Drivers of community and functional assemblages in rocky intertidal ecosystems of the Goan coast

by

Shreyas Prashant
Enrolment no: 50BB24A73027

Dissertation Thesis

Submitted to

Academy of Scientific and Innovative Research

For the partial fulfilment of the degree

Master of Science

in

Wildlife Science

Under the supervision of

Ms Chinmaya Ghanekar, Scientist-C

Dr Sutirtha Dutta, Scientist-E

Dr JA Johnson, Scientist-F

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

AcSIR

July 2026

DECLARATION

I hereby declare that the work conducted under the thesis entitled **"Drivers of community and functional assemblages in rocky intertidal ecosystems of the Goan coast",** is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Master's in Wildlife Science** at the **Academy of Scientific and Innovative Research**. This research work has been carried out under the guidance and supervision of **Ms Chinmaya Ghanekar, Scientist - C** and co-supervision of **Dr Sutirtha Dutta, Scientist – E** and **Dr JA Johnson, Scientist – F,** of Wildlife Institute of India, Dehradun. The work has not formed the basis for the award of any other degree, diploma, or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding and the particulars given in it are true to the best of my knowledge.

Shreyas Prashant

Enrolment No: 50BB24A73027

Place: Dehradun

Date: 14th July, 2026

Ms. Chinmaya Ghanekar
Supervisor

Dr. Sutirtha Dutta
Co- Supervisor

Dr. JA Johnson
Co- Supervisor

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE

This is to certify that the thesis by **Shreyas Prashant** entitled **"Drivers of community and functional assemblages in rocky intertidal ecosystems of the Goan coast"** is an original and independent research work submitted to the **Academy of Scientific and Innovative Research**, for the award of the degree of **Master's in Wildlife Science**.

Shreyas Prashant has put one semester of research work embodied in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted to any other University or Institute for the award of any degree, diploma or distinction.

Ms. Chinmaya Ghanekar
Supervisor

(Dr. Ruchi Badola)
Dean
Faculty of Wildlife Science

पत्रपेटी सं 18 चन्द्रबनी देहरादून-248001, उत्तराखण्ड, भारत
Post Box No. 18, Chandrabani, Dehradun-248001, Uttarakhand, INDIA
ई.पी.ए.बी.एक्स .+91-135-2640111 से 2640115, फैक्स :0135-2640117
EPABX +91-135-2640111 to 2640115, Fax · 0135-2640117
ई–मेल/E-mail wii@wii.gov.in, वेब/website . www.wii.gov.in

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE OF PLAGIARISM CHECK

It is certified that the Master's dissertation thesis titled **"Drivers of community and functional assemblages in rocky intertidal ecosystems of the Goan coast"** submitted by **Shreyas Prashant** has been examined by us for plagiarism check as per UGC (Promotion of Academic Integrity and Prevention of Plagiarism in Higher Educational Institutions) Regulations. The following inferences are drawn from this check:

a) Thesis has significant new work/knowledge as compared to already published work or work under consideration for publication elsewhere.
b) No sentence, equation, diagram, table, paragraph or section is found to have been copied verbatim from previous work unless it was placed under quotation marks and the source was duly cited.
c) The work presented is original work of the author (i.e., there is no plagiarism) and there is no fabrication of data or result by manipulating research materials, equipment or processes, or by changing or by omitting data or results such that the research is not accurately represented.

The similarity indices as reported by the software Drillbit are as follows:

Software used	Date	Total world count	Similarity index
Drillbit	15.07.2026	21072	4%

The similarity index came as above. Scientific names, measuring units (SI) and references have been excluded from documents.

15/7/26

Mr. Manohar Pathak
Librarian

मनोहर पाठक / Manohar Pathak
पुस्तकालयाध्यक्ष / (Librarian)
पुस्तकालय एवं प्रलेखन केन्द्र
Library and Documentation Centre
भारतीय वन्यजीव संस्थान
Wildlife Institute of India
चन्द्रबनी, देहरादून, उत्तराखंड
Chandrabani, Dehradun - 248 001

Ms Chinmaya Ghanekar,
Supervisor

पत्रपेटी सं. 18, चन्द्रबनी, देहरादून-248 001, उत्तराखण्ड, भारत
P.B. No. 18, Chandrabani, Dehradun-248 001, Uttarakhand, INDIA
ई.पी.ए.बी.एक्स. :+91-135-2640114, 2640115, 2646100, फैक्स : 0135-2640117
EPABX : +91-135-2640114, 2640115, 2646100, Fax : 0135-2640117
ई–मेल/E-mail : wii@wii.gov.in, वेब/website : www.wii.gov.in

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENT

Sitting at the Shyampur FRH after a few fleeting glimpses of leopards and more close calls with elephants than I would've preferred, I finally found a moment of respite to write these acknowledgements following the many unnerving field-less weeks since my return from Goa. It is my privilege to put in print the names of those without whom this thesis would never have come to be.

Were it not for the many brainstorming sessions with Ms Chinmaya Ghanekar over the course of two term papers, I might never have arrived at research questions about marine communities for my dissertation. She also made sure those questions translated into a real research project. Then, of course, I wish to thank Dr Sutirtha Dutta, who patiently worked through my ventures beyond the terrestrial systems he knows so well and helped me shape them into a methodologically sound study. I am also grateful to Dr JA Johnson for meticulously reviewing everything I wrote, from the concept note to the final thesis, and for the lessons I shall carry with me. I would be remiss not to thank Dr Rohan Arthur, who was always just a phone call away and whose insights continually challenged and refined my questions, methods and inferences. I owe my thanks to Dr Anant Pande, without whose encouragement I would never have dared to undertake the experimental section of this study. I extend my gratitude to Dr Swapnali Gole, Pranay Sawant, Gaurav Patil, Ameya Bhojane, Abhishek Jamalabad and Nester Fernandes for helping me anticipate challenges I might encounter during fieldwork and adjust my ideas accordingly.

My time in Goa introduced me to a remarkable group of people whose support became indispensable to this study. Diksha Mandlik, who helped me navigate the inevitable hurdles of early fieldwork. Om for his assistance during fieldwork, and for the daily anecdotes through which I learnt much about life in Goa. Abhidyu and Vinayak, for readily assisting me whenever

needed. Vignesh, for coming down from WII and being great company during his brief time in the field. At the basecamp by the bog, Motilalji and Vasudev Raikar made life immeasurably easier. Peter, for the scrumptious ros omelette every morning. Omkar for introducing me to the faculty at NIO. Raniya and Navita for their assistance with gastropod and barnacle identification. Aashish, Rajendra and Aatma for helping me build and deploy the experimental setup on that chilly pre-dawn low tide. I would also like to thank the Goa Forest Department for permitting me to carry out my research along the Goan coast.

None of this would have felt quite right without a group of people to come back to in Dehradun. To my batchmates, thank you for all the times we shared. Bryan, Srinjan, Gayathri, Srajal, Himani, Tanya and Mencho for the conversations that stretched into the night and the days we spent travelling. For turning our post-field pilgrimage to McDonald's into a ritual as sacred as fieldwork itself. For the lavish cookouts and the late-night matches. Akshay, for being a better roommate than I could ever be. And Joshika, for sharing every high and low with me, amplifying the moments of joy and softening every moment of despair.

Life at WII wouldn't have been the same if it hadn’t been for the professors who broadened my perspective on the natural world. I am grateful to Dr Vishnupriya Kolipakam for furthering my interest in evolution, Dr Bivash Pandav for teaching me to read the forest, and Dr Bilal Habib for making mammalian ecology, a subject I once found uninteresting, deeply fascinating. I am equally grateful to Dr Sutirtha Dutta and Dr Amit Kumar, our course directors, for putting together a wonderful course. And to Varun Kher, for helping me identify errors in my analyses before it was too late. I also thank the Director, Dean and Registrar for giving me the opportunity to undertake this study.

Above all, no words can adequately express my gratitude to Ma, Appa, Thatha and Paati. They kindled and nurtured in me a curiosity about the living world. Without their

encouragement and interest, I wouldn't possess the conviction to follow my passion for ecology. Ma, for joining me in the field and patiently making sense of her son's fascination with tiny organisms on seemingly desolate rocks. I must also acknowledge them for tolerating my perpetual unavailability as I navigated the last few months.

It only seems fitting that I end where all of this began: with the ocean and its inhabitants that continue to reward curiosity with wonder. To the tides that shaped the last few months of my life, and that have shaped innumerable lives over the course of evolution. To the magnificent moray, the resilient limpet, the brilliant coral, the enigmatic nudibranch, and the myriad other beings that go about their ebb-and-flow existence. Here's to the *intertidal*.

Shreyas Prashant

June, 2026

SUMMARY

Rocky intertidal ecosystems have long served as natural laboratories for testing fundamental ecological theories. However, much of our understanding of community assemblages in these systems comes from temperate shores. In contrast, tropical intertidal ecosystems remain largely understudied. The disparity in environmental conditions between the temperate and the tropical zones limits our understanding of ecological processes. Therefore, investigating how environmental and biotic factors drive tropical community assemblages is critical for assessing the generalizability of existing ecological theory. This study examines the effects of environmental stress gradients ranging from the upper to the lower intertidal zones on community and functional assemblages in Goa's rocky intertidal ecosystem. The influence of predation on community composition is also investigated within this ecosystem.

To understand the effects of the environmental stress gradient and multiple fine-scale habitat characteristics on the community, a transect-quadrat method was employed across three study sites. The environmental stress gradient was found to be the main factor influencing community composition and structure, while sand cover, wave action and substrate complexity operated at finer scales within the broader gradient. Functional traits were compiled for the organisms found within the quadrats. This trait matrix was then used to assess whether motile and sessile animals respond differently to gradients of environmental stress and algae cover. Motile animals showed functional dispersion along the biotic gradient, while sessile animals showed a functional trait shift along the stress gradient. This suggests that motile animals may respond through biotic facilitation, driven by the combined effects of decreased stress and increased algal cover. Lastly, predator-exclusion cages were deployed to investigate whether predators considerably affect community composition. The experiment used *Indothais*

blanfordi, a predatory sea snail, as the focal predator of *Brachidontes* mussels. *Indothais* had a strong effect on both *Brachidontes* mussels and community composition.

Together, the results show that the environmental stress gradient structured the community through environmental filtering. However, the mechanisms through which this occurs are nuanced and depend on organismal life histories, biotic interactions and fine-scale habitat mediators. These findings extend environmental stress gradients and environmental filtering theory, developed primarily along temperate shores, into an understudied tropical system. In doing so, it provides an ecological foundation and methodological framework from which further questions can now be pursued.

INTRODUCTION

The intertidal zone is a transitional area between land and sea, occupying the space between the low and high tide lines. Due to daily tidal oscillations, this ecosystem and its inhabitants are in a constant state of flux (Palmer, 1973). This dynamic condition results in an exceptionally diverse and species-rich system and has previously been explained by the intermediate disturbance, habitat heterogeneity, and non-equilibrium hypothesis proposed by Connell (1978). The gradients in the intertidal zone are short and sharp, with tightly clustered communities distributed across them. These communities comprise species adapted to the constant environmental fluctuation, leading to distinct evolutionary and physiological adaptations. They consist largely of macroscopic, sessile, or slow-moving species that interact at small spatial scales. Consequently, these features make manipulative, mechanistic, and comparative studies highly generalizable and feasible. For these reasons, this ecosystem is often referred to as a natural laboratory (Underwood, 2000; Tomanek et al., 2002).

Several major ecological theories have been derived through studies in this ecosystem, including the keystone predation concept (Paine, 1966) and the stress-gradient concept (Menge & Sutherland, 1987). The intertidal has also served as a model system for testing many overarching ecological theories, such as competition, predation, disturbance-diversity relationships, succession, top-down and bottom-up control, and trophic cascades (Connell, 1961, 1978; Paine, 1966, 1980; Sousa, 1979; Menge, 1992; Underwood, 2000).

An observable trend across these studies is that they have primarily been conducted in the temperate zone, with tropical areas gradually catching up. Some studies in western tropical systems have investigated community and functional composition (Menge & Lubchenco, 1981; Murley et al., 2024), while others have examined species responses to stress (Bertness, 1981). Studies from Panama have examined biotic interactions in the intertidal (Menge &

Lubchenco, 1985, 1986). Similar research from Brazil and Australia has also contrasted temperate to tropical shores, adding to the broader understanding of intertidal ecology (Zamprogno et al., 2012). Despite these advances, comparable process-based studies remain scarce across much of the tropical Indo-Pacific region, particularly along the Indian coastline.

