 2005
	Mexico	5m-27m	Lehnert 1998
	Venezuela	Not informed	Diaz et al. 1990
	Southern Caribbean - Netherlands Antilles (Bonaire)	18-30m	Kobluk 1989
	Cuba	6-30m	Buznego 1987
	Bimini (Bahamas) and Jamaica	2-3m; 10-25m	Pulitzer-Finali 1986
	Grand Cayman Island - (UK, Caribbean)	9-11m	Rose and Risk 1985

	Belize	Not informed	Highsmith et al. 1983
	Netherlands Antilles	5-30m	Van Soest 1981
	Discovery Bay (Jamaica)	22-34m	Pang 1973

CHAPTER 02 - New records of the Order Clionaida D'Orbigny, 1851 (Porifera: Demospongiae) from Equatorial Southwestern Atlantic coast (Ceará State, Brazil)

This paper will be submitted to Zootaxa in February.

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Abstract

The order Clionaida Morrow & Cárdenas (2015) is poorly documented along the tropical Southwestern Atlantic coast, particularly in the equatorial intertidal, shallow, and mesophotic reefs, where only the *Cliona celata* species complex had previously been recorded. In this study, we report four new records of Clionaida for this low-latitude region: *Cliothosa delitrix* (Topsent 1892), *Cliona carteri* (Ridley 1884), *Spirastrella hartmani* Boury-Esnault 1971, and *Placospongia giseleae* Mácola & Menegola, 2021 expanding the known distribution of these species in the southwestern Atlantic. *Cliona carteri* is redescribed based on newly examined material, with detailed scanning electron microscopy (SEM) images of its skeletal architecture and spicules. The occurrence of bioeroding species, including *C. delitrix*, associated with building corals is documented, contributing to the understanding of bioerosion processes in this reef region. These results substantially increase the known diversity of Clionaida in the tropical South Atlantic and highlight the need for further taxonomic surveys in under-sampled reef environments.

Keywords: taxonomy; sponges; diversity

1 Introduction

The order Clionaida Morrow & Cárdenas 2015 comprises three extant families: Clionaidae d'Orbigny 1851 (ten genera), Placospongiidae Gray, 1867 (three genera), Spirastrellidae Ridley & Dendy, 1886 (two genera), and one extinct family, Acanthochaetetidae Fischer, 1970 (de Voogd *et al.* 2025). All taxa belong to the subclass Heteroscleromorpha and are characterized by tylostyles as principal megascleres (Morrow & Cárdenas 2015).

The families show distinct morphological traits. Clionaidae are bioeroding sponges with various microscleres (spirasters, amphiasters, microxeas) (Rützler 2002a). Placospongiidae possess selenasters or amphinaster-like sterrasters forming a protective surface crust (Rützler 2002b). Spirastrellidae exhibit an encrusting habit and robust streptasters forming dense cortical layers (Rützler 2002c). Acanthochaetetidae differ by possessing a basal calcareous skeleton (Morrow & Cárdenas 2015).

Clionaida plays a fundamental ecological role through bioeroding sponges that influence reef dynamics (Scoffin *et al.* 1980; Schönberg *et al.* 2017a) and function as environmental bioindicators under climate change conditions (Carballo *et al.* 2013; Chaves-Fonnegra *et al.* 2014). Despite their importance, taxonomy presents significant gaps in under-sampled tropical regions (Muricy *et al.* 2011) like tropical Southwestern Atlantic (Spalding et al. 2007), though recent revisions of *Cliona* and *Cliothosa* have improved diagnoses (de Paula *et al.* 2012; Schönberg *et al.* 2017b, Schönberg *et al. 2024*).

According to de Voogd *et al.* (2025), approximately 209 species comprise Clionaida globally. Clionaidae includes 79 *Cliona*, 38 *Spheciospongia*, 22 *Pione*, and ten other genera. Spirastrellidae comprises nine *Diplastrella* and 18 *Spirastrella*. Placospongiidae includes 15 *Placospongia* and three other species.

In Brazil, 22 species have been recorded. Clionaidae includes 12 species (six *Cliona*, two *Spheciospongia*, and four other genera). Spirastrellidae comprises two *Diplastrella* and two *Spirastrella*. Placospongiidae includes six *Placospongia* species (Mácola & Menegola 2021; Muricy *et al*. 2011; Sandes *et al*. 2024).

Of the 60 sponge species recorded in equatorial Southwestern Atlantic (Ceará coast, Brazil), only *Cliona celata* complex belongs to Clionaida (Salani *et al*. 2021). Here we report four new records (*Cliothosa delitrix*, *Cliona carteri*, *Spirastrella hartmani*, and *Placospongia giseleae*) and redescribe *C. carteri* with SEM images.

2 Material and Methods

Sponges were collected during different research projects conducted along the coast of Ceará, northeastern Brazil (Fig. 1), at depths ranging from 0 to 50 m (intertidal, shallow, and mesophotic reef habitats). Some specimens were obtained through active search and free diving in intertidal zones during low tide, while others were collected via scuba diving as part of the GEFMAR monitoring project at Pedra da Risca do Meio. Additional specimens were already available in the Porifera Collection of the Laboratório de Invertebrados Marinhos do Ceará (LIMCE–POR). In total, 13 specimens were analyzed (Table 1).

For detailed collection data, see the "Examined Material" section for each species. All specimens were fixed in 80% ethanol and deposited in the Porifera Collection of the Universidade Federal do Ceará (LIMCE–POR) and in the Museu de História Natural do Ceará Professor Dias da Rocha (MHNC–POR). However, specimens collected during the Mar XV expedition (see Examined material) were initially fixed in formalin and subsequently transferred to 80% ethanol.

FIGURE 1 Locations where specimens were collected along the coast of equatorial Southwestern Atlantic Ocean(Ceará state, Brazil).

Spicule slides and perpendicular sections of the skeleton surface were prepared by hand following protocols described by Hajdu *et al.* (2011). Thirty spicules of each type were measured in micrometers (length × shaft width × head width for megascleres; length × width for microscleres), reported as minimum–mean–maximum with standard deviation in parentheses (±SD).

The most representative characteristics of the specimens, such as spicule diversity, skeletal morphology, presence of ostia or oscula, and whether the specimen was alive or fixed, were photographed using a digital camera (Nikon D3100) coupled to an optical microscope (Olympus CH30). Spicular material that could not be observed under light microscopy was sent for scanning electron microscopy (SEM) at two institutions: the Analytical Center of the Federal University of Ceará (UFC), using a QUANTA 450-FEG (FEI) microscope, and the Laboratory of Microscopy and Microanalysis of the Cell Biology Department at the University of Brasília (UnB), using a JSM-7001F microscope with metallization performed on a Sputter Coater (Leica, EM SCD 500).

