

An epibiotic association between burrowing and sessile bivalves on the Amazon continental shelf: implications for ecological facilitation in sediment-dominated environments

Jonata de Arruda Francisco^{1,2}, Flavio de Almeida Alves-Júnior^{2,3}, Karolina Ferreira Rodrigues^{1,2}, José Carlos Nascimento Barros⁴, Jonathan Stuart Ready^{1,2}

¹ Grupo de Investigação Biológica Integrada (GIBI), Universidade Federal do Pará - UFPA, Pará, Brazil

² Programa de Pós-Graduação em Ecologia Aquática e Pesca -PPGEAP - UFPA

³ Laboratório de Crustacea (LabCrus), Universidade Federal Rural da Amazônia - UFRA, Pará, Brazil

⁴ Departamento de Pesca, Universidade Federal Rural de Pernambuco - UFRPE, Pernambuco, Brazil

Corresponding author: jonata.francisco@neap.ufpa.br, jonatafrancisco@gmail.com

Keywords Epibiose, Ecological facilitation, Soft-bottom ecosystems, Amazon continental shelf, Benthic communities, Biogenic substrates.

Abstract

From the perspective of ecological facilitation theory, we report an epibiotic association between two mollusk species with contrasting lifestyles, *Chama macerophylla* **Gmelin, 1791 (sessile)** and *Tucetona pectinata* **(Gmelin, 1791) (burrowing)**, on the Amazon continental margin. Specimens were collected using a Van Veen dredge near the shelf break and in the vicinity of AP3 blocks recently offered for offshore oil exploration. The observed interaction suggests that semi-infaunal bivalves may act as mobile hard substrates, facilitating the establishment of sessile organisms and increasing habitat heterogeneity in soft-bottom environments. This record provides a baseline for future environmental monitoring of ecological interactions in the region.

Introduction

Epibiotic interactions are defined as the use of the external surface of one organism by another as a living substrate (Martin et al., 2020; Dvoretzky & Dvoretzky, 2022). These interactions contribute to the structuring of benthic communities by generating secondary substrates and modifying local habitat conditions (Majewska et al., 2023). In many cases, epibiosis acts as a mechanism of ecological facilitation, increasing spatial complexity and

allowing the persistence of sessile organisms in environments where consolidated substrates are scarce (Bruno et al., 2003).

Substrate limitation is a critical factor in unconsolidated bottom systems, where the availability of hard surfaces restricts larval settlement and the ontogenetic development of sessile invertebrates (Fernandez-Leborans, 2010). Most settlement is associated with reef or rocky environments, where stable surfaces favor colonization (Buschbaum & Reise, 1999; Schejter & Bremec, 2007; Vasconcelos et al., 2007; Souto et al., 2012; Schejter et al., 2014a). In contrast, records of epibiotic associations are particularly relevant in environments where consolidated substrates are naturally scarce such as sedimentary sea beds (Mikkelsen & Bieler, 2008; Rios, 2009; Redfern, 2013). In this context, external hard body parts of living organisms may act as mobile substrates, generating ephemeral habitat patches within relatively homogeneous muddy bottoms. The Amazon continental shelf represents an important system (both for biodiversity and for fisheries resources) dominated by fine sediments under strong fluvial influence (Nittrouer et al., 2021; Vale et al., 2022), where recent studies have reported epibiotic organisms, indicating increasing scientific attention to these interactions (Alves-Júnior et al., 2022; 2023). At the same time, this region is increasingly exposed to anthropogenic pressures, particularly due to expansion of offshore oil exploration, reinforcing the need to understand baseline ecological processes.

This study aims to characterize an epibiotic association in unconsolidated bottom systems of the Amazon continental shelf and explore its potential ecological role in sediment-dominated environments, providing a baseline for future environmental monitoring.

Materials and Methods

The sampling area is located in the Amazon Shelf ecoregion and is characterized by predominantly sandy-muddy bottoms under strong influence of the Amazon sediment plume (Fig. 1). This environment exhibits a high load of suspended particulate matter and intense continuous deposition of fine sediments, constituting a system of high sedimentary dynamics (Nittrouer et al., 2021; Vale et al., 2022). This study site is located near the shelf break and in the vicinity of AP3 blocks that were recently offered for offshore oil exploration (ANP, 2026).