In India, intertidal ecology remains largely in a checklist-science phase. Early Indian intertidal studies emerged in the 1950s, with work on barnacles, succession, and sandy beach fauna (Daniel, 1955; Raja, 1959; Ganapati & Rao, 1962). Since then, progress has been slow. Despite India's 11,098 km of coastline, we have yet to derive fundamental ecological insights from this natural laboratory. This is largely due to a limited understanding of the factors influencing our coastal systems. We have extensive taxonomic knowledge with some autecological knowledge. However, species interactions and their role in the ecosystem, that is, synecological information, remain largely unexplored.

Tropical intertidal systems exhibit different ecological processes compared to temperate ones due to dissimilarity in seasonality, disturbance regimes, and recruitment dynamics (Murley et al., 2024), making studies in the tropics even more essential. Systematic, long-term studies addressing various abiotic, biotic, and anthropogenic factors that shape Indian intertidal ecosystems are required. However, understanding the effects of key abiotic factors on community assemblages, recruitment, and species interactions must come first; without this knowledge, progress will remain limited.

To address this gap, the study investigates how select abiotic and biotic factors influence the community and functional assemblages of the rocky intertidal ecosystem. To do so, a theoretical framework that links environmental stress, functional assembly, and biotic interactions is required. This conceptual basis is developed in the next section.

1.1 CONCEPTUAL UNDERPINNINGS

1.1.1 Environmental stress gradients and community structure

Before delving into the theoretical manifestations of "environmental stress," it is critical to understand what it means. "Stress" in ecology has a specific meaning distinct from the word's everyday use. Ecological stress may refer to any abiotic condition that reduces the growth, survival, or reproduction of organisms below their potential maximum (Grime, 1977). Although this definition explains stress in an autecological context, it is not synergetic with community ecology. Environmental stress at a community level would be a characteristic of a site relative to what the regional species pool can tolerate. Environmental stress would then be the degree to which abiotic conditions determine which members of the regional species pool can persist at a given site (Menge & Sutherland, 1987; Scrosati et al., 2011).

Environmental stress in the intertidal zone manifests primarily as desiccation and thermal stress. Due to bi-daily tidal oscillations, the upper intertidal zone experiences prolonged aerial exposure very often, while the lower zone remains submerged longer and more frequently. This exposure to the aerial environment inevitably results in increased thermal, desiccation, and osmotic stress (Valdivia et al., 2011). Early work described vertical zonation patterns across shores (Stephenson & Stephenson 1949), with later studies demonstrating that the stress gradient mediates both species distribution directly and species interaction indirectly (Connell 1961; Menge 1978). Figure 1, modified from Raffaelli & Hawkins (1996), depicts a conceptual visual for the same. Similar zonation categories will be used in the present study.

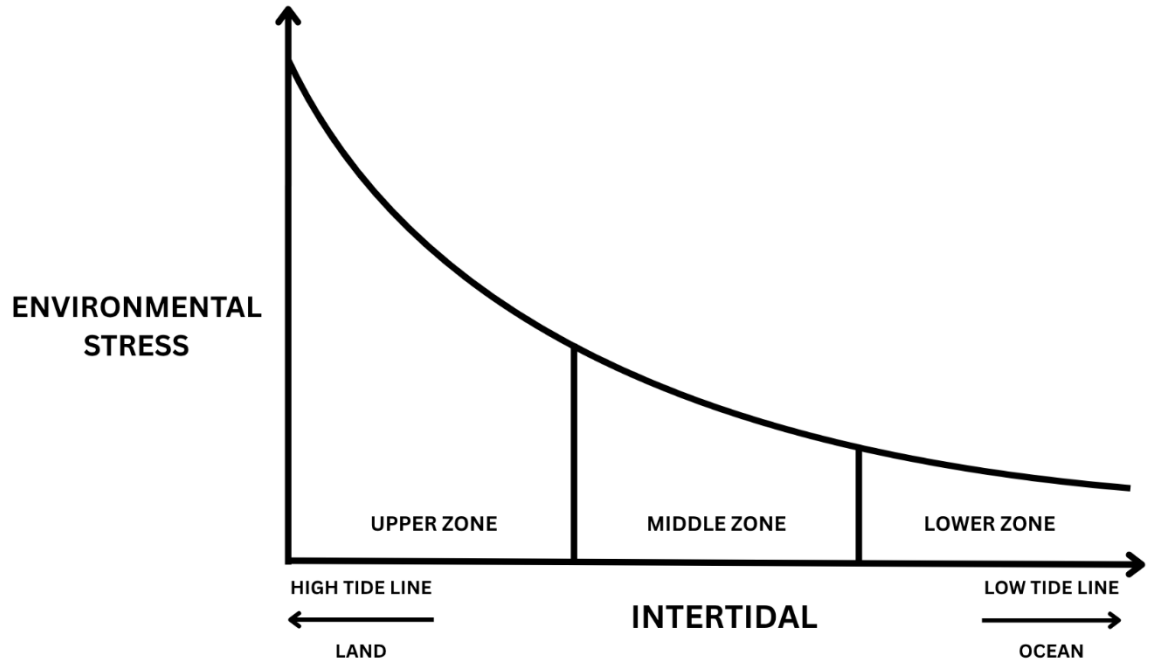


Figure 1 *A conceptual visual depicting the decline of environmental stress from upper to lower intertidal zone; Modified from Raffaelli & Hawkins 1996.*

In light of this, Menge & Sutherland (1987) proposed the environmental stress model (ESM). According to this, high-stress areas are controlled mostly by environmental factors, intermediate-stress areas are mostly shaped by competition, whereas in low-stress environments, predation dominates as the key factor shaping communities (Paine, 1966; Luckens, 1970; Connell, 1972). Extending this framework, Bruno et al. (2003) argued that, alongside the aforementioned factors, facilitative interactions play a greater role in high-stress areas. The mechanisms driving these patterns are described in the following paragraph (Menge & Sutherland, 1987).

At higher stress levels, only species that can tolerate physically harsh conditions can persist. Therefore, only a few species with similar traits find it possible to survive, leading to limitations on biotic interactions such as competition. This selective process, through which environmental conditions restrict which members of the regional pool can persist, is termed environmental filtering and represents the dominant community assembly mechanism under

high stress. Additionally, most consumers also find it hard to colonise this zone, ultimately curbing interactions such as predation and herbivory. As a result, communities in the upper intertidal become simplified, often dominated by a few stress-tolerant species. These species benefit from facilitative interactions, wherein neighbouring species can ameliorate harsh conditions, e.g., oyster beds create microhabitats that help other taxa withstand desiccation (McAfee et al., 2018). On proceeding to lower stress levels, there comes a transition zone where populations build up, which in turn intensifies competition for space. However, continued abiotic stress limits predator abundance and efficiency, preventing strong top-down control. Lastly, at lower stress regimes, all trophic levels can persist, and predation becomes a major factor in shaping the intertidal community. Keystone predation also reduces prey abundances and prevents monopolisation of space by a single prey species. In doing so, predators alleviate the effect of competition, therefore becoming the main driver of community assemblages at lower stress regimes.

Collectively, the environmental stress gradient represents spatial and temporal variation in physical and physiological conditions that alter mortality risk and regulate community structure by shifting the relative importance of physical disturbance, predation and competition (Menge et al., 1987, 1990, 2002).

Hence, the environmental stress model attributes community assemblages to a set of deterministic processes whose relative importance varies along a gradient of environmental stress. In doing so, it provides a framework for examining how abiotic factors shape assemblages in the present study (Chapter 1).

1.1.2 Environmental filtering and functional assemblages

The environmental stress gradient operates through the process of environmental filtering (Fattorini & Halle, 2004). Keddy (1992) best describes this as analogous to the process of evolution through natural selection. As habitats filter out less-fit genotypes while allowing

better-suited ones to propagate, environmental factors filter out specific species traits, eliminating those that are unable to withstand environmental conditions. The resultant set of species that comprise the community are those that survive the filter. In the intertidal context, the intertidal stress gradient acts as a primary filter, wherein communities at any given position along this gradient consist of taxa whose functional trait combinations confer enough tolerance to persist there.

Consequently, in areas with higher environmental stress, only taxa sharing specific stress-tolerant trait combinations can persist. This restriction of viable trait space leads to functional convergence, wherein communities are composed of taxa that are more functionally similar to one another than expected by chance (Keddy, 1992; Cornwell, 2006). The upper intertidal, subjected to prolonged aerial action and higher physiological stress, is therefore expected to hold functionally convergent communities dominated by a narrow set of stress-tolerant strategies.

With a decrease in stress towards the lower intertidal, environmental filters are relaxed, and a greater range of functional strategies becomes feasible. Additionally, as stress decreases, populations grow, and competition intensifies. The relaxed environmental filters, along with increased competition, lead to functional divergence through the mechanism of limiting similarity. This idea posits that species that coexist cannot be too functionally similar without competitive exclusion, which, in turn, results in functional differentiation as a mechanism of coexistence (MacArthur & Levins, 1967; Chesson, 2000). Therefore, filtering and coexistence through limiting similarity work concurrently at opposite ends of the intertidal gradient; convergence under high stress and divergence under low stress.

Biotic interactions such as competition, predation and herbivory may also lead to filtering alongside the primary environmental stress gradient, resulting in biotic filtering

(Keddy, 1992; Boet et al., 2020; Bauer, 2021). Additionally, biotic facilitation may also occur along a biotic stress gradient depending on the ecology of a species group. Positive interactions between species can ameliorate harsh conditions, leading to a wider range of viable functional strategies and thereby causing functional divergence (Bertness & Callaway, 1994; Bruno et al., 2003). Therefore, depending on the species group in question, the biotic gradient may act as a filter or a facilitator.

Previous studies along an intertidal stress gradient have shown that communities shift towards functional convergence under high stress and diverge under low stress (Valdivia et al., 2017). This is consistent with filtering and limiting similarity concepts, respectively. Although differential responses of motile and sessile taxa to abiotic gradients are well established (Sousa, 1984; Scrosati et al., 2011), studies comparing their functional responses to a biotic gradient remain scarce and, to my knowledge, have not been explicitly studied.

The present study investigates how these filtering mechanisms influence two functionally distinct groups of animals: motile and sessile taxa (Chapter 2). Both groups experience the same environmental stress gradient, but their interaction with the biotic algal gradient differs fundamentally.

1.1.3 Keystone predation

In previous sections, the environmental stress model posits that predation increases with a decrease in environmental stress (Menge & Sutherland, 1987) and environmental filtering was also shown to operate through biotic interaction (Bauer, 2021), including predation. Therefore, where predation is strong, identifying the predator and understanding its effect on the community is as essential as the stress gradient itself (Boaden & Kingsford, 2015).

Paine's (1966) *Pisaster* (predatory sea stars) removal experiments revealed how a predator can maintain community diversity by preventing monopolisation of space (a limited

resource in the intertidal). In the absence of the predatory sea stars, mussels monopolised space and excluded most taxa, leading to a collapse of the food web. The concept of a keystone predator was an outcome of this experiment (Paine, 1969). A keystone predator has a disproportionately large effect on the community relative to its abundance (Power et al., 1996). The mechanism involves interspecific competitive release among primary consumers: by suppressing the dominant consumer, predators reduce competitive exclusion and allow weaker competitors to persist, resulting in coexistence (Paine, 1974).

Predator effects have been largely tested in temperate intertidal systems, but tropical shores lack studies. There is a need to understand the effect of predation in tropical intertidal systems because they differ greatly from temperate shores in two ways. Firstly, it is well established that biotic interactions, including predation, increase in strength at lower latitudes (Sousa, 1981; Schemske et al., 2009; Freestone et al., 2013). Secondly, tropical ecosystems support more diverse communities (Brown, 2014), by virtue of which they have greater functional redundancy (Mouillot et al., 2014). Thus, removal of a dominant competitor by a predator may be neutralised by another species assuming that role, buffering the community against strong top-down effects. The effect of a candidate keystone predator cannot be predicted from temperate shores alone, as strong predation pressure may be counterweighed by higher prey redundancy.

One manipulative ichthyofaunal predation study in India uses tethering experiments in mesotidal mangroves (Namboothri, 2015). Apart from this, there are no published predator-exclusion experiments conducted anywhere on the Indian coast, leaving the role of top-down control entirely unresolved. The present study addresses this by conducting predator-exclusion experiments on the rocky shores in Goa (Chapter 3).