Taxonomic comparisons were conducted based on a bibliographic survey of all species of the genera *Cliona*, *Cliothosa, Spirastrella*, and *Placospongia* available in the World Porifera Database (de Voogd *et al.* 2025). Comparative tables were prepared to facilitate the analysis and identification of species, and for *Placospongia*, the dichotomous key proposed by Sandes *et al.* (2024) was applied.

3 Results

Taxonomy and Description

Phylum Porifera Grant, 1836

Class Demospongiae Sollas, 1885

Order Clionaida Morrow & Cárdenas, 2015

Family Clionaidae D’Orbigny, 1851

Genus *Cliona* Grant, 1826

Cliona celata complex Grant, 1826
(Figure 2; Table 1)

Synonymy. *Cliona celata* sensu De Paula *et al.* 2012; Muricy *et al.* 2011 (for other synonyms).

Examined material. Ceará State, Brazil, intertidal zone: **LIMCEPOR–243,** Praia do Náutico, Fortaleza, 3º43'26"S–38º29'24"W, March 29th, 2012, coll. Filho, R.; **LIMCEPOR–308**, Praia do Pecém, 3º32'30.1"S-38º48'44.0"W, October 8th, 2021, coll. Salani, S., Oliveira, M., Regis, L.; **LIMCEPOR–315**, Praia da Pedra Rachada, Paracuru, 3º23'57"S–39º00'42"W, January 30th, 2021, coll. Oliveira, M. & Regis, L.; **LIMCEPOR–316**, Praia da Pedra Rachada, Paracuru, 3º23'57"S–39º00'42"W, January 30th, 2021, coll. Oliveira, M. & Regis, L.; **LIMCEPOR–320**, Praia da Sabiaguaba, 3°47'32.3"S 38°25'18.1"W, Fortaleza, December 3rd, 2021, coll. Regis, L.; **MHNCEPOR–7**, Praia da Sabiaguaba, 3°47'32.3"S 38°25'18.1"W, Fortaleza, December 3rd, 2021, coll. Regis, L.

Description. The sponges were found in all three growth forms: alpha, beta, and gamma (Fig. 2a–c, respectively). Sponge in alpha stage (LIMCEPOR–320; MHNCPOR–7) is slightly compressible, rough surface, color in life is yellow-orange and after preservation is brown, it was associated with sandstone reefs. The papilla is oval and measures 2 to 5 mm in diameter. Sponge in beta stage (LIMCE–POR 308) is slightly compressible, rough surface, after preservation in ethanol the papillae became conules measuring 1.5 mm in diameter and 0.5mm in height, color in life is bright yellow and in alcohol is brown-orange and was encrusting calcareous algae. The oscula range from 10 to 20 mm in diameter. Sponge in gamma stage (LIMCEPOR–243) is slightly compressible and elastic, smooth surface with papillae ranging from rounded to oval, measuring 2.0-3.0-5.5mm. Surface hispid and ectosoma is not detachable. The color of all specimens in alcohol is brown. The sponges (LIMCEPOR–315 and LIMCEPOR–316) were not observed *in situ*, only the presence of their spicules, they were bioeroding the mollusks *Cassis tuberosa* and *Turbinella laevignata*, respectively.

Skeleton. It is confusing (Fig. 2d), without clear differentiation into ectosomal and internal skeletons. The tylostyles are arranged randomly in the spongin fibers and projecting through the ectosome. The papillae skeleton is a perpendicular arrangement of ectosomal spicules, with points directed outward, forming a palisade with some tylostyles arranged horizontally between them.(Fig. 2e).

Spicules. Megascleres only. Subtylostyles (110–550/2,5–12,5 µm, tyle 2–12.5 µm in width, are smooth, straight to slightly curved, with heads that vary from globular (Fig. 2f – black arrow) to ovoid and hastate point (Fig. 2g – lilac arrow).

Ecology. The specimens were found in three stages and it was bioeroding rocks (sandstone reefs) and for the first time, they were seen drilling into species of mollusks *Cassis tuberosa* and *Turbinella laevignata.*

Distribution. Brazil. Northeast Region. Alagoas, Bahia, Ceará, Rio Grande do Norte, Pernambuco. Southeast Region. Rio de Janeiro, São Paulo, Espírito Santo Statestate (Muricy *et al.* 2011). **World.** Adriatic Sea, Aegean Sea, Alboran Sea, Argentina, Azores, Canaries, Madeira, Cape Verde, Cargados Carajos/Tromelin Island, Celtic Seas, Chatham Island Delagoa, East China Sea, Greater Antilles, Indian, Ionian Sea Levantine Sea, Maldives, Namibia, Netherlands, North Atlantic Ocean, North Patagonian Gulfs, North Sea, Northeastern New Zealand, Northern Gulf of Mexico, Republic of the Congo, Saharan Upwelling, Sea of Japan/East Sea, Seychelles, South Africa, South Atlantic Ocean, South European Atlantic Shelf, South India and Sri Lanka, South Korea, Southern Gulf of Mexico, Tunisia, Tunisian Plateau/Gulf of Sidra, Virginian, Western Mediterranean, White Sea, Yellow Sea (de Voogd *et al.* 2025).

Remarks. *Cliona celata* belongs to a species complex with a broad geographic distribution. In South America, four species are currently recognized within this complex: *C. celata Grant 1826*, *Cliona chilensis* Thiele, 1905, *C. diversityla*, and *C. lisa* Cuartas, 1991, with the first two being the most frequently reported in South America (De Paula 2012). Due to the scarcity of diagnostic morphological characters and the wide distribution of these sponges, such attributes have proven insufficient for accurate species delimitation. De Paula *et al*. (2012) emphasized the importance of incorporating genetic markers to revise these descriptions, as the diversity of clionids in South America is considerably greater than previously assumed. According to the same authors, the population of the Northeast, including that of Ceará, is part of clade D, which is closer to the Caribbean.