Sampling was carried out aboard the research vessel R/V Soloncy Moura, on March 3, 2025, using a Van Veen dredge to collect loose sediments at approximately 70 m depth

(2°29'26.00"N; 47°35'35.00"W). The survey was conducted as part of a partnership between the Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul (CEPSUL) and the Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Norte (CEPNOR), both affiliated with the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

After sampling, the individuals were frozen and subsequently transported to the Laboratório de Crustáceos (LabCrus) at the Universidade Federal Rural da Amazônia (UFRA), where they were sorted, identified, and deposited in the Coleção de Invertebrados Aquáticos Amazônicos - Mollusca subárea (CIAA-MOL-009). Additionally, the taxonomic identification was based on diagnostic conchological characters, as described by Rios (2009), Mikkelsen & Bieler (2008), Redfern (2013), and Chagas et al. (2020).

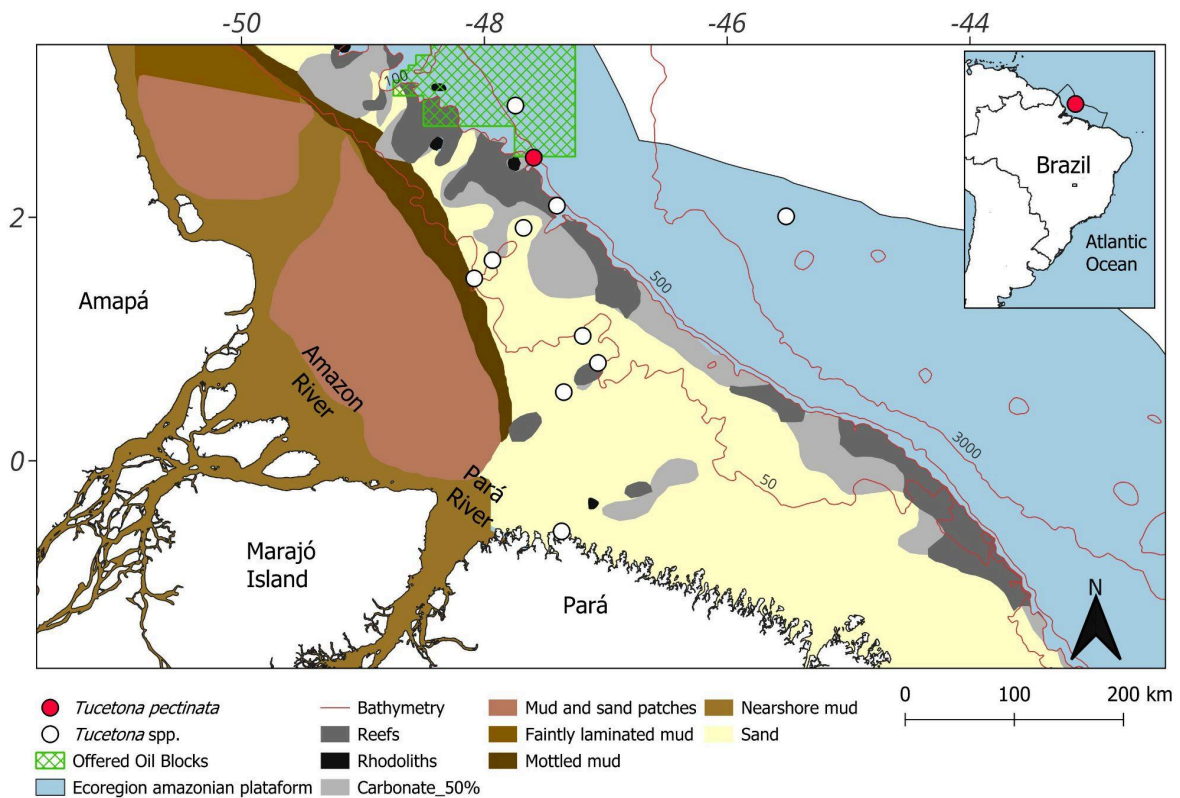


Figure 1. Map of the Amazon continental shelf showing occurrences of *Tucetona pectinata* (red dots, new records) and *Tucetona* spp. (white dots, literature records from Chagas et al., 2020). Environmental layers include the location of offshore oil blocks (ANP, 2026), the extent of the Amazon platform ecoregion (Spalding et al., 2007), and bathymetry and substrate types (Vale et al., 2022).