1.2 SIGNIFICANCE OF THE STUDY

The environmental stress models and environmental filtering theories have been developed and largely tested in the temperate zones of the world. Whether these models apply in warmer, seasonally driven, tropical ecosystems remains underexplored. The present study addresses both community composition and functional trait assembly, along with the influence of predators in tropical intertidal ecosystems. It further aims to elucidate the mechanisms that shape community assemblages, taking into account both broad and fine-scale drivers. Finally, the study establishes a methodological foundation for community ecology and predator exclusion studies attuned to the nature of the Indian intertidal. Understanding how these factors influence the communities is essential for detecting environmental change and evaluating the ecological consequences of coastal disturbance. The results provide a framework for advancing hypothesis-driven intertidal ecology in India.

OBJECTIVES AND RESEARCH QUESTIONS

1. **To examine the effect of the environmental stress gradient and fine-scale habitat drivers on the community assemblages of the rocky intertidal ecosystem.**

   How do community composition and structure change across intertidal zones?

   What mechanisms and taxa drive the shift in community composition?

   How do fine-scale habitat drivers such as substrate complexity, sand cover and wave action influence community structure within the broader effects of intertidal zonation?

2. **To assess the functional trait assemblages of motile and sessile animals in response to environmental stress gradients.**

   Do motile and sessile animals exhibit different functional responses to environmental and biotic gradients?

   Which functional trait combinations are associated with specific environmental factors?

3. **To understand the influence of predation on the community assemblage of the rocky intertidal system through predator exclusion experiments.**

   How do top-down effects like predation shape the community assemblages of rocky intertidal ecosystems?

   Do keystone predators exist in tropical intertidal ecosystems?

STUDY AREA

Goa lies on the western coast of India, bounded by the Arabian Sea to the west and the Western Ghats to the east. It has a coastline of 193.95 km and is ecologically part of the larger Arabian Sea marine biome (Rajendra et al., 2026). The rocky intertidal patches, particularly in central Goa, are primarily composed of lateritic and basaltic substrates, forming platforms, crevices, boulder fields, and tidepools that create diverse microhabitats for intertidal species (Figure 4). Species assemblage in Goa is strongly shaped by monsoonal seasonality, with heavy rainfall influencing sediment load, freshwater input, and salinity dynamics across the coast. The state is drained by nine rivers, which form estuarine systems that influence nutrient supply and larval recruitment to coastal intertidal habitats (Usmani et al., 2020).

The rocky intertidal habitats of Siridao, Cacra, Hollant, and Odxel beaches were selected as the study sites (Figure 2). The observational part (Chapters 1 & 2) of this study was conducted in Siridao (15.4451° N, 73.85497° E), Cacra (15.4428° N, 73.8346° E) and Hollant (15.3544° N, 73.8839° E), whereas the experimental part (Chapter 3) of the study was undertaken in Odxel (15.453716° N, 73.829868° E). Sites were selected based on similar environmental conditions to avoid confounding effects outside the scope of the study. Specifically, all sites were wave-sheltered and characterised by laterite rock as the main substrate. The supratidal zone was sandy in nature, whereas the intertidal areas under study were entirely rocky (Figure 3). Each of these sites was mostly visited by locals and had low tourism pressure. Siridao had an intertidal patch that was 220 meters long and 90 meters wide, Cacra, 400 meters long and 90 meters wide, and Hollant, 400 meters long and 50 meters wide. Odxel lacked a continuous intertidal gradient but presented a large exposed middle intertidal suitable for predator-exclusion cage placement.

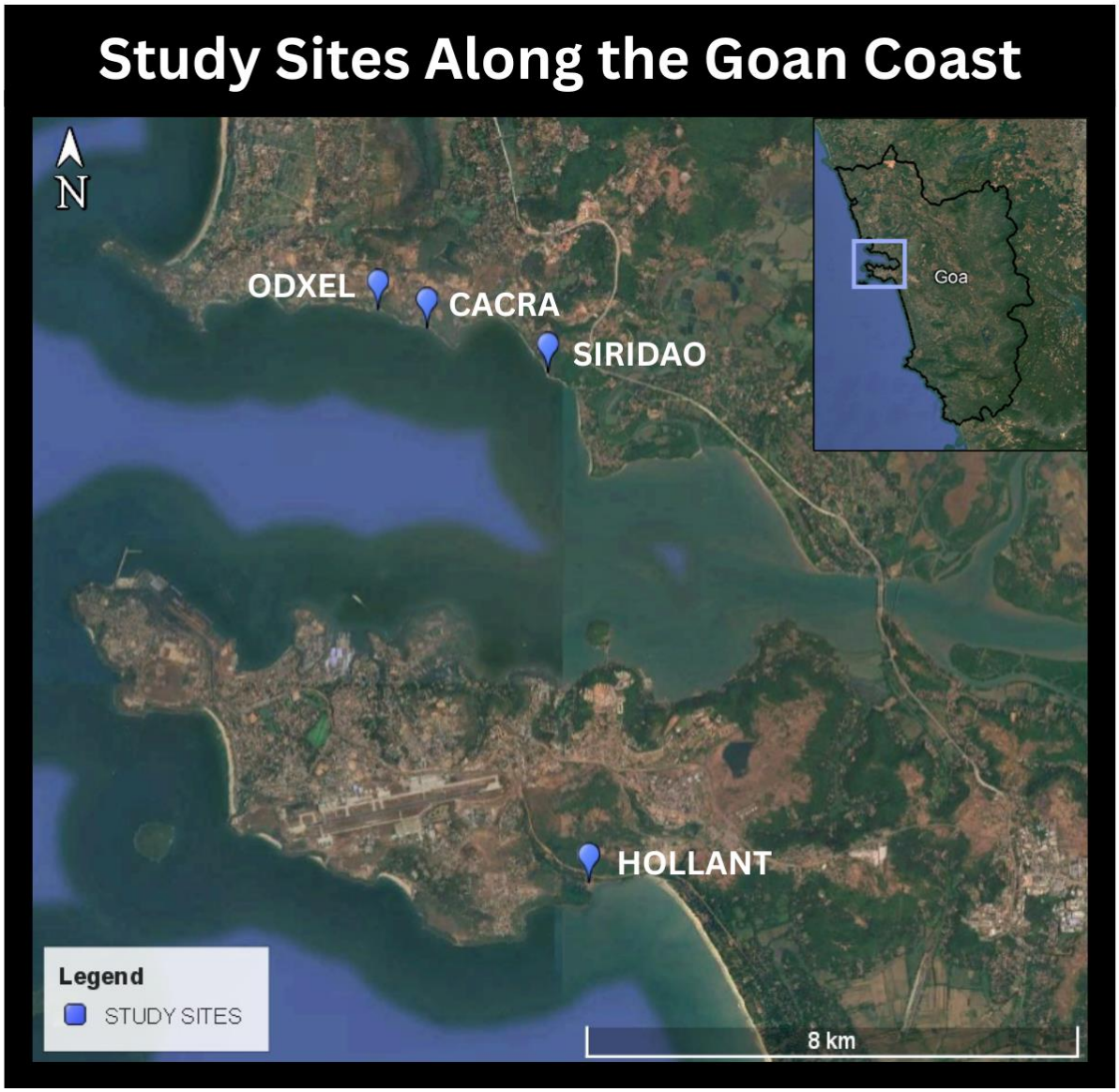


Figure 2 *Location of study sites on the Goan coast*

Figure 3 *Typical rocky intertidal habitat sampled during the study (Siridao).*

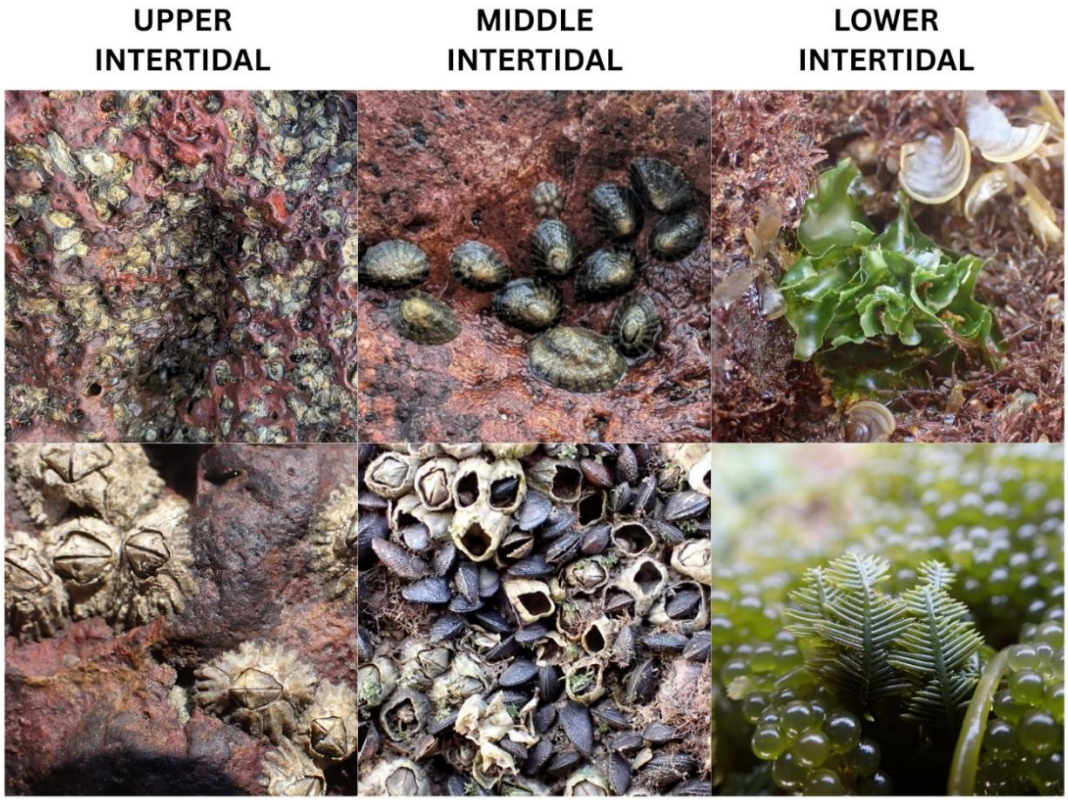


Figure 4 *Representative assemblages across the upper, middle and lower intertidal zones. Top row (left to right): Oyster beds, Siphonaria false limpet congregations, and an algal bed comprising Padina, Dictyota, Centroceras and Ulva. Bottom row (left to right): Chthamalus barnacles, Amphibalanus barnacle-Brachidontes mussel beds, and Caulerpa spp. algal beds.*

Chapter 1
Drivers of Community Assemblages

4.1 INTRODUCTION

In light of the environmental stress gradient discussed earlier, this chapter aims to understand how community assemblages change in composition and structure along the gradient in an Indian intertidal ecosystem. A strong compositional shift is expected from the high-stress upper zone to the lower-stress zone (Heaven & Scrosati, 2008). The upper intertidal is expected to hold a subset of the downshore communities (Bertness et al., 1999). Additionally, a decrease in stress is predicted to increase richness and diversity (Scrosati & Heaven, 2007). Beyond the environmental stress gradient, additional abiotic factors are expected to modulate intertidal community structure at finer spatial scales. These factors include substrate complexity, sand cover and wave action.

Substrate complexity includes features such as crevices, pits, ridges and variation in surface relief (Meager et al., 2011). It creates microhabitats that provide stress refugia and support higher species richness (McGuinness & Underwood, 1986; Loke & Todd, 2016). A more volatile factor is sand cover, which refers to the deposition of a shallow layer of sand on the predominantly rocky substrate due to seasonal changes, sediment availability and substrate structure. Sand cover is known to have varying effects on intertidal community assemblages, depending on its location in the intertidal and the taxa in question (Littler et al., 1983). Sand can provide refugia for certain species while causing burial-induced mortality in others. Therefore, sand has a variable effect on intertidal communities (Taylor & Littler, 1982; D'Antonio, 1986). Lastly, wave action pertains to the hydrodynamic forces generated by waves (Denny, 1988). Much like sand cover, the effect of wave force on intertidal communities is nuanced. Negative effects include mechanical stress (Jonsson et al., 2006), while positive

effects include increased nutrient supply (Flores et al., 2015). A more context-dependent effect of wave action is its ability to mediate species interactions like predation (Menge, 1978) and herbivory (Jonsson et al., 2006) by causing disturbance (Kraufvelin, 2007).

All the aforementioned factors are expected to be mediated by intertidal zonation. Sand cover and wave action may have variable effects on the community depending on stress levels. Substrate complexity is expected to have a greater positive effect in the high-stress upper zone. How these factors interact with the intertidal stress gradient to shape community composition and diversity is explored through an information-theoretic approach. Furthermore, understanding which environmental factors structure communities will provide the ecological context necessary to ask the deeper mechanistic question of how these gradients shape the functional organisation of communities, addressed in Chapter 2.