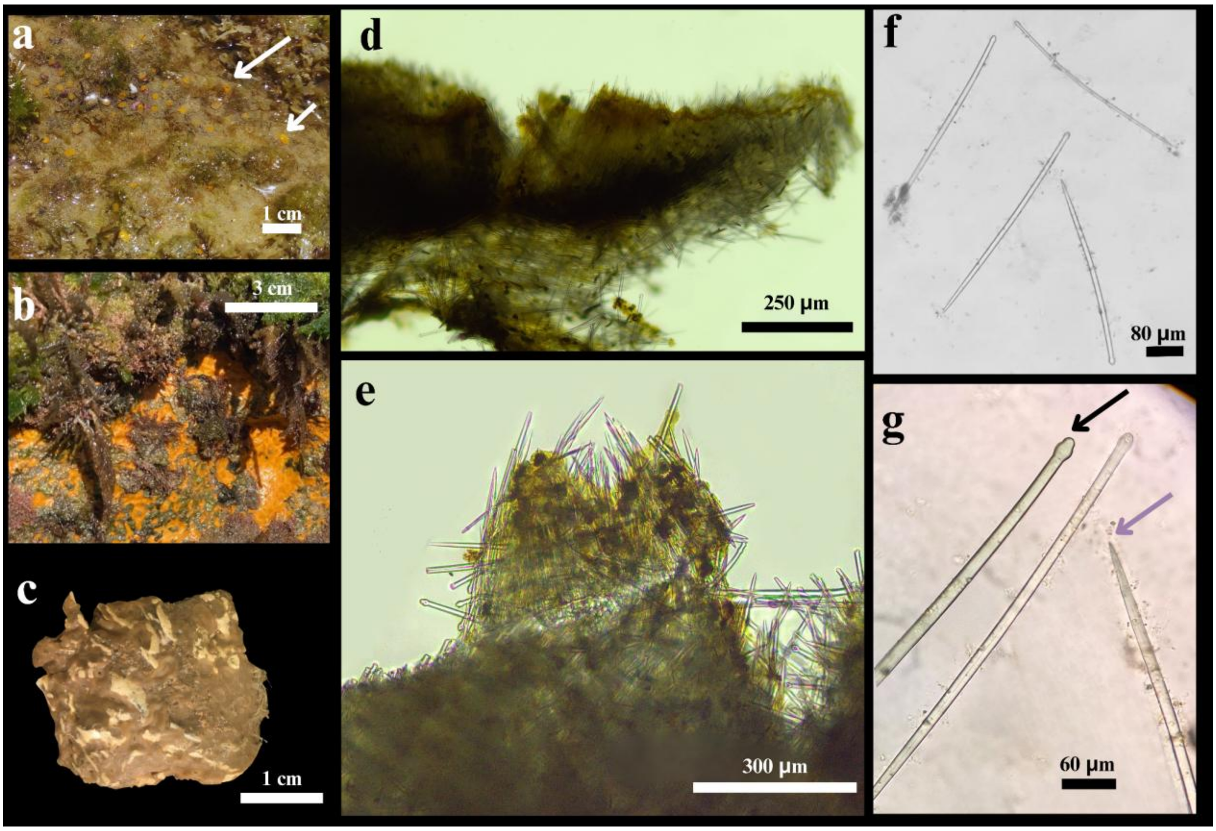

FIGURE 2 Complexo *C. celata* **a** LIMCEPOR–320 in alpha stage. **b** LIMCEPOR–308 in beta stage. **c** LIMCEPOR–243 in gamma stage. **d and e** Skeleton architecture. **f and g** Tylostyles.

***Cliona carteri* (Ridley, 1881)**
(Figure 3; Table 1)

Synonymy. See Muricy *et al.* 2011 for other synonyms

Examined material. Ceará State, Brazil. **LIMCEPOR - 319**, Guyot platform,1°36,5'S Long. 38°42,0'W, 50m deep, 1990, coll. Noc. Victor Hensen.

Description. Excavating sponge. Color in alcohol is purple (Fig. 3a), was observed in the alpha stage of growth bioeroding rhodoliths. The specimen was fragile to the touch.

Skeleton. Tylostyles were observed primarily in the choanosome; however, due to the calcareous substrate, only their tips were visible emerging from the ectosome (Fig. 3b).

Spicules. Spicules consist of tylostyles and with rare spirasters (Fig. 3c–d). **Megascleres. Tylostyle** (240–380/5–15µm), smooth and slightly curved, hastate, globular tyle (10–20 µm) (Fig. 3c). Malformation spicules were occasionally observed, including polytylote forms (Fig.

3d).

Microscleres. Spirasters 22–42.5 µm, with three turns bearing 2–6 simple, conical spines unilaterally disposed along the longitudinal axis of the rays (Fig. 3e), some spines bifurcate at their distal ends (3e - setae).

Ecology. This sponge was bioeroding rhodoliths at 50m deep (present study), and calcareous algae and dead coral (Ridley 1881).

Distribution. Brazil. Northeast region: Ceará State (present study) and Fernando de Noronha archipelago (Mothes & Bastian 1993). Southeastern region: Espírito Santo State: Vitória Bank (type locality) (Ridley 1881).

Remarks. The specimen collected along the coast of Ceará is assigned to *Cliona carteri* based on its agreement with the original description, particularly the presence of a single type of spiraster (Ridley 1881). *C.carteri* has historically been confused with *C. schmidtii* (Ridley 1881) due to their strong morphological similarity. When describing *C. carteri*, Ridley (1881) noted in a footnote (p. 130) that material previously referred to as *Vioa johnstonii* Schmidt (1870) should be separated into two distinct taxa, *C. carteri* and *C. schmidtii*. The most reliable distinction between these species lies in the microsclere complement: *C. carteri* possesses only one type of spiraster, whereas *C. schmidtii* has two distinct types, including a slender form. The Ceará specimen exhibits tylostyles measuring 240–380/5–15 µm and a single type of spiraster measuring (22-30-42,5/0.8 - 1.5 µm), supporting its identification as *C. carteri*.