Results

We found an epibiotic interaction between two species with contrasting lifestyles *Chama macerophylla* (sessile) and *Tucetona pectinata* (burrowing). Three live specimens of *T. pectinata* were collected at 70 m depth in soft-bottom habitats near the Great Amazon Reef System and the AP3 offshore exploration blocks (Figs. 1, 2). All specimens had well preserved soft tissues providing evidence that they were alive shortly before sampling (Fig. 2). One specimen also presented an individual of *C. macerophylla* firmly attached to the right valve (Fig. 2A–B) that similarly showed well preserved soft tissues, indicating that it was a living epibiont close to the time of collection. The epibiont was attached near the ventral margin of the shell, close to the opening region and showed preserved soft tissues. The other two individuals of *T. pectinata* also exhibited well-defined scars at similar locations on the ventral margin of the shell with rounded outlines and absence of periostracal regeneration, consistent with areas previously occupied by encrusting organisms, indicating a common attachment site for epibionts. No evident structural deformities or asymmetries were observed in the valves of the three basibionts.

Discussion

These new records show that living molluscs can act as structural substrates in systems dominated by fine sediments. The epibiotic association between *Chama macerophylla* and *Tucetona pectinata* demonstrates that species with contrasting burrowing and sessile lifestyles can functionally interact even under strong sedimentary influence.

Tucetona pectinata is a species of bivalve in the family Glycymerididae and is a typically endopsammic organism that inhabits sedimentary environments, living partially or completely buried in the substrate (Ansell & Trueman, 1967; Thomas, 1975, 1976; Chagas et al., 2020). Its burrowing behavior and semi-infaunal lifestyle characterize it as a dynamic component of soft-bottom ecosystems. In contrast, *Chama macerophylla* (Chamidae) is a sessile epilithic species that permanently cements one of its valves to hard substrates (Allen, 1977; Vance, 1978; Campbell et al., 2004; Mikkelsen & Bieler, 2008), and is commonly found in reef and rocky environments where substrate stability favors suspension feeding (Yonge, 1967; LaBarbera & Chanley, 1971; Castrejón-Ríos et al., 2023).