4.2 METHODS

4.2.1 Field methods

The field work for this objective was conducted from 4th December 2025 to 1st March 2026 across 3 rocky shores (Siridao, Cacra & Hollant) along the Goan coast. Sites were selected based on accessibility and representation of key environmental gradients. Sampling was undertaken during low tide conditions (0.3 meters or less) to ensure full access to all intertidal zones. To equitably distribute effort over time, each site was visited equally in every low-tide cycle. However, this was not always possible due to erratic field conditions and shortened low-tide cycles.

The transect-quadrat method was employed for sampling rocky intertidal organisms. Four transects were placed at each site perpendicular to the waterline. The location for these transects was chosen based on accessibility and the presence of a contiguous rocky intertidal area. Transects were spatially fixed and spanned the upper, middle, and lower intertidal zones (Gonor & Kemp, 1978; Underwood, 1981; Miller & Ambrose, 2000).

25 × 25 cm quadrats (0.0625 m^2) were placed on rock surfaces along the transect at 10-meter intervals. Two a priori placement criteria were applied: (1) quadrats could not be placed within tidal pools, as pools retain water through tidal emersion and support community assemblages that are substantially different from those on emergent rocks, making them ecologically isolated from the desiccation-driven stress gradient under study (Raffaelli & Hawkins, 1996). (2) The intertidal stress gradient is determined by the duration and frequency with which a point along the gradient remains submerged. Therefore, each quadrat had to be at a lower elevation than the quadrat immediately landward of it, ensuring that the transect consistently descended toward the sea, and the assumption of this gradient was met (Valdivia et al., 2011). Placing a quadrat at a relatively higher position (such as on a protruding rock) within the lower intertidal would have disrupted this gradient, as it would remain submerged for shorter times than at other points in the same zone. Where either criterion wasn't met, the quadrat was repositioned laterally until both were satisfied (Menge et al., 1999), with a maximum lateral displacement of 2 m from the transect. Quadrats were not permanently fixed; positions were re-established at each visit using the aforementioned criteria. This approach samples the assemblage extensively at each relative position rather than repeatedly measuring a single fixed microsite, consequently improving ecological representation. The high-tide line was taken to be the last rocky point beyond which the supratidal sandy system began, while the low-tide line varied daily with that day's low-tide height.

Organisms that formed continuous cover across the substrate (mat-forming taxa) were quantified as per cent cover (resolution: 5 x 5 cm), while other taxa were recorded as counts. Multiple images of every organism were taken using an Olympus TG-6 camera. Each image had a unique code that linked the recorded organism to its image. These uniquely coded images were used to identify organisms post hoc. Organisms were identified up to the genus level. When taxonomic identification could not be achieved, a morphospecies approach was used to

assign it a unique label (Oliver & Beattie, 1996; Brind'Amour et al., 2014). This is a well-established method employed in numerous ecological studies from regions where taxonomic expertise for certain taxa is limited (Loke & Todd, 2016; Raijman-Nagar et al., 2024). Identification was undertaken using multiple field guides (Agadi & Untawale, 1978; Joseph, 2007; Jha et al., 2009; Apte, 2012; Sonak, 2017; Palanasamy & Yadav, 2022), online databases like AlgaeBase (Guiry & Guiry, 2026), WoRMS (2026) and iNaturalist (2026) and through expert communication. Ichthyofauna and fast-moving taxa like *Brachyuran* crabs were not quantified, as the former are transient visitors rather than permanent residents (Gibson, 1982) in the intertidal, while the latter are capable of actively tracking tidal movement, thereby avoiding prolonged exposure to the desiccation and thermal stress that structure the assemblages of less mobile taxa (McIntire & Miller, 2025).

Variables, such as relative distance to high tide line, rugosity, undulation, crevice availability, sand cover and wave action level, were recorded for every quadrat. Relative distance was essentially the distance of a quadrat from the high tide line divided by the maximum length of the transect; this maximum length was taken to be the length of the transect at the lowest tide throughout sampling sessions. Relative distance to the high-tide line served as a proxy for the stress gradient; quadrats located farther away from the high-tide line experienced lower stress (Raffaelli & Hawkins, 1996; Tomanek & Helmuth, 2002; Viejo, 2009; Scrosati et al., 2011; Valdivia et al., 2011; Eckersley & Scrosati, 2012). Rugosity, undulation and crevice availability captured different aspects of habitat structure. Rugosity quantifies the overall surface roughness of the substrate. Undulation refers to broad substrate features that materialise at the quadrat scale, including slopes, troughs and crests that influence desiccation patterns. Conversely, crevices are microhabitats within the quadrat, including fissures and other narrow cavities that provide refugia from abiotic stressors and biotic interactions. These variables were subsequently converted into an index of substrate complexity as described in

the Analytical Methods section. Rugosity was measured using the chain-and-tape method along the quadrat's diagonals (Risk, 1972). These values were then averaged for every quadrat to give an index of rugosity. Undulation, crevice availability, sand cover and wave action level were evaluated on a scale of 1 to 4, estimated ocularly. The criteria for the ocular scores are displayed in the table below.

Table 1 *Grading criteria for ocularly estimated habitat variables.*

Variable	*Score*	*Description*
Undulation	1	Flat
	2	Gentle irregularities
	3	Distinct undulation
	4	Strong undulation
Crevice availability	1	No crevices
	2	Rare small cracks
	3	Several crevices
	4	Abundant crevices
Sand Cover	1	Rock surface free of sand
	2	1–25% of rock surface covered by sand
	3	26–66% of rock surface covered by sand
	4	66–100% of rock surface covered by sand
Wave Action	1	Sheltered: Quadrat sits behind a large rock, where the force of the waves is mostly blocked.
	2	Slightly Exposed: Quadrat is on a flatter surrounding substrate with some wave splash but low force.
	3	Exposed: Quadrat is in an open area that is regularly subject to direct wave action.
	4	Highly Exposed: Quadrat lies in the active wave-crash zone where waves break with strong force.

4.2.2 Analytical methods

Relative position for each quadrat along the intertidal gradient was calculated by dividing its distance to the high tide line by the maximum length of the same transect. This made relative position a standardised scale ranging from 0 to 1; 0 for the uppermost quadrats and 1 for the lowermost ones. Quadrats were then assigned to upper, middle and lower intertidal using relative position values: Upper intertidal < 0.33, Middle intertidal >= 0.33 and < 0.66,

Lower intertidal >= 0.66 (Scrosati & Heaven, 2007; Valdivia et al., 2011). This zonation framework was used for community composition, structure and modelling analyses.

A presence-absence community matrix was used to assess sampling adequacy using species accumulation curves. Chao2 was used to estimate asymptotic richness. Wisconsin double standardisation was utilised to ensure comparability between taxa quantified in counts and those recorded as per cent cover for each quadrat (McCune & Grace, 2002). To evaluate whether data could be pooled across sampling occasions, a PERMANOVA was run using month-wise data using Bray-Curtis dissimilarities (9999 permutations). Spatial autocorrelation was assessed by plotting within-transect Bray-Curtis dissimilarities against their quadrat separation distance within each intertidal zone, with significance evaluated using a Mantel test. Subsequently, NMDS ordination was plotted. It was used to visualise the shift in community composition across zones. The effect of zone on community composition was tested using PERMANOVA with 999 permutations, both for zone alone and for site and zone together. Additionally, pairwise PERMANOVA was used to compare zone pairs, and betadisper was used to compare the homogeneity of dispersion among zones as a diagnostic test. Betapart was then used to decompose total beta diversity into turnover and nestedness components, to assess the mechanisms underlying the Bray-Curtis dissimilarity. Furthermore, similarity percentage analysis (SIMPER) was used to identify the taxa contributing most strongly to the dissimilarity. Complementing this, an indicator species analysis (IndiVal) was used to identify taxa most strongly associated with specific intertidal zones.

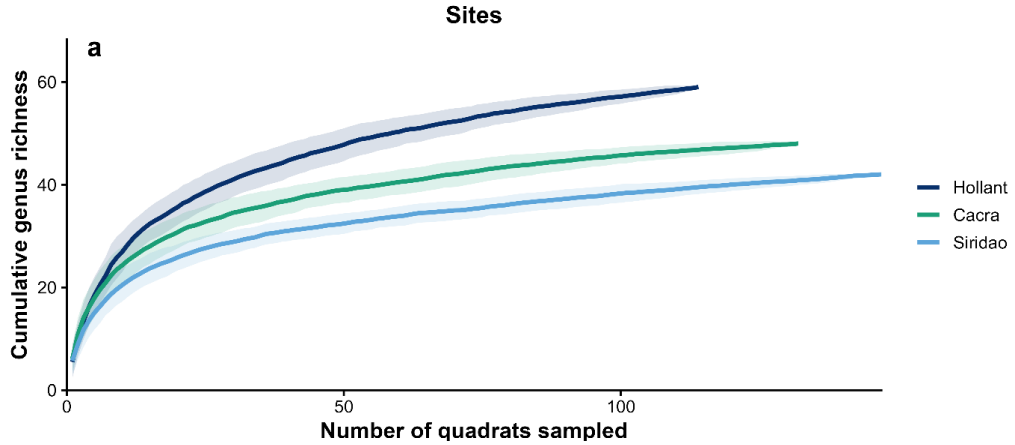
Following this, to understand differences in communities across zones, indices for community structure were calculated. Quadrat-level taxa richness and Wisconsin-standardised Shannon diversity were pooled by zone and plotted with boxplots. To statistically test for zonal differences in richness and diversity, Kruskal-Wallis tests were used. Additionally, zone-wise

boxplots were plotted separately for algal and animal taxa to assess whether consumer and producer assemblages respond differently to the environmental stress gradient.

To understand how environmental variables shape quadrat-level richness and diversity, generalised linear models (GLMs) were used. Before this, undulation, rugosity, and crevice availability were z-standardised and averaged to form a substrate complexity index (Rescaled 0-1), and predictor multicollinearity was assessed using Pearson correlations. The nested sampling structure was first assessed by fitting GLMMs with site and transect random effects. Poisson and Gaussian GLMs were then run using taxa richness and Shannon diversity, respectively, with Zone, Sand cover, Wave action and Substrate complexity as predictors. Model selection used Akaike information criteria (AICc) values (MuMIn::model.sel), overdispersion was checked via the deviance/degrees of freedom ratio, and predicted associations from the best supported models were visualised. All analyses were performed in RStudio using the vegan, dplyr, tidyr, ggplot2, ggeffects, Hmisc and corrplot packages.

4.3 RESULTS

Over the course of this study, from 4th December 2025 to 1st March 2026, 412 quadrats were sampled along 12 transects across 3 sites. Species accumulation curves were plotted to understand whether the communities across the 3 sites (Figure 5 a), as well as the three zones (Figure 5 b) within these intertidal sites, were adequately sampled.



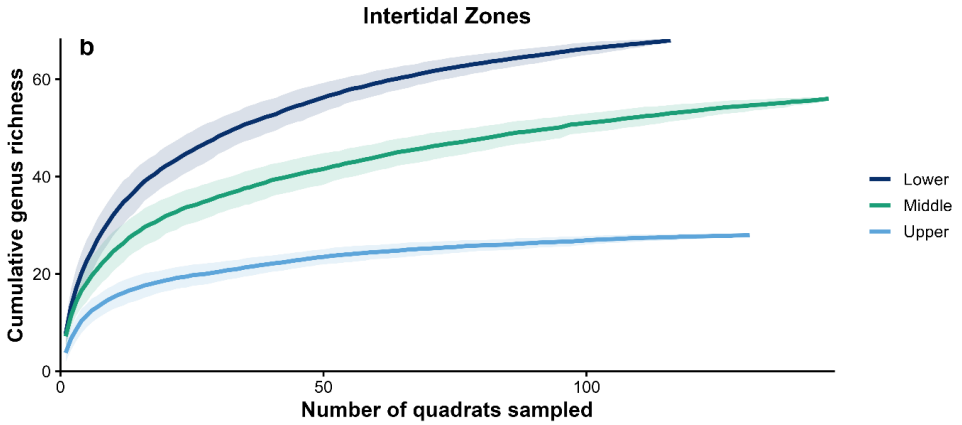


Figure 5 *(a) Site-wise species accumulation curve. (b) Zone-wise species accumulation curve.*

Species accumulation curves approached their asymptotes at all three sites and all three zones. Chao2 estimates (Table 2) indicated that Siridao was the most undersampled site, followed by Cacra and Hollant. It is important to note that Siridao's Chao2 estimate is associated with a large standard error value. According to the zonation Chao2 estimates, the middle intertidal was the most undersampled.