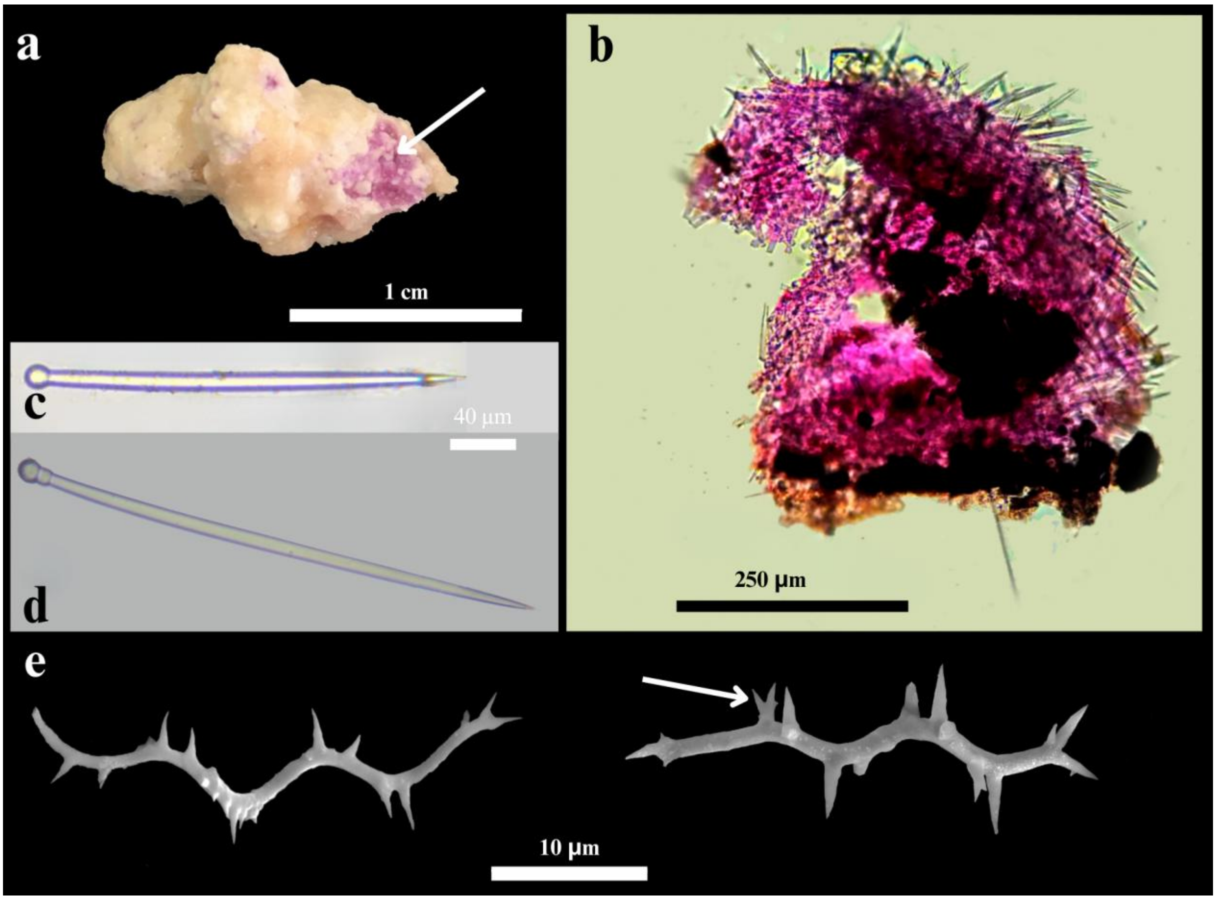

FIGURE 3 Spicules and skeleton of *Cliona carteri*. **a** Specimen in alcohol, (LIMCEPOR – 319). **b** Skeleton organization in transversal section showing tylostyles emerging from the ectosome; **c and d** tyle variations. **e** spirasters presents three turns with 2-6 rays.

Genus *Cliothosa* Grant, 1826

***Cliothosa delitrix* (Pang 1973)**
(Figure 4; Table 1).

Synonym. See Muricy *et al*. 2011 for other synonyms

Examined material. Ceará State, Brazil. **LIMCEPOR-413**; Cabeço do Balanço Reef, Parque Marinho Estadual da Pedra da Risca do Meio, Fortaleza, Ceará (03º 34' 44"S; 38º23'14"W), **LIMCEPOR-414**; Pedra Nova Reef, Parque Marinho Estadual da Pedra da Risca do Meio, Fortaleza, Ceará (–3° 34' 44.4"S; 38° 22' 59.34"W). December 10, 2024, coll. Gurgel, A and Bleuel, J.

Description. Reddish-orange color in life after fixation is orange brown. Firm consistency, not elastic, but brittle. Presence of circular and slightly elevated oscula with 1 centimeter of length, after fixation it appears retracted (Fig. 4a–b).

Skeleton. The tylostyles completely fill the choanosomal skeleton without a well–defined organization and they are oriented towards the ectosome, crossing its surface (Fig. 4c). It is possible to observe that the sponge was in the beta stage going to the gamma stage

Spicules. Megascleres only. Subtylostyles are smooth, straight and the head width ranging from slightly curved to more rounded (118–507/1,4–5,9µm), head width, 1,2–6,5µm and the tips are hastate with rare, stepped tips (Fig. 4d – black arrow).

Ecology. *Cliothosa delitrix* was observed excavating the coral *Siderastrea stellata* in high abundance. The formation of galleries within the coral skeleton was evident, particularly in bleached colonies. This species had not been previously recorded at the study site. However, in the Caribbean, *C. delitrix* has been reported as highly detrimental, contributing to the mortality of several coral species, including *Siderastrea siderea*, *Montastraea cavernosa*, *Diploria strigosa*, and *Porites astreoides*, especially in the context of ongoing global climate change (Chaves-Fonnegra & Zea 2011).

Distribution. Brazil. Northeast region. Ceará (present study), Bahia and Rio Grande do Norte state. **World.** Type locality is Greater Antilles (de Voogd *et al*. 2025).

Remarks. The specimen reported here was described based on the few studies available in scientific literature. Live color, shape, spicule type, measurements and skeleton of the sponge fit well with previous studies (Pang 1973). This species appears to be influenced by global climate change (Chaves–fonnegra *et al.* 2014). Therefore, more specific taxonomic and ecological studies in the study area are necessary to understand this species more specifically.