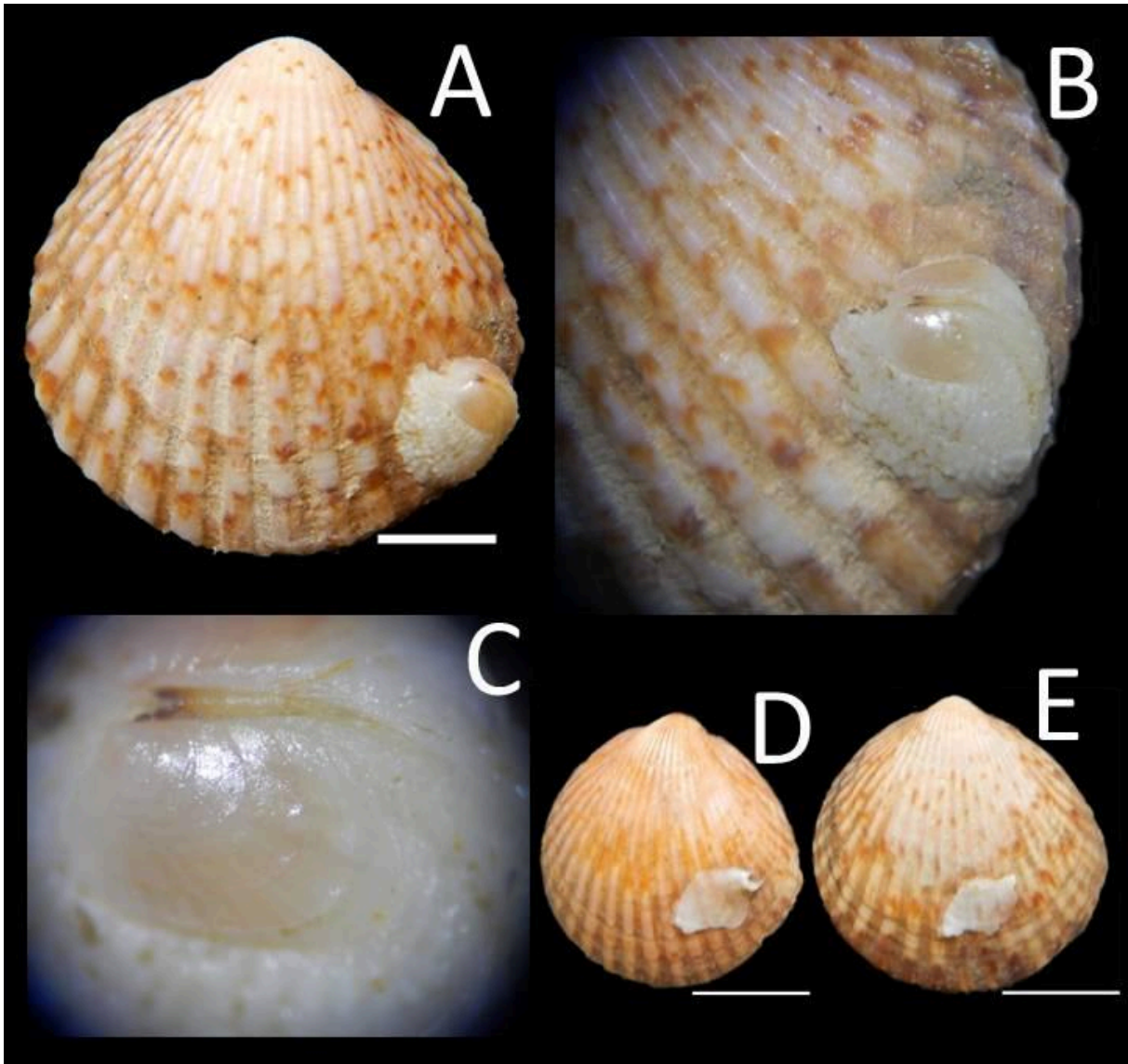


Figure 02. Epibiotic association between the burrowing bivalve *Tucetona pectinata* (Gmelin, 1791) and the sessile bivalve *Chama macerophylla* Gmelin, 1791, collected on the Amazon continental shelf. (A) external view of *T. pectinata* with an attached specimen of *C. macerophylla*; (B) detail of epibiont attachment on the host shell; (C) view of the prodossoconch of *C. macerophylla*; (D–E) comparative external view of additional individuals of *T. pectinata*. Scale bars: (A) 0.5 cm; (D–E) 1 cm.

From the perspective of “ecological facilitation” (Bruno et al., 2003), this interaction can be interpreted as a process in which one species modifies the physical environment in a way that increases the probability of establishment of another (Bruno et al., 2003; Majewska et al., 2023). In sediment-dominated systems (Vale et al., 2022), the need for a substrate is a critical limiting resource for epibiotic organisms (Mikkelsen & Bieler, 2008), and the partially

exposed shell of *Tucetona pectinata* may function as an emergent structure within a muddy matrix. Thus, the burrowing glycymeridid (Ansell & Trueman, 1967) may act as a structural facilitator by providing a surface for larval settlement of chamids (LaBarbera & Chanley, 1971).

The presence of epibionts on all three samples of *Tucetona pectinata* suggests that semi-infaunal bivalves may regularly act as mobile hard substrates, facilitating sessile organisms and increasing habitat heterogeneity (Bruno et al., 2003). Although based on three individuals, the consistency of the attachment site for epibionts suggests that this interaction does not represent an isolated or random event, but rather that the association is facilitated by the usual orientation of the burrowing species within the substrate. The fixation site may be related to the settlement of epibionts on surfaces that are more regularly exposed beyond the sediment or may be associated with current flows generated by or related to the burrowing activity of the basibont. The position of the encrustation near the shell opening also suggests potential interference with the burrowing capacity of *T. pectinata*, although the mechanics of valve opening and closing did not appear to be compromised. Epibionts may interfere with movement and affect shell opening processes of basibionts (Wahl, 1989; Souto et al., 2012). For the epibiont, access to a hard substrate in a muddy environment represents a potential benefit, although there may be risks associated with alterations in host mobility (Fernandez-Leborans, 2010). Thus, this interaction may involve a balance between structural facilitation for the epibiont and potential mechanical costs for the basibiont (Fernandez-Leborans, 2010; Dvoretzky & Dvoretzky, 2022). Even interactions with potential individual costs may, at the community scale, contribute to increased benthic structural complexity (Souto et al., 2012).