Table 2 *Site and zone-wise Chao2 estimates.*

Sites	*Taxa Observed*	*Chao2 estimates*
Siridao	42	62.03 ± 17.31
Cacra	48	57.92 ± 8.31
Hollant	59	69.79 ± 7.55
Zone	*Taxa Observed*	*Chao2 estimates*
Upper	28	28.74 ± 1.26
Middle	56	65.32 ± 6.76
Lower	68	75.14 ± 5.41

Within the 412 quadrats sampled across these sites, a total of 66 genera and 13 morphospecies were identified (Appendix 1). These comprised 51 animal taxa and 28 algal taxa. Seven phyla contributed to the 51 animals, whereas three phyla contributed to the 28 algae. The seven animal phyla were *Annelida* (6 genera/morphospecies), *Arthropoda* (3 genera), *Bryozoa* (2 genera), *Chordata* (1 genus), *Cnidaria* (4 genera), *Mollusca* (30

genera/morphospecies), and *Porifera* (5 genera). The 3 algal phyla were *Chlorophyta* (green alga), *Ochrophyta* (brown alga), and *Rhodophyta* (red alga), contributing 7, 8 and 14 genera/morphospecies, respectively.

The six annelid genera/morphospecies comprised polychaete worms, while the three arthropod genera were barnacles. A tunicate represented the chordate genus, and the five poriferan genera were sponges. The four cnidarian genera include two genera of sea anemones and two genera of soft corals. The 30 molluscan genera/morphospecies comprised six bivalve genera, two limpet genera, and one genus each of chitons, tube snails, and sea slugs, in addition to 19 genera of marine sea snails. The distribution of these genera across intertidal zones and the environmental factors structuring this distribution are examined in the sections below.

Before examining spatial factors driving community composition, a PERMANOVA was utilised to assess temporal variation among sampling months. Although community composition differed significantly among months (PERMANOVA, $F = 2.16$, $p < 0.001$), months explained a negligible proportion of the total variation in assemblages ($R^2 = 0.016$). Consequently, temporal variation was considered minor relative to the spatial patterns investigated below, and data from all sampling months were pooled for subsequent analyses without introducing meaningful temporal bias. Additionally, distance-decay analysis revealed statistically significant but negligible distance-decay relationships across all three zones (Mantel $r = 0.097 – 0.118$, $p < 0.001$). The baseline Bray-Curtis dissimilarity already exceeded 0.80 at minimum quadrat separations, indicating that spatial autocorrelation was negligible in magnitude and did not represent any biologically meaningful source of non-independence at the scale of the sampling design (Appendix 2).

To visualise community composition across intertidal zonation, an NMDS ordination was plotted using Wisconsin double-standardised data (Figure 6). It revealed a clear separation of assemblages across intertidal zones.

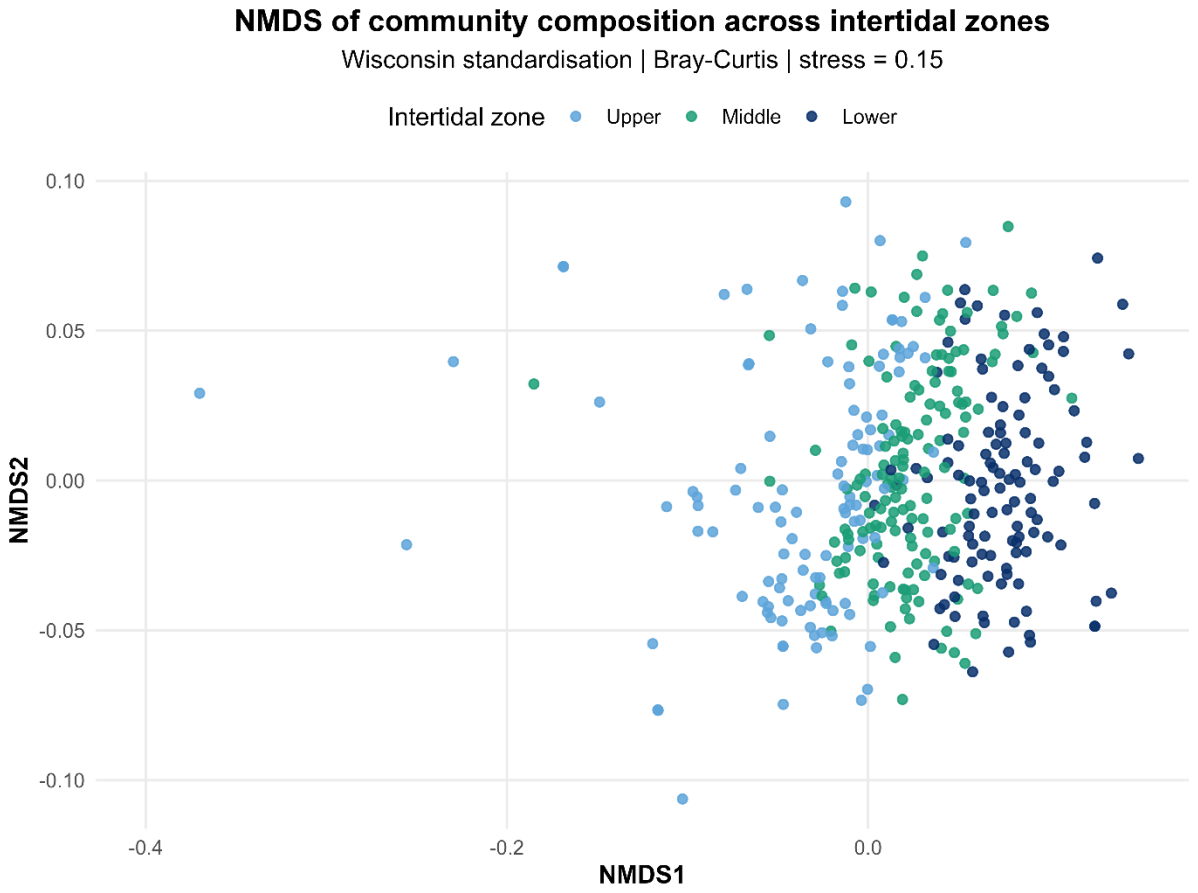


Figure 6 *Non-metric multidimensional scaling (NMDS) ordination of intertidal community composition across upper, middle, and lower intertidal zones based on Bray-Curtis dissimilarities calculated from a Wisconsin-standardised community matrix. Each point represents a quadrat, and colours indicate the intertidal zone. The two-dimensional ordination provided an acceptable representation of community dissimilarity.*

A PERMANOVA showed community composition differed significantly among intertidal zones (PERMANOVA: $F = 25.03$, $R^2 = 0.114$, $p = 0.001$). In a PERMANOVA including site and zone, both site ($F = 15.68$, $R^2 = 0.066$, $p = 0.001$) and zone ($F = 27.81$, $R^2 = 0.117$, $p = 0.001$) remained significant. Pairwise comparisons showed significant differences among all zone pairs, with the strongest separation between upper and lower zone assemblages ($F = 31.90$, $R^2 = 0.115$, $p = 0.001$), followed by middle and lower zones ($F = 24.41$, $R^2 = 0.086$, $p = 0.001$), while upper and middle zones showed the weakest separation ($F = 19.26$, $R^2 =$

0.065, p = 0.001). Beta dispersion analysis revealed a significant difference in within-zone community variability between zones (F = 6.2, p = 0.005). Given the significant zonal differences in community composition identified by NMDS and PERMANOVA, beta diversity was subsequently partitioned to evaluate the relative contributions of taxa turnover and nestedness to patterns of community dissimilarity (Table 3).

Contrast	*βSOR (Total dissimilarity)*	*Turnover*	*Nestedness*
Upper-Middle	0.405	0.107	0.298
Middle-Lower	0.258	0.179	0.079
Upper-Lower	0.542	0.214	0.328

Table 3 *Pairwise beta-diversity decomposition across intertidal zones. Higher turnover values indicate greater taxa replacement between zones, whereas higher nestedness values indicate that assemblages in one zone largely comprise subsets of those occurring in another zone.*

Beta diversity varied across zones, with the largest compositional dissimilarity between the upper and lower zones and the lowest between the middle and lower zones. Dissimilarity involving the upper zone was primarily driven by nestedness, while turnover contributed most strongly to differences between middle and lower zone assemblages.

Given the significant differences in community composition and the contrasting contributions of turnover and nestedness to the zonal differences, subsequent analyses were conducted to identify the taxa contributing most strongly to this dissimilarity. Similarity percentage analysis (SIMPER) identified taxa that contributed disproportionately to community dissimilarity among intertidal zones (Figure 7). The Upper-Middle zone contrast was primarily driven by *Saccostrea* oysters, followed by algal taxa and *Siphonaria*, a false limpet. Differences between the middle and lower zones were mainly associated with a suspension feeder and three red algae. Lastly, the dissimilarity between upper and lower intertidal was primarily driven by both the suspension feeder and *Saccostrea* oysters, followed by two biofilm-grazing sea snails, *Planaxis* and *Echinolittorina.*

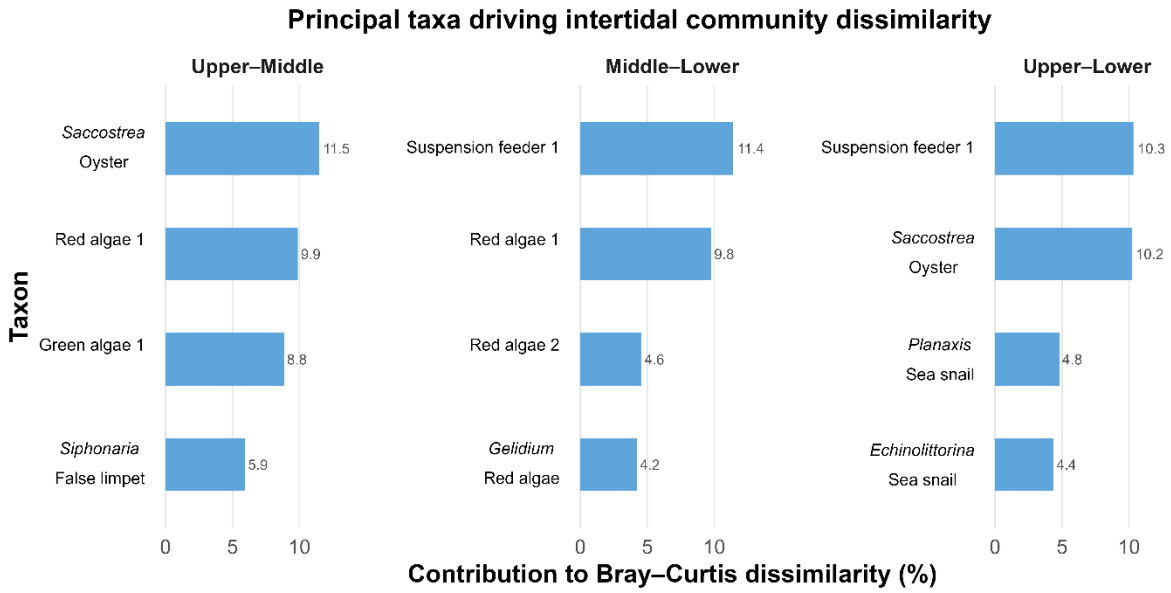


Figure 7 *Principal taxa contributing to Bray-Curtis dissimilarity among intertidal zones as identified by SIMPER analysis. Bars indicate the percentage contribution of each taxon to average community dissimilarity for each pairwise zonal comparison.*

To complement SIMPER analysis and identify taxa most strongly associated with particular shore zones, an indicator species analysis (IndVal) was undertaken. This analysis identified taxa that were significantly associated with a specific intertidal zone. The upper intertidal was characterised by *Chthamalus* barnacles (IndVal = 0.471), and three biofilm-grazing sea snails, *Planaxis* (0.457), *Echinolittorina* (0.331) and *Littoraria* (0.228). The middle intertidal showed association with only two taxa, red algae 1 (0.556) and *Ergalatax* (0.556), an omnivorous sea snail. In contrast, the lower intertidal consisted of the greatest number of significant indicator taxa and was most strongly associated with Suspension feeder 1 (IndVal = 0.697), a predatory sea snail, *Indothais* (0.559), and two genera of brown algae, *Padina* (0.542) and *Dictyota* (0.580). Altogether, the indicator taxa reflected clear zonation patterns, with the lower intertidal holding a large number of characteristic taxa in contrast to the middle and upper intertidal.