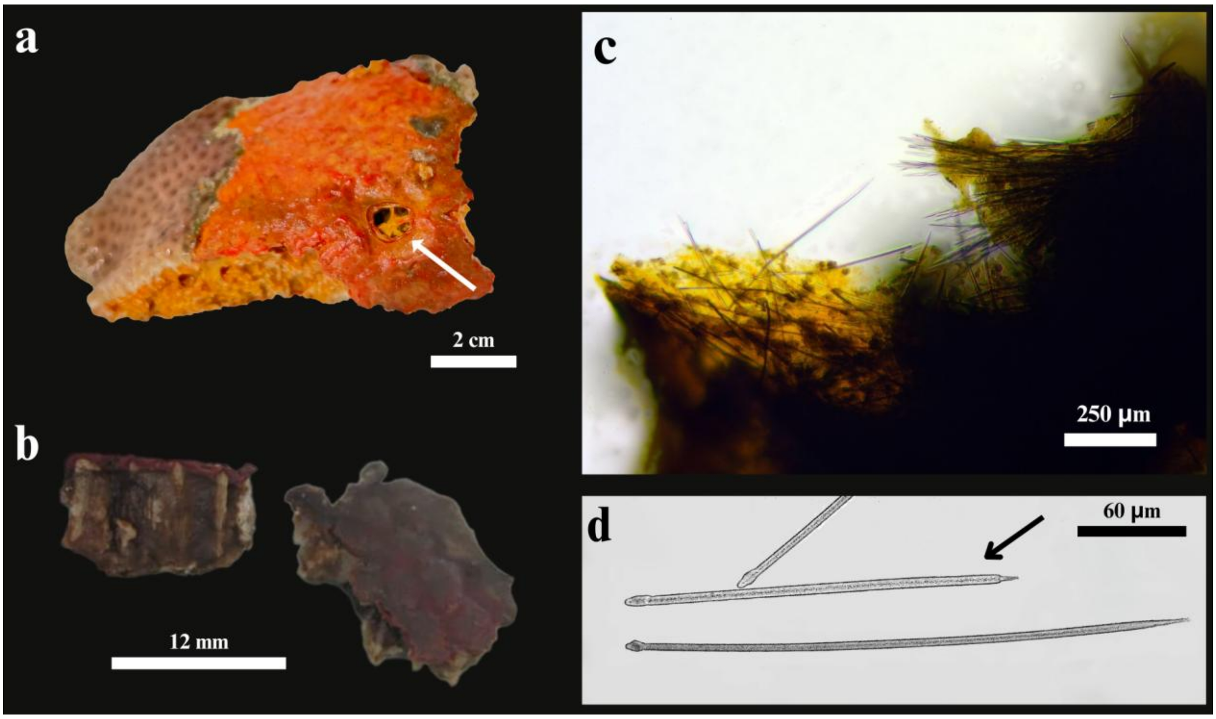

FIGURE 4 *Cliothosa delitrix.* **a** LIMCEPOR–413 showing oscules. **b** specimen fixated**. c** transversal section of skeleton showing tylostyles present in the ectosome and choanosome. **d** Tylostyles and tips morphology.

Phylum Porifera Grant, 1836

Class Demospongiae Sollas, 1885

Order Clionaida Morrow & Cárdenas, 2015

Family Placospongiidae

Genus Placospongia Gray, 1867

Placospongia giseleae Mácola & Menegola, 2021
(Figure 5; Table 1)

Synonymy. *absent*

Examined material. Ceará State, Brazil, Intertidal zone. **LIMCEPOR–191; LIMCEPOR–187**, Praia do Pacheco, coll. Oliveira, M and Salani, S. August, 2019. **LIMCEPOR–309**, Praia do Pecém, coll. Oliveira, M and Salani, S. October, 2021.

Description. Specimens collected exposed at low tide. Color varies: LIMCEPOR–191 dark brown both in vivo and after fixation (Fig. 5a); LIMCEPOR-187 and LIMCEPOR–309 salmon in vivo (Fig. 5b), becoming light pink when fixed. Consistency rigid, stone-like after fixation. Oscules are not observed, likely due to contraction while exposed out of water. Surface covered by smooth, rigid cortical plates separated by contractile grooves.

Skeleton. The choanosome has bundles of multispicule tylostyles that support the ectosome (Fig. 6a). The tylostyles cross the choanosome, supporting the cortex formed by a large number of selenasters present (Fig. 6b) Some microrhabds were visualized on the ectosome and coanosome surface (LIMCEPOR–309; LIMCEPOR–191). The ectosome (1 mm thick) has a selenaster layer.

Spicules. Tylostyles in two categories, selenasters and acanthomicrorrabdos. **Megasclere.** Tylostyles in two categories. **Type I** (Fig. 6c) are large, straight, smooth, with rounded tips and globular terminal tyles (Fig. 6e–f) (400–900/10–25 µm; tyle diameter 7.5–22.5 µm). Malformations include angulate shafts and stepped terminal tip. **Type II** (Fig. 6d) are smaller, straight, smooth, with a hastate tip, (160–370/7.5–12.5 µm); tyles range from oval to globular, 7.5–12.5 µm in diameter (Fig. 6g–h).

Microscleres. Microrhabds are straight to slightly sinuous, densely covered with numerous spines, measuring 5–22.5/2.5–5 µm (Fig. 6i–j). **Selenasters,** which range from oval to spherical (Fig. 6k); younger forms are bean-shaped, and the surface is composed of a star-like mesh (Fig. 6l), measuring 15–22.5 × 10–20 µm.

Ecology. Found associated with other sponges and polyplacophorans attached to rocks in the intertidal zone. In the Southwest Atlantic, this constitutes the first record for the state of Ceará. It was observed in association with *Phragmatopoma* reefs, and at the time of collection, an epibiotic colonial ascidian was also present. According to Mácola & Menegola (2021), this species was found in the lower part of the rocks (0–20 m depth).

Distribution. Brazil. Northeast region. Ceará (present study), Bahia and Pernambuco state. Type locality is Eastern Brazil (Mácola & Menegola, 2021)

Remarks. The analyzed specimens exhibit the same spicule types and size ranges as those reported in the original description of *P. giseleae* (Mácola & Menegola 2021). Different growth stages of selenasters and microrhabds were observed. However, the latter spicule type appears to be rare, being absent in specimen LIMCEPOR–187, present in low abundance in LIMCEPOR–191, and abundant in LIMCEPOR–309. The reduced formation of microscleres in the examined specimens may be related to the availability of silica in the environment

(Schröder *et al*. 2005). However, this factor was not assessed in the present study, and further investigations are required to test this hypothesis. We also observed that specimen coloration ranges from dark brown to lighter brown. The darker specimen changes color after fixation, becoming dark purple (Fig. 5 a–b), while the lighter specimen retains the same color (Fig. 5 c–d).