Although the present records represent an interaction at a single location, it is possible that similar structural facilitation processes also occur in other areas of continuous fine-sediment deposition on the Amazon continental shelf (Nittrouer et al., 2021; Vale et al., 2022), as previous records of species of the genus *Tucetona* at a broader scale reinforce the presence of these shells along most of the continental shelf and their availability as relevant structural elements providing opportunity for settlement across this extensive sedimentary system (Chagas et al., 2020). The record of this association in an area adjacent to offshore exploration blocks (ANP, 2026) adds further relevance to this finding due to its novelty (Allen, 1977; Vance, 1978; Campbell et al., 2004; Mikkelsen & Bieler, 2008). Such ecological interactions may act as sensitive indicators of environmental change, as the weakening or

collapse of these relationships may precede local species loss (Valiente-Banuet et al., 2014). Thus, documenting these associations provides an ecological process for monitoring the environmental integrity of the Amazon continental shelf under potential anthropogenic pressures.

Epibiotic interactions with bivalve basibionts are already known from other regions. Pectinid bivalves have been shown to play this functional role, acting as ecological facilitators and increasing the structural heterogeneity of the seafloor in the South West Atlantic. Soft-bottom pectinids frequently support diverse epibiotic communities on their shells, even in areas with mixed unconsolidated bottoms (Schejter & Bremec, 2007; Souto et al., 2012; Schejter et al., 2014a,b) with the species *Flexopecten felipponei* (Dall, 1922), found to host encrusting organisms including serpulids, barnacles, and oysters (Schejter & Bremec, 2007). Additionally, 91% of examined individuals of *Aequipecten tehuelchus* (A. d'Orbigny, 1846) hosted epibionts, indicating a high frequency of association (Souto et al., 2012), and *Zygochlamys patagonica* has been associated with increased benthic biodiversity in deep environments of the continental shelf (Schejter et al., 2014a,b). These examples reinforce the role of bivalve shells as substrates for other taxa.

In conclusion, the interaction between species with contrasting lifestyles highlights the role of mobile biogenic substrates in generating structural complexity in soft-bottom ecosystems. In regions as vast and complex as the Amazon continental margin, each documented interaction contributes to a better understanding of the ecological dynamics and functional heterogeneity of these environments.

Acknowledgements

We thank the research team of the research vessel *R/V Soloncy Moura* and the team of the Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Norte (CEPNOR) for their essential support during field sampling.

Funding

This study was supported by the Serrapilheira Institute (FUNARBE Project 8835/ Fapespa T.O. 169/2024/Processo 00001.0.000418/2024) through a postdoctoral fellowship and research grant awarded to Jonata de Arruda Francisco.

Ethics Statement

The author has nothing to report.

Conflicts of Interest

The author declares no conflicts of interest.

Data Availability Statement

Data are available from the corresponding author upon reasonable request.