The analyses presented above reveal differences in community composition along the environmental stress gradient, the processes underlying beta diversity, and the characteristic taxa associated with each zone, as well as the ones driving community dissimilarity. Having

established how key taxa identities and community composition vary across the stress gradient, the following section investigates changes in community structure through patterns of richness and diversity.

Boxplots were used to ascertain the patterns of community richness and Wisconsin-Standardised Shannon diversity across the intertidal gradient (Figure 8 a, b). Taxa richness differed significantly among intertidal zones (Kruskal-Wallis: $\chi^2 = 160.4$, df = 2, $p < 0.001$). Pairwise Wilcoxon tests indicated that richness was significantly different between all zone pairs (all $p < 0.05$). Median richness increased from the upper to the middle intertidal and remained high in the lower intertidal, although substantial variation was observed within each zone (Figure 8 a). Similarly, Wisconsin-standardised Shannon diversity differed significantly among zones (Kruskal-Wallis: $\chi^2 = 153.98$, df = 2, $p < 0.001$), with all pairwise zone comparisons remaining significant (all $p < 0.001$). Diversity increased from the upper to the lower intertidal, with the highest median values observed in the lower zone (Figure 8 b).

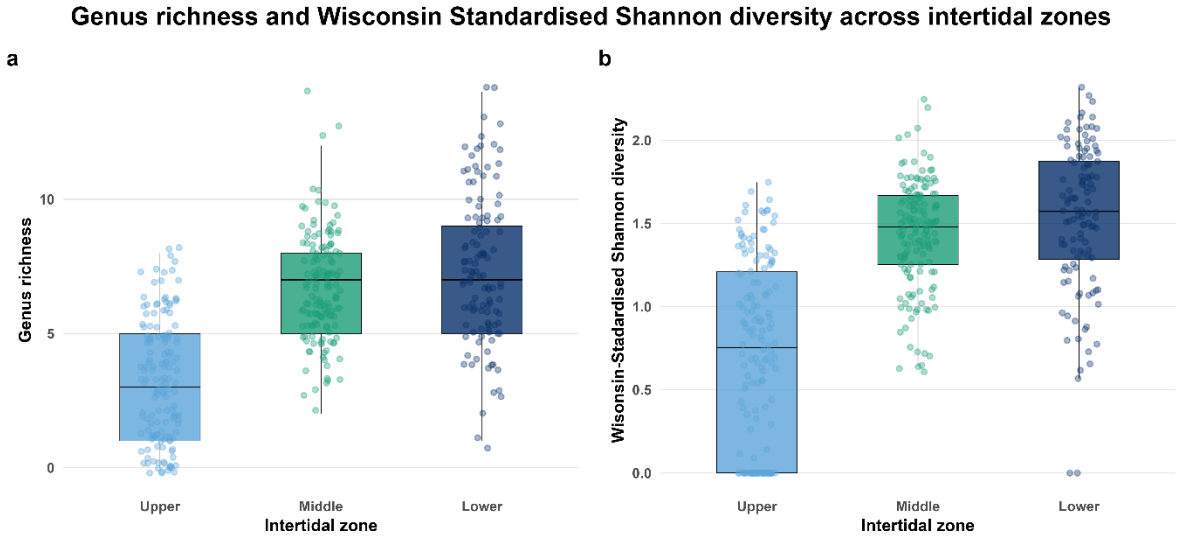


Figure 8 *Boxplots showing (a) taxa richness and (b) Wisconsin-standardised Shannon diversity across intertidal zones. Indices were calculated for individual quadrats and are displayed as boxplots.*

Building on this, to determine whether the observed diversity patterns were consistent across ecologically dissimilar components of the community (consumers and producers), Wisconsin-Standardised Shannon diversity was examined using boxplots separately for animal and algal communities (Figure 9 a, b).

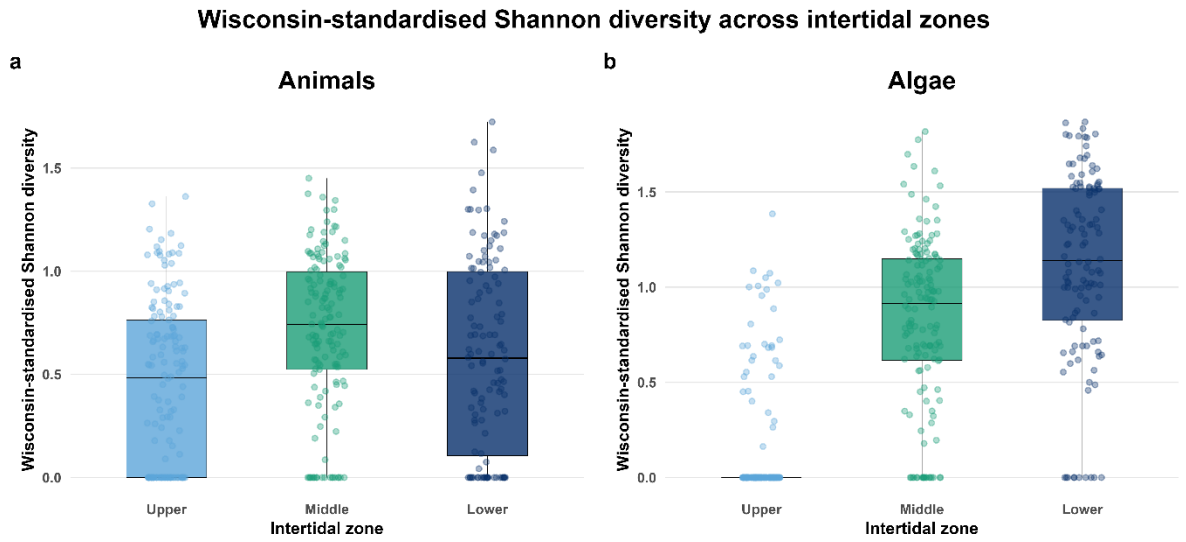


Figure 9 *Boxplots showing (a) Wisconsin-standardised diversity for animal communities and (b) Wisconsin-standardised Shannon diversity for algal communities across intertidal zones. Indices were calculated for individual quadrats and are displayed as boxplots.*

Animal diversity differed significantly among intertidal zones (Kruskal-Wallis: χ^2 = 28.11, df = 2, $p < 0.001$), with pairwise comparisons also indicating significant differences between all zone pairs (all $p < 0.005$). However, changes in animal diversity across the intertidal gradient were relatively modest (Figure 9 a). In contrast, algal diversity demonstrated a stronger zonation pattern and differed significantly among zones (Kruskal-Wallis: $\chi^2 = 194.4$, df = 2, $p < 0.001$; all pairwise comparisons $p < 0.001$) (Figure 8 b). Algal diversity increased substantially from the upper to the lower intertidal, as opposed to animal diversity.

The analyses presented above investigated patterns of community structure across broader zonal differences but did not examine the influence of local habitat characteristics on richness and diversity. To determine whether the nested sampling design introduced non-

independence among observations, taxa richness was first analysed using a generalised linear mixed model (GLMM) framework, with substrate complexity, wave action, and sand cover as fixed effects and site and transect as random effects. Random effects variance was negligible at both the site (SD = 0.036) and transect (SD = 0.063) levels, suggesting that observations were largely independent across quadrats. Consequently, general linear models (GLMs) were used to investigate the effects of substrate complexity, wave action, and sand cover on richness and diversity, and to determine whether these relationships differed among intertidal zones.

Table 4 *Model selection results for candidate Poisson GLMs explaining taxa richness across the intertidal gradient. Models were ranked using the corrected Akaike's Information Criterion (AICc).*

Model	*Predictors*	*df*	*AICc*	*ΔAICc*	*Weight*
Sand–Wave	Zone × Sand cover + Zone × Wave action + Substrate complexity	10	1841.5	0.00	0.728
Global	Zone × Sand cover + Zone × Wave action + Zone × Substrate complexity	12	1844.5	2.98	0.164
Sand	Zone × Sand cover + Wave action + Substrate complexity	8	1845.8	4.26	0.087
Sand–Complexity	Zone × Sand cover + Zone × Substrate complexity + Wave action	10	1848.6	7.07	0.021
Wave	Zone × Wave action + Sand cover + Substrate complexity	8	1868.2	26.71	<0.001
Wave–Complexity	Zone × Wave action + Zone × Substrate complexity + Sand cover	10	1869.0	27.44	<0.001
Additive	Zone + Sand cover + Wave action + Substrate complexity	6	1876.3	34.80	<0.001
Complexity	Zone × Substrate complexity + Sand cover + Wave action	8	1876.3	34.84	<0.001
Zone-only	Zone	3	1879.9	38.43	<0.001

Model selection (Table 4) strongly supported the Sand-Action model (AICc = 1841.5, weight = 0.728), which included zonal interactions with both sand cover and wave action, with substrate complexity as an additive predictor of taxa richness (Table 2). The global model received some support (ΔAICc = 2.98, weight = 0.164), whereas all remaining models received substantially less support (ΔAICc > 4).

There was no meaningful indication of overdispersion in the selected model (Dispersion ratio = 1.09). The model also explained 41.9% of the variation in taxa richness (pseudo-R^2 = 0.419). Residual diagnostics showed no substantial divergence from model assumptions. Variable estimates for the selected model are presented in Table 5.

Table 5 *Estimates from the selected GLM explaining variation in taxa richness. Estimates are presented on a log scale, along with standard errors (SE) and Z-values.*

Predictor	*Estimate*	*SE*	*Z-value*
Intercept	1.028	0.153	6.701
Zone (Middle)	0.805	0.188	4.290
Zone (Lower)	0.882	0.205	4.302
Sand cover	0.225	0.044	5.114
Wave action	-0.110	0.045	-2.431
Substrate complexity	0.366	0.119	3.082
Zone (Middle) × Sand cover	-0.256	0.052	-4.900
Zone (Lower) × Sand cover	-0.290	0.051	-5.717
Zone (Middle) × Wave action	0.121	0.057	2.128
Zone (Lower) × Wave action	0.170	0.059	2.877

Consistent with previous findings, taxa richness differed among intertidal zones (Table 5). Relative to the upper intertidal, both middle and lower intertidal zones exhibited higher richness values (Figure 10 a). Furthermore, substrate complexity had a positive effect on taxa

richness (Figure 10 b). The effect of sand cover varied across intertidal zones. In the upper intertidal, richness increased with sand cover, whereas the relationship was negative in the middle and lower intertidal zones (Figure 10 c). Lastly, the effect of wave action was highly variable across intertidal zones. Wave action was negatively associated with taxa richness in the upper intertidal, while effects were minimal in the middle intertidal and positive in the lower intertidal (Figure 10 d).