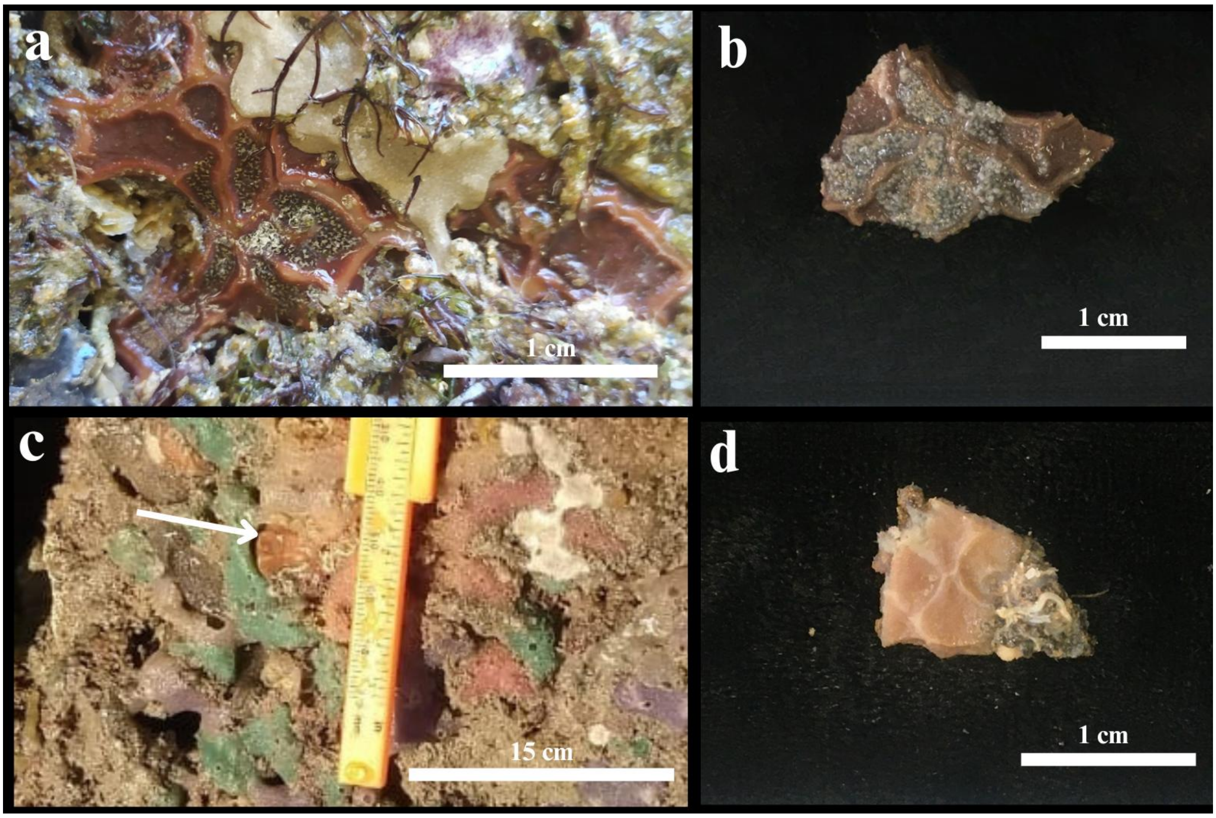

FIGURE 5 Specimens of *Placospongia giseleae.* **a and b** LIMCEPOR–191 in vivo and in alcohol. **c and d** LIMCEPOR–309 in vivo and in alcohol.

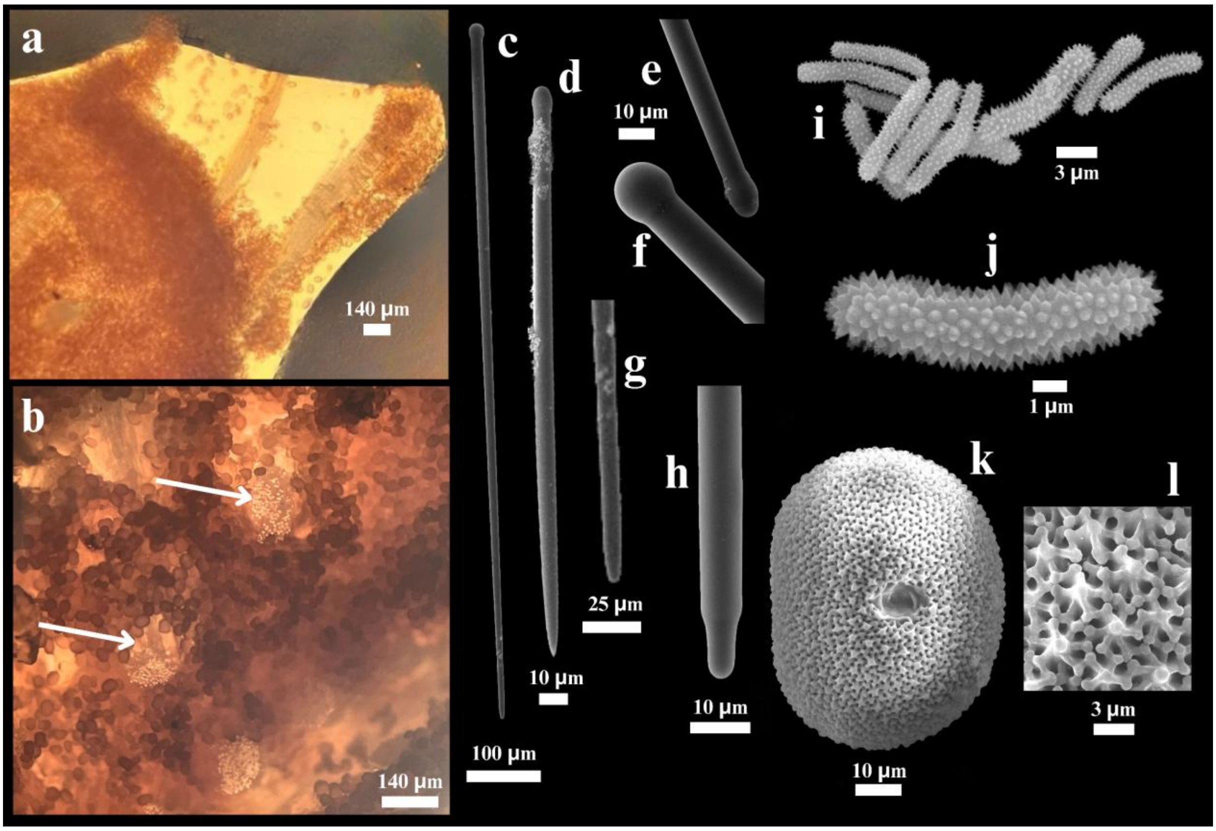

FIGURE 6 Skeleton and spicular types of *P. giseleae* (LIMCEPOR–191) . **a** Skeleton architecture (LIMCEPOR–191); **b** Tylostyle bundle; **c, d, e, f, g and h** the morphology of tylostyles, highlighting the heads and tips (LIMCEPOR–187; LIMCEPOR–191; LIMCEPOR–309). **i and j** microrhabds (LIMCEPOR–191; LIMCEPOR-309). **k and l** selenaster morphology.

Phylum Porifera Grant, 1836

Class Demospongiae Sollas, 1885

Order Clionaida Morrow & Cárdenas, 2015

Family Spirastrellidae

Spirastrella hartmani Schmidt, 1868
(Figure 8; Table 1)

Synonymy. Absent

Examined material. LIMCEPOR–50, Guyot platform, 1°36,5'S Long. 38°42,0'W, Ceará State, 50m deep, 1990, coll. Noc Victor Hensen.

Description. Smooth surface, soft and easy to break. Oscules not observed. Color is cream after fixation (Fig. 7a).

Skeleton. The ectosome contains densely packed spirasters forming a conspicuous cortical crust. Tylostyles protrude through the surface with their terminal points visible, giving the surface a hispid texture (Fig. 7b). In the choanosome confused, chanels can be observed.

Spicules. Tylostyles and Spiraster in two types. **Megascleres.** Tylostyles are slightly curved to straight, point hastate (360–600/10–25 µm); head width is oval to globular, 10–20 µm (Fig. 7c–e).