References

- Allen, J. A. (1977). On the biology and functional morphology of *Chama gryphoides* Linné (Bivalvia: Chamidae). *Vie et Milieu*, 26(2A), 243–260. <https://hal.science/hal-02989628v1>
- Alves-Júnior, F., Martins, D. E. G., Araújo Silva, K. C., Macedo Klautau, A. G. C., & Cintra, I. H. A. (2022). Barnacles as epibionts in crustaceans from the Great Amazon Reef System (GARS), northern Brazil: New records and new host associations. *Thalassas*, 38, 1–8. <https://doi.org/10.1007/s41208-022-00480-y>
- Alves-Júnior, F. A., Martins, D. E. G., Monteiro, B. S., Francisco, J. A., Klautau, A. G. C. M., & Cintra, I. H. A. (2023). Two in one: Report of two epibiont groups on *Callinectes bocourti* A. Milne-Edwards, 1879 (Decapoda: Portunidae) from the Amazon province. *Environmental Smoke*, 6, 1–8. <https://doi.org/10.32435/envsmoke-2023-0001>
- ANP - Agência Nacional do Petróleo, Gás Natural e Biocombustíveis. (2026). GeoMaps ANP. <https://geomaps.anp.gov.br/geoanp/>
- Ansell, A. D., & Trueman, E. R. (1967). Observations on burrowing in *Glycymeris glycymeris* (L.) (Bivalvia, Arcacea). *Journal of Experimental Marine Biology and Ecology*, 1(1), 65–75. [https://doi.org/10.1016/0022-0981\(67\)90007-X](https://doi.org/10.1016/0022-0981(67)90007-X)
- Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, 18, 119–125. [https://doi.org/10.1016/S0169-5347\(02\)00045-9](https://doi.org/10.1016/S0169-5347(02)00045-9)
- Buschbaum, C., & Reise, K. (1999). Effects of barnacle epibionts on the periwinkle *Littorina littorea* (L.). *Helgoland Marine Research*, 53, 56–61. <https://doi.org/10.1007/PL00012138>
- Campbell, M. R., Steiner, G., Campbell, L. D., & Dreyer, H. (2004). Recent Chamidae (Bivalvia) from the western Atlantic Ocean. *Malacologia*, 46, 381–415. <https://www.biodiversitylibrary.org/page/28112961>

Castrejón-Ríos, A. R., Ramírez, C. T., Flores-Garza, R., Rodríguez, P. F., Cornelio, J. C. C., & Serrato, J. G. P. (2023). Estimation of individual growth of the violet oyster *Chama coralloides* (Bivalvia: Chamidae) using Schnute model cases. *Turkish Journal of Zoology*, 47(5), Article 3. <https://doi.org/10.55730/1300-0179.3141>

Chagas, A. R., Castro, L. R., Santos, W. J. P., Barros, M. R. F., & Bezerra, A. M. (2020). Ocorrências de *Glycymeris* spp. (Bivalvia: Glycymerididae) no litoral paraense, região Norte do Brasil. *Revista Ciência & Desenvolvimento*, 13, 756–763. <https://doi.org/10.11602/1984-4271.2020.13.3.13>

Dvoretzky, A. G., & Dvoretzky, V. G. (2022). Epibiotic communities of common crab species in the coastal Barents Sea: Biodiversity and infestation patterns. *Diversity*, 14(1), Article 6. <https://doi.org/10.3390/d14010006>

Fernandez-Leborans, G. (2010). Epibiosis in Crustacea: An overview. *Crustaceana*, 83, 549–640. <https://doi.org/10.1163/001121610X532657>

LaBarbera, M., & Chanley, P. E. (1971). Larval and postlarval development of the corrugated jewel box clam *Chama congregata* Conrad (Bivalvia: Chamidae). *Bulletin of Marine Science*, 21(3), 733–744.

Majewska, R., Dobretsov, S., Robinson, N. J., & Thompson, F. (2023). Editorial: Marine epibioses. *Frontiers in Ecology and Evolution*, 11, 1229173. <https://doi.org/10.3389/fevo.2023.1229173>

Martin, M. V., Venkatesan, R., Beyline, M., Limma Mol, V. P., & Divya, L. (2020). Influence of environmental factors on macrofouling assemblages on moored buoys in the eastern Arabian Sea. *PLoS ONE*, 15(1), e0223560. <https://doi.org/10.1371/journal.pone.0223560>

Mikkelsen, P. M., & Bieler, R. (2008). *Seashells of Southern Florida: Living marine mollusks of the Florida Keys and adjacent regions. Bivalves*. Princeton University Press.