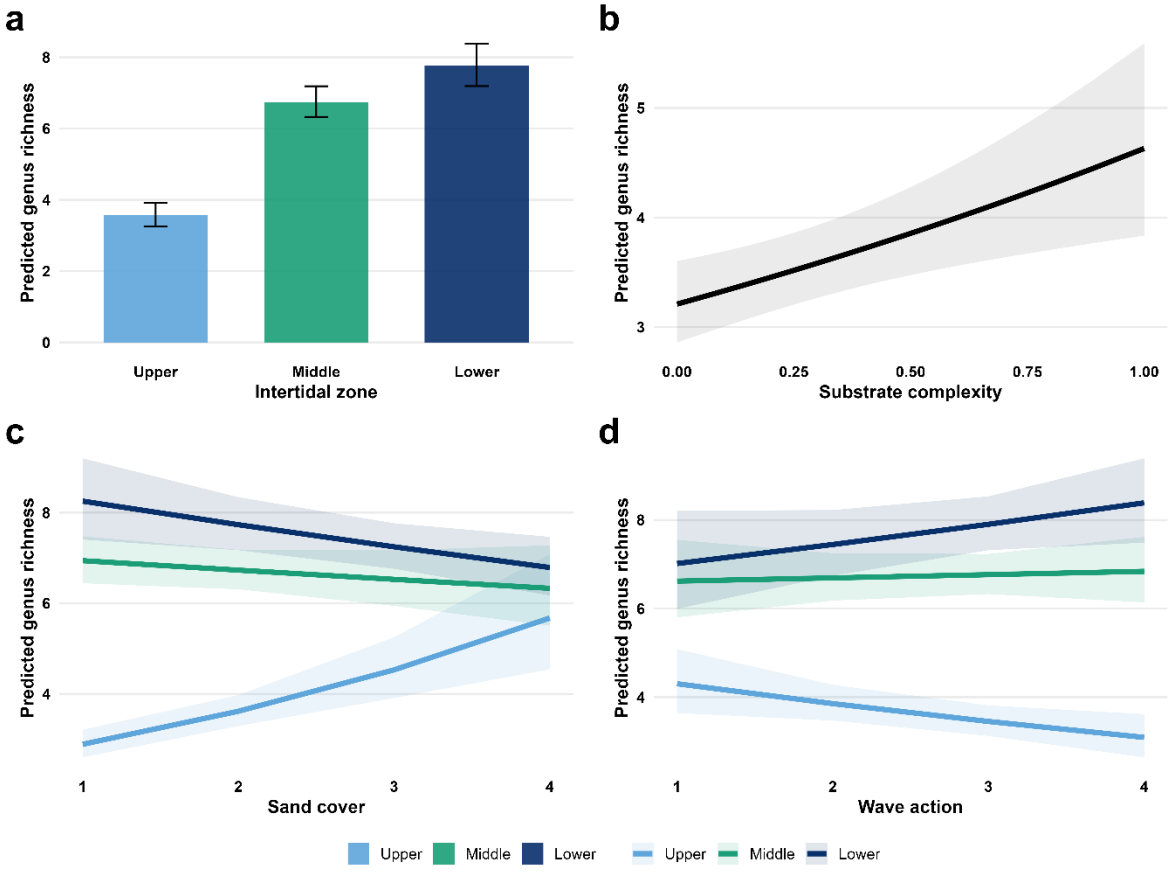


Figure 10 *Effects of intertidal zone, substrate complexity, sand cover and wave action on taxa richness. (a) Variation in taxa richness with zonation is presented as boxplots with overlaid quadrat-level observations. (b) Predicted relationship between substrate complexity and taxa richness, with the shaded area representing 95% confidence intervals. (C) Predicted effects of sand cover on taxa richness across intertidal zones, displaying a significant interaction between sand cover and zone. (d) Predicted effects of wave action on taxa richness across intertidal zones, displaying a significant interaction between action level and zone. Predictions are shown with 95% confidence intervals and were derived from the best supported model identified using AICc-based model selection.*

Overall, taxa richness was significantly influenced by intertidal zone, substrate complexity, sand cover and wave action. Furthermore, to determine whether the environmental drivers of community diversity differed from those influencing richness, a similar modelling framework was applied to Wisconsin-standardised Shannon diversity. Candidate models were compared using an information-theoretic approach, and the selected model was subsequently examined to identify the key environmental variables associated with varying diversity. The diversity results were identical to those for richness, with the Sand-Wave model being the best supported. The direction and magnitudes of all predictors were also similar. (Appendix 3, 4 & 5).

Taken together, these analyses demonstrated how community composition varied along the intertidal gradient and identified the taxa contributing most strongly to the observed patterns of beta diversity. They further revealed patterns of richness and diversity along the gradient, including contrasting patterns between animal and algal communities, and identified taxa that were characteristic of each intertidal zone. Finally, the effect of local habitat characteristics on taxa richness and diversity was examined alongside the broader effects of intertidal zonation.

4.4 DISCUSSION

The environmental stress gradient strongly drives the compositional and structural shifts in community assemblages. The three zones: upper, middle and lower showed a different community composition and held communities of varying richness and diversity. The upper intertidal showed the lowest richness, which increased in the middle intertidal and was maintained in the lower intertidal. Diversity shows a similar pattern but increases even more in the lower intertidal. Scrosati & Heaven (2007) found an identical relation of richness and diversity with the environmental stress gradient. The further increase in diversity denotes a similarly rich community with taxa abundances more evenly distributed compared to the middle intertidal (Krebs, 1999). This corroborates well with the environmental stress model,

wherein the middle intertidal is characterized by tense competition due to species abundance build up, leading to a few taxa dominating the assemblages, whereas in the lower intertidal, the competition is alleviated by lower stress as well as the effect of predation, leading to a more equitable distribution amongst taxa that make up the community (Menge & Sutherland, 1987).

The decomposition of pairwise beta diversity into turnover and nestedness components demonstrated a clear distinction in mechanisms driving community-level shifts. Dissimilarity between the middle and lower zones was dominated by taxon turnover (0.179), indicating that these communities differ mainly through taxa replacement. This pronounced turnover is consistent with the shift from stress-driven environmental filtering to biotic interactions structuring community composition (Menge & Sutherland, 1987). In contrast, the dissimilarity between the upper zone and both the middle and lower zones was driven by nestedness (Upper–Middle: 0.298; Upper–Lower: 0.328), suggesting that the upper intertidal harbours a diminished subset of the taxa found in less stressed zones. This aligns with the environmental stress gradient hypothesis, which posits that in high-stress zones, environmental filtering will restrict community composition to a few stress-tolerant taxa (Menge & Sutherland, 1987; Valdivia et al., 2011).

The SIMPER and Indicator species analysis help understand these concepts at the taxon level. *Chthamalus* barnacles, along with three sea snails, *Planaxis*, *Echinolittorina* and *Littoraria*, were associated with the upper intertidal. *Chthamalus* barnacles have been famously demonstrated to be competitively excluded in the lower intertidal by other barnacles (Connell, 1961); this aligns with field observations. Additionally, the three sea snails are all highly stress-tolerant taxa (Han, 2019; Marshall, 2015). Furthermore, the upper-middle intertidal SIMPER results show that the Oysters from the upper intertidal and the algal taxa from the lower intertidal drive the dissimilarity between the zones. The shift from oyster beds to the Red algae 1 and Green algae 1 beds signify a shift from hard-bodied heat-tolerant animals to soft-bodied

animals. The middle intertidal is strongly associated with only two taxa, an omnivorous gastropod, *Ergalatax* and the Red algae 1. This aligns with the idea that the middle intertidal acts as a transitional zone and doesn't host many zone specialists. The differences between middle and lower are driven by Suspension feeder 1 and 3 kinds of red algae. The indicator species analysis shows *Indothais*, a predatory gastropod, and brown macroalgae (*Padina* & *Dictyota*) as representatives of the lower intertidal. Lower stress also allows for the growth of larger habitat-forming algal taxa, as indicated by the analysis. The presence of *Ergalatax* in the middle intertidal and *Indothais* in the lower intertidal signifies a gradual accumulation of trophic types as predicted by the environmental stress hypothesis.

Fine-scale habitat characteristics strongly shaped community structure within the broader intertidal stress gradient. Through an information-theoretic approach, the best model fit found that the effects of sand cover and wave action on richness differ among zones. Whereas substrate complexity increased taxa richness similarly across zones. The observed pattern for substrate complexity deviated from the prediction that it would have a greater influence in the high-stress zones. A structurally complex substrate can produce refugia from desiccation and thermal stress, making it all the more essential in high-stress zones and relatively obsolete in low-stress ones (Helmuth & Hofmann, 2001). The finding suggests that substrate complexity plays an important role even in low-stress environments. This could be due to complex surfaces providing escape terrain for prey taxa or even an increase in available niches (Kohn & Leviten, 1976). Sand cover decreases richness in the middle and lower intertidal zones, while having the opposite effect in the upper intertidal zone. The decrease in richness could be attributed to burial under sand (Airoldi, 2003). However, the positive effect of sand cover on richness may be due to its moisture-retaining nature, which alleviates stress. Lastly, wave action showed a negative association with richness in the upper intertidal, which is likely due to the exclusive presence of oyster beds along the high wave action zones in the upper intertidal, as observed

in the field. The middle intertidal did not show a biologically meaningful relationship with wave action. Whereas the lower intertidal showed a mild positive relation, which could be attributed to high taxa turnover due to mechanical stress caused by wave force (Sousa, 1979). Similar patterns were also found for taxa diversity, indicating that the community's abundance structure does not substantially differ with fine-scale habitat characteristics.

Put together, the findings point to a hierarchically structured community in which broad-scale zonation patterns serve as primary drivers of community assemblages, with finer-scale habitat characteristics operating within the boundaries set by zonation. The fact that this pattern holds across three intertidal sites improves its generality across Goan rocky intertidal zones. However, compositional and structural patterns alone cannot reveal why particular taxa occupy particular zones. Understanding which functional assemblages characterise each zone within the environmental stress gradient is the question addressed in Chapter 2.

Chapter 2
Drivers of Functional Assemblages

5.1 INTRODUCTION

The previous chapter reported a differential response to the reduction of environmental stress between animals and algal taxa. Animals persisted across much of the intertidal zone, whereas algae appeared to thrive primarily in lower-stress conditions. This pattern may reflect the inability of algal taxa to evade stress through locomotion, resulting in distributions that are more tightly constrained by stress gradients, especially in high-stress zones such as the upper intertidal (Huey et al., 2002).

Within animals, both motile and sessile forms occur in the intertidal. Motile animals are composed mainly of slow-moving organisms that contribute to food-web structure by grazing on algae, preying on grazers and other sessile animals, and scavenging dead matter. For these taxa, food availability is the limiting resource, whereas the dominant pressures are imposed by the environmental stress gradient discussed in Chapter 1. Sessile animals, in contrast, are mostly suspension feeders, although some are capable of predating and photosynthesising through mutualistic microorganisms. For these taxa, space is the principal limiting factor, while their main stressors are similar to those experienced by motile animals. As a result, sessile animals compete with both algal taxa and one another for space in the intertidal, since the availability of suitable substrate largely governs their larval settlement (Jenkins et al., 2009). To summarise, motile animals encounter algae as a food resource that expands trophic opportunity, whereas sessile ones encounter algae as a competitor for the same limiting resource (substrate).

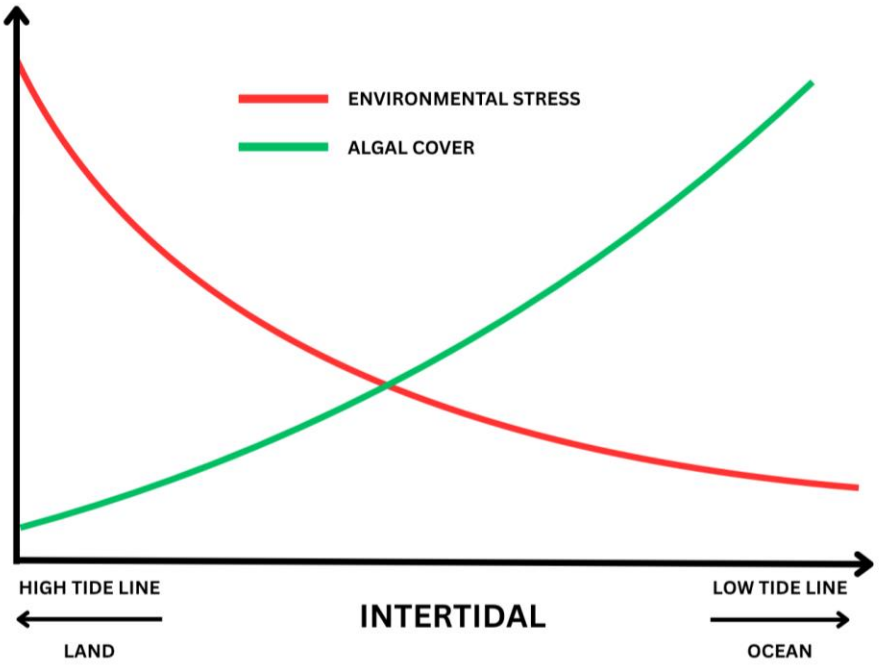


Figure 11 *Conceptual illustration showing variation in environmental stress and algal increase (biotic gradient) across the intertidal zone.*

Consequently, motile taxa are expected to benefit not only from reduced stress but also from greater resource availability in the lower intertidal zone. However, for sessile taxa, coexistence with highly specialised algal taxa inhabiting lower intertidal zones may lead to intense competition for space. Thus, reduced environmental stress in the intertidal may not have the same alleviating effect on sessile taxa as it does on motile taxa. Instead, sessile taxa may experience a biotic stress gradient that has the opposite effect of the abiotic stress gradient.

Based on environmental filtering theory, as discussed in the Conceptual underpinnings section, motile taxa are predicted to show functional divergence in high-algal zones, where algal cover facilitates a wider range of foraging strategies by expanding resource availability. Sessile taxa, by contrast, are predicted to show functional convergence in high-algal zones, where competition for primary substrate intensifies and filters communities toward effective space-holding strategies. The environmental stress gradient, therefore, is expected to exert a similar directional effect on both groups, while the biotic gradient drives them in opposite functional directions.