Microscleres. Spiraster type I: are smaller and have one to three curvatures (10–25/2.5–7.5 µm) (Fig. 6f – green arrow). **Spiraster type II**: are larger and have only one curvature (37.5–55/ 10–17.5µm) (Fig. 6f – black arrow).

Ecology. This sponge was associated with rhodolits at 50 m deep.

Distribution. Brazil. Northeast (Fernando de Noronha, Atol das Rocas, Island São Pedro and São Paulo, Rio Grande do Norte, Alagoas). Type locality is Southwestern Caribbean. (De Voogd *et al.* 2025; Muricy *et al*. 2008).

Remarks. Our description is based on the examination of the holotype previously described by Boury-Esnault *et al.* (1999) and specimen decribed by Moraes (2011). The spicule measurements fall within the ranges reported in those earlier studies.

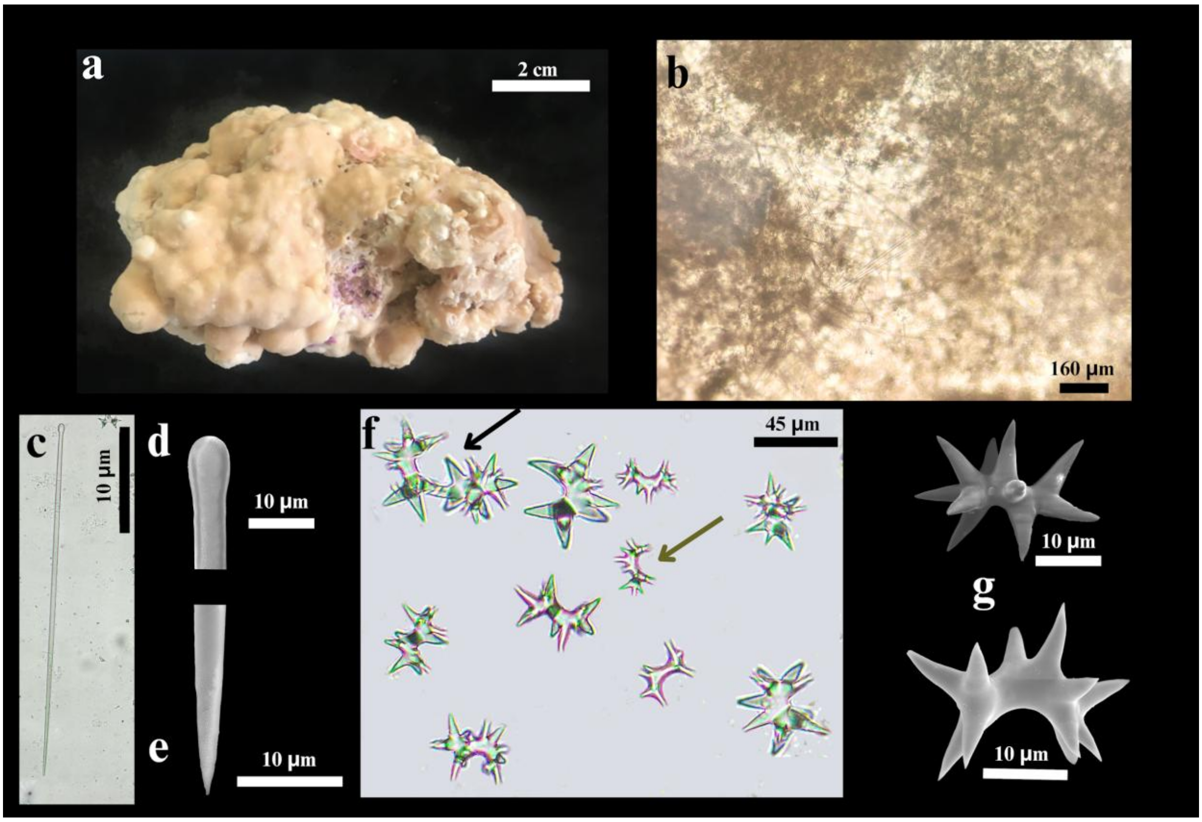

FIGURE 7 *Spirastrella hartmani* **a** LIMCEPOR–50 in situ. **b** skeleton architecture. **c, d and e** tylostyle morphology. **f** spirasters type I (green arrow) and spirasters type II (black arrow). **g** spiraster type II.

In this study, we report for the first time four species of the order Clionaida (*Cliothosa delitrix, Cliona carteri, Spirastrella hartmani,* and *Placospongia giseleae*) from the Equatorial Southwestern Atlantic (Ceará), expanding knowledge of regional sponge biodiversity. In addition, we redescribed *C. carteri* based on scanning electron microscopy (SEM) and updated the geographic distribution of these species in intertidal reefs.

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TABLE 1. Comparative table of the specimens found with measurements of length, width and standard deviation of their spicules, color, growth stages and depth.

Species	**Megascleres (tylostyles)**	**Microscleres**	**Color**	**Growth stages**	**Site (depth)**	**Vouches**
Cliona celata (Grant 1886)	210–**308**–350µm(35.10)/2.5–**7.8**–12.5µm(2.4)/2–**4.2**–5µm(0.77)	absent	bright yellow (in vivo); brown-orange (fixated)	Alpha	Praia do Pecém - Pecém, Ceará / Brazil (intertidal zone)	LIMCEPOR–308
Cliona celata (Grant 1886	180–**290**–342µm(39,6)/3,5–**8,5**–12,5µm (1,6) /head width, 5–**9,5**–12,5µm (1,5)	absent	yellow-orange (in vivo); brown (fixated)	Beta	Praia da Sabiaguaba - Fortaleza, Ceará State / Brazil (intertidal zone)	MHNCEPOR–7
Cliona celata (Grant 1886)	210–**311**–350µm (25,47) / 7,5–**10,4**–12,5µm (1.32) / head with, 7,5–**10**–12,5µm (1,4)	absent	brown (fixated)	Gamma	Praia do Náutico - Fortaleza, Ceará State / Brazil (intertidal zone)	LIMCEPOR–243
Cliona celata (Grant 1886)	110–**216**–280µm (33,3) / 5–**9,5**–12,5µm (1,6) / head width, 7,5–**10**–12,5µm (1,4)	absent	brown (fixated)	Alpha	Praia da Pedra Rachada - Paracuru, Ceará State / Brazil (intertidal zone)	LIMCEPOR–315