Nittrouer, C. A., DeMaster, D. J., Kuehl, S. A., Figueiredo, A. G., Jr., Sternberg, R. W., Faria, L. E. C., Silveira, O. M., Allison, M. A., Kineke, G. C., Ogston, A. S., Souza Filho, P. W. M., Asp, N. E., Nowacki, D. J., & Fricke, A. T. (2021). Amazon sediment transport and accumulation along the continuum of mixed fluvial and marine processes. *Annual Review of Marine Science*, 13, 501–536. <https://doi.org/10.1146/annurev-marine-010816-060457>

Redfern, C. (2013). *Bahamian seashells: 1161 species from Abaco, Bahamas*. Bahamianseashells.com.

Rios, E. de C. (2009). *Compendium of Brazilian sea shells*. Evangraf.

Schejter, L., & Bremec, C. S. (2007). Epibionts on *Flexopecten felipponei* (Dall, 1922), an uncommon scallop from Argentina. *American Malacological Bulletin*, 22, 75–82. <https://doi.org/10.4003/0740-2783-22.1.75>

Schejter, L., Bremec, C., & Escolar, M. (2014a). Epibionts increase benthic richness associated with the Patagonian scallop *Zygochlamys patagonica* on the Argentine continental shelf. *Journal of the Marine Biological Association of the United Kingdom*, 94, 917–925. <https://doi.org/10.1017/S002531541300XXX>

Schejter, L., Lopez Gappa, J., & Bremec, C. S. (2014b). Epibiotic relationships on *Zygochlamys patagonica* (Mollusca, Bivalvia, Pectinidae) increase biodiversity in a submarine canyon in Argentina. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 104, 252–258. <https://doi.org/10.1016/j.dsr2.2013.10.010>

Souto, V. S., Schejter, L., & Bremec, C. C. (2012). Epibionts on *Aequipecten tehuelchus* (d'Orbigny, 1846) (Pectinidae) in shelf waters off Buenos Aires, Argentina. *American Malacological Bulletin*, 30(2), 261–266. <https://doi.org/10.4003/006.030.0205>

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., Robertson, J., & (others). (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience*, 57, 573–583. <https://doi.org/10.1641/B570707>

Thomas, R. D. K. (1975). Functional morphology, ecology, and evolutionary conservatism in the Glycymerididae (Bivalvia). *Paleontology*, 18(2), 217–254. <https://doi.org/10.5281/zenodo.16567309>

Thomas, R. D. K. (1976). Constraints of ligament growth, form and function on evolution in the Arcoidea (Mollusca: Bivalvia). *Paleobiology*, 2, 64–83. <https://doi.org/10.1017/S0094837300003304>

Vale, N. F., Braga, J. C., Moura, R. L., Salgado, L. T., Moraes, F. C., Karez, C. S., Carvalho, R. T., Salomon, P. S., Menandro, P. S., Amado-Filho, G. M., & Bastos, A. C. (2022). Distribution, morphology and composition of mesophotic ‘reefs’ on the Amazon continental margin. *Marine Geology*, 447, 106779. <https://doi.org/10.1016/j.margeo.2022.106779>

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M., & Zamora, R. (2014). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, 29(3), 299–307. <https://doi.org/10.1111/1365-2435.12356>

Vance, R. R. (1978). A mutualistic interaction between a sessile marine clam and its epibionts. *Ecology*, 59(4), 679–685. <https://doi.org/10.2307/1938770>

Vasconcelos, P., Cúrdia, J., Castro, M., & Gaspar, M. B. (2007). The shell of *Hexaplex (Trunculariopsis) trunculus* (Gastropoda: Muricidae) as a mobile hard substratum for epibiotic polychaetes (Annelida: Polychaeta) in the Ria Formosa (Algarve coast, southern Portugal). *Hydrobiologia*, 575, 161–172. <https://doi.org/10.1007/s10750-006-0367-x>

Wahl, M. (2009). Epibiosis: Ecology, effects and defences. In M. Wahl (Ed.), *Marine hard bottom communities: Patterns, dynamics, diversity, and change* (pp. 61–72). Springer. https://doi.org/10.1007/978-3-540-92704-4_4

Yonge, C. M. (1967). Form, habit and evolution in the Chamidae (Bivalvia) with reference to conditions in the rudists (Hippuritacea). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 252(775), 49–105. <https://doi.org/10.1098/rstb.1967.0003>