Cliona celata (Grant 1886)	120–**231,4**–550µm (144,3) / 5–**10**–12,5µm (2,5) / head width,7,5–**10**–12,5µm (2)	absent	brown (fixated)	Alpha	Praia da Pedra Rachada - Paracuru, Ceará State / Brazil (intertidal zone)	LIMCEPOR–316
Cliona celata (Grant 1886)	180–**290**–342µm (39,6)/3,5–**8,5**–12,5 µm (1,6) /head width, 5–**9,5**–12,5µm (1,5)	absent	yellow-orange (in vivo); brown (fixated)	Beta	Praia da Sabiaguaba - Fortaleza, Ceará State / Brazil (intertidal zone)	LIMCEPOR–320
Cliona carteri (Ridley 1881)	240–**315**–380µm (36,45) / 5–**12**–15µm (2,54) / head width, 10–**16**–20µm (2,64)	22–**30**–42,5/ x 0.8 - 1.5 µm **(n=5)**	purple (fixated)	Beta	Guyot platform - Ceará State / Brazil (50m)	LIMCEPOR–319
Cliothosa delitrix (Pang 1973)	118–**253**–321µm (52,3) / 1,4 – **3,5** – 5,9µm (1,1); head width, 1.4–**3,5**–5,9 (1,2)	absent	red-orange (in vivo); dark brown (fixated)	Beta	Pedra Nova Reef - Fortaleza, Ceará state / Brazil (18m)	LIMCEPOR–414
Cliothosa delitrix (Pang 1973)	173–**269**–507µm (56,8) / 2,5–**3,8**–4,9µm (0,55); head width, 1,2–**3,7**–6,5 (1,0)	absent	red-orange (in vivo); orange brown (fixated)	Beta	Cabeço do Balanço Reef - Fortaleza, Ceará state /Brazil (18m)	LIMCEPOR–413

Placospongia giseleae	Type I:400–**712**–900µm (154.3)/10–**14.5**–25µm (2.8); head width, 7.5–**14.5**–22.5µm(3.3); Type II: 160–**248.6**–370µm(60)/7.5–**9.1**–12.5µm(0.75); head width, 7.5–**9.25**–12.5µm(1.6)	Selenaster: 27.1–**52.3**–95.6–(34.7)/10.7–**29.9**–58.9(19.6) Microrhabd:5.7–7.6–**9.1** (0.9)/ 1.1–**1.3**–1.8 µm (0.2)	Dark brown (in vivo and fixated)	Encrusting	Praia do Pecém (Intertidal zone) Ceará, Brazil)	LIMCEPOR–309
Placospongia giseleae	Type I: 527,9–**764,7**–985.9µm (187.1)/10–**14.3**–20µm (0.8); head width, 9–**.95**–13.6µm (2.01) Type II: 380–**482**–654,3 (133,2)/3.**9**–**4.8**–6.8 (1.36); head width, 7.1–**8.8**–9.6µm (1.04)	Selenaster: 50–**56,77**–71,0µm (5,41)/30–**39,97**–50µm (4.06) microrhabd: 12,4 µm **(n=1)**	salmon (in vivo); light pink (fixated);	Encrusting	Intertidal zone (Praia do Pacheco - Ceará State / Brazil	LIMCEPOR–187

Placospongia giseleae	Type I: 726.6–**868.7**–1245.5 µm (145.8) / 7.4–**11.1**–12.6 µm (1.4); head width, 10.8–**14.1**–16.8 µm (1.5) Type II: 243,2–**407.6**–493.2µm (93) / 4,16–**7**–8.8 µm (1.75), head width 6.9–**8.15**–12µm)	Selenaster: 50-**60,91**-70µm (5,26)/40-**47,17**-60µm (10.04) microrhabd: 8.1 x 1.2µm **(n=1)**	Dark brown (in vivo and fixated)	Encrusting	Intertidal zone (Praia do Pacheco - Ceará State / Brazil	LIMCEPOR–191
Spirastrella hartmani	360–**478**–600µm (72.3)/ 10–**15**–25µm(0.7) / head width, 10–**19.6**–20µm (1.8)	Spiraster type I: 10–**16.6**–25µm (4.55) x 2.5–**4.46**–7.5µm (1.44) ; Spiraster type II: 37.5–**44.6**–55µm (4.87) x 10–**12.6**–17.5 (2.38)µm	cream color (fixated)	Encrusting	Guyot platform - Ceará State / Brazil (50m)	LIMCEPOR–50

4. CONCLUSÃO GERAL E CONSIDERAÇÕES FINAIS

Os resultados desta dissertação contribuem de forma significativa para o conhecimento da espongiofauna e para a conservação dos ecossistemas recifais do Atlântico Sudoeste, especialmente em um contexto de intensificação das mudanças climáticas globais nas regiões tropicais e equatoriais do planeta. Ambos os capítulos foram fundamentados em dados primários e na compilação crítica de estudos prévios, sobretudo aqueles conduzidos no Brasil e no Grande Caribe, que subsidiaram a interpretação dos padrões ecológicos observados e escritos em inglês visando publicação em revistas de qualidade internacional.

No Capítulo 1, foi registrada a bioerosão do coral *Siderastrea stellata* por *Cliothosa delitrix*, sendo observadas taxas mais elevadas em colônias branqueadas, padrão semelhante ao documentado para recifes caribenhos durante ondas de calor marinhas recentes. Esses resultados foram obtidos na única unidade de conservação marinha submersa do Ceará. Além disso, foram caracterizados os estágios de desenvolvimento de *C. delitrix* e sua distribuição ao longo do gradiente batimétrico do recife. Esses achados permitiram discutir aspectos ecológicos relevantes da espécie e reforçar a necessidade de ampliar estudos regionais, bem como de incorporar as esponjas bioerosivas em programas de monitoramento e planos de manejo de unidades de conservação marinhas, diante da aceleração de eventos climáticos extremos que intensificam processos de erosão, degradação estrutural e mortalidade de corais construtores.

No Capítulo 2, foram registrados pela primeira vez para o Atlântico Sudoeste Equatorial (Ceará) representantes de quatro espécies da ordem Clionaida (*Cliothosa delitrix*, *Cliona carteri*, *Spirastrella hartmani* e *Placospongia giseleae*), além da redescrição de *C. carteri* com base em microscopia eletrônica de varredura (MEV) e da atualização da distribuição geográfica dessas espécies em recifes entremarés.

De modo geral, os resultados reforçam a importância da continuidade dos estudos taxonômicos e ecológicos sobre esponjas nos recifes brasileiros, especialmente diante da ausência prévia de registros de taxas tão elevadas de bioerosão em corais termorresistentes no Atlântico Sudoeste. As esponjas bioerosivas emergem como potenciais bioindicadoras do aumento da temperatura oceânica, embora seja fundamental a implementação de programas de monitoramento de longo prazo para confirmar esses padrões e compreender suas implicações ecológicas em escala regional e global.