5.2 METHODS

5.2.1 Compilation of Functional Trait Data

To achieve Objective 2, functional trait information (Table 6) was compiled for all taxa from the kingdom Animalia using published literature and scientific databases. Key sources include AlgaeBase (Guiry & Guiry, 2026), WoRMS (2026) and expert communication. A fuzzy-coded matrix was used (Chevene et al., 2024), wherein every trait modality was scored on a scale from 0 to 3 (Table 7) (Mondy et al., 2014).

Table 6 *Functional trait categories and associated modalities used in the study.*

Trait	*Categories*
Body Size	S < 2cm · M 2–6cm · L 6–10cm · XL 10–20cm · XXL > 20cm
Growth Form	Conical · Encrusting · Fusiform · Globose · Prostrate · Colonial mat · Tubular
Feeding Mode	Autotroph · Suspension feeder · Grazer · Predator · Detritivore
Reproductive Mode	Planktonic Egg Laying · Planktonic Broadcast · Non-Planktonic Development
Attachment Mechanism	Cement · Byssus · Pedal adhesion · Basal disc · Free-living
Calcification	Calcareous · Non-calcareous

Table 7 *Fuzzy coding scoring criteria. Adapted from Patrohay et al., 2022.*

Code	*Explanation*
3	Taxon has total and exclusive affinity for a certain trait modality.
2	Taxon has a high affinity for a certain trait category, but other categories can occur with equal (2) or lower (1) affinity.
1	Taxon has a lower affinity for a certain trait category.
0	Taxon has no affinity for a certain trait category.

Trait compilation for algal taxa was attempted but was unsuccessful due to a lack of detailed trait literature for Indian marine algae. The available traits were too similar for all algal taxa, leading to inevitable clustering in functional space. As a result, algal taxa were not included in functional analysis.

5.2.2 Analytical methods

Within each trait category in the fuzzy-coded matrix, scores were normalised so that they sum to one per taxon. Taxon abundances (cover and counts) were rescaled using a max-standardisation wherein the abundance was divided by the taxon's maximum observed value across all quadrats (Oksanen, 2015; Uno et al., 2025). Quadrats with fewer than three taxa were excluded, as subsequent functional dispersion analyses require a minimum of taxa for stable estimation (Laliberté & Legendre, 2010). Trait modalities with zero variance within a given subset (motile or sessile) were excluded as they could not contribute to distinguishing taxa. Pairwise functional distances between taxa were computed using Gower's distance (Gower, 1971) with inverse block-size weighing (Pavoine et al., 2009) applied across trait categories, to ensure that categories with more modalities did not disproportionately drive the distance matrix.

Functional dispersion analysis within the FD package (Laliberté & Legendre, 2010) was used to understand how environmental gradients shape functional trait space. Functional dispersion (FDis) measures the mean distance of community assemblages from the abundance-weighted centroid of the occupied trait space of that community. To evaluate whether observed FDis exceeded or fell below what would be expected in the case of random assembly, standardised effect sizes (SES-FDis) were calculated by comparing observed values against a null distribution generated from 999 randomised communities (Swenson, 2014; Valdivia et al, 2017). Independent swap randomisations (Gotelli, 2000) were used to produce randomised taxa

co-occurrence matrices that preserved both the rarity of taxa and quadrat richness. This generated a null model, representing an unfiltered community, allowing comparisons between the filtered observed communities and the unfiltered null community. Additionally, to generate ecologically realistic null abundances, the observed abundances of each taxon were then resampled from its observed distribution across sites and assigned to the independently swapped null cells (Bernard-Verdier et al., 2012; Laliberté & Legendre, 2010). This abundance shuffle null was chosen over a presence-absence null to account for dominance structure; not doing so would ignore the dominant role of a few abundant taxa in shaping community trait space. Analyses were conducted separately for motile and sessile animal assemblages, since these groups were expected to respond differently to the abiotic and biotic gradients. SES-FDis was then regressed against relative position and algal cover, using generalised mixed models with site as a random effect.

Subsequently, RLQ analysis (Dolédec et al., 1996; Beauchard et al., 2022) was conducted separately for motile and sessile assemblages using the ade4 package (Dray & Dufour, 2007). RLQ analysis identifies the trait combinations associated with different environmental gradients across the community. Before ordination, environmental variables (R matrix) were z-standardised, since they were originally measured in different ranges. This ensured that no single variable dominated the ordination because of a larger numerical range. Taxon abundances (L matrix) were also Wisconsin double-standardised, in addition to max-standardisation, to prevent numerically dominant taxa and high-abundance quadrats from disproportionately driving the ordination. The environmental variables (R matrix), taxon abundances (L matrix), and their traits (Q matrix) were simultaneously ordinated to identify the major trait-environment relationships structuring the assemblages (Gusha & McQuaid, 2025). For the sessile and motile subsets, trait ordination (Q matrix) used the Hill-Smith method (dudi.hillsmith), as this method accommodates mixed and non-continuous trait data

more appropriately than standard PCA (Hill & Smith, 1976; Dray & Dufour, 2007). A preliminary fourth-corner screen was run before ordination to identify trait modalities with meaningful associations to the environmental matrix, which were retained in the final RLQ (Gusha & McQuaid, 2025). The overall significance of each RLQ ordination was tested using Monte Carlo permutation (999 permutations; randtest, ade4). Lastly, fourth-corner analysis (Legendre et al., 1997; Dray & Legendre, 2008) was used to test the statistical significance of trait-environment associations identified by the RLQ ordinations, using 9999 permutations with Benjamini-Hochberg correction for multiple testing. This analysis evaluates whether particular trait combinations are associated with specific environmental variables to a greater extent than expected by chance. Together, the RLQ and fourth-corner approaches were used to determine both the direction and significance of trait responses along environmental gradients (Dray et al., 2014; Gusha & McQuaid, 2025).

All analyses were performed in RStudio. Packages used include FD, lme4, ade4, ggplot2 and ggeffects.

5.3 RESULTS

To set the premise for the forthcoming analysis, algal cover was plotted against relative position (Figure 12). A strong, significant positive association was found between the two ($\beta = 1.059 \pm 0.090$ SE, $t = 11.78$, $p < 0.001$). Due to this relationship, algal cover and relative position were treated as potentially collinear predictors with different biological effects; relative distance served as a proxy for environmental stress, and algal cover represented a biotic gradient. Therefore, these were tested separately in the following analysis.

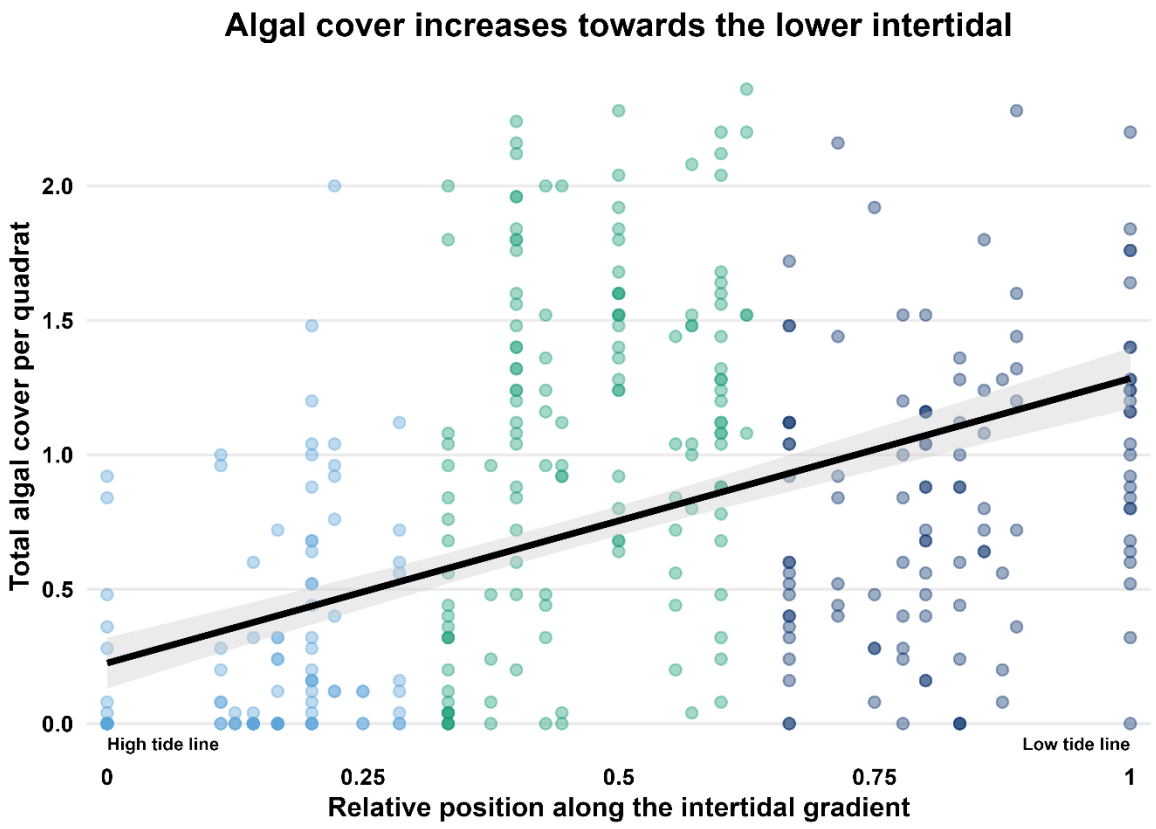


Figure 12 *Summed algal cover per quadrat plotted against relative position.*

As algal cover increased, a biotic gradient materialised along the environmental stress gradient represented by relative position. To test whether animal communities were more or less functionally dispersed than expected by chance, standardised effect sizes of functional dispersion (SES-FDis) were computed using an abundance-shuffle null model. SES-FDis values for these communities were then plotted against relative position and algal cover to reveal their variations in functional space. Positive values are associated with communities where taxa occupy more functional space than random assembly would predict (functional dispersion). In contrast, negative values indicate communities that occupy less functional trait space than would be expected under random assembly.

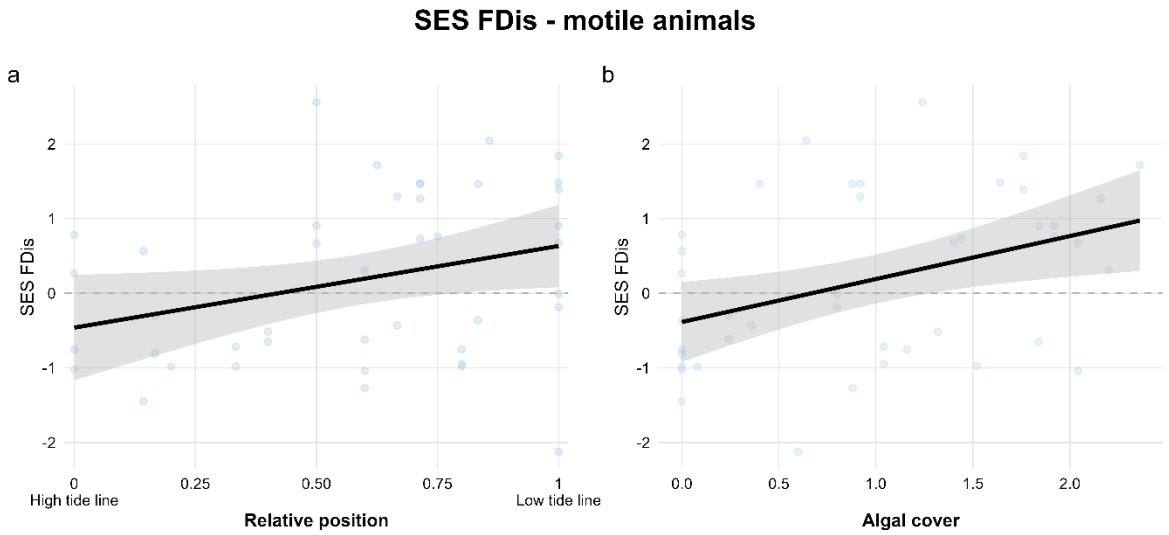


Figure 13 *Relationship between SES functional dispersion (SES-FDis) of motile taxa and (a) relative position along the intertidal gradient and (b) algal cover. The fitted line represents fitted linear models, and shaded areas indicate 95% confidence intervals.*

A SES-FDis analysis was run for sessile and motile animals separately. The SES-FDis plots for motile taxa (Figure 13) showed significant functional dispersion when plotted against algal cover (GLMM: p = 0.022, Site SD = 0.523); however, relative position did not generate a significant result (GLMM: p = 0.269, Site SD = 0.527). Motile animal communities in higher algal cover showed greater functional dispersion than expected by chance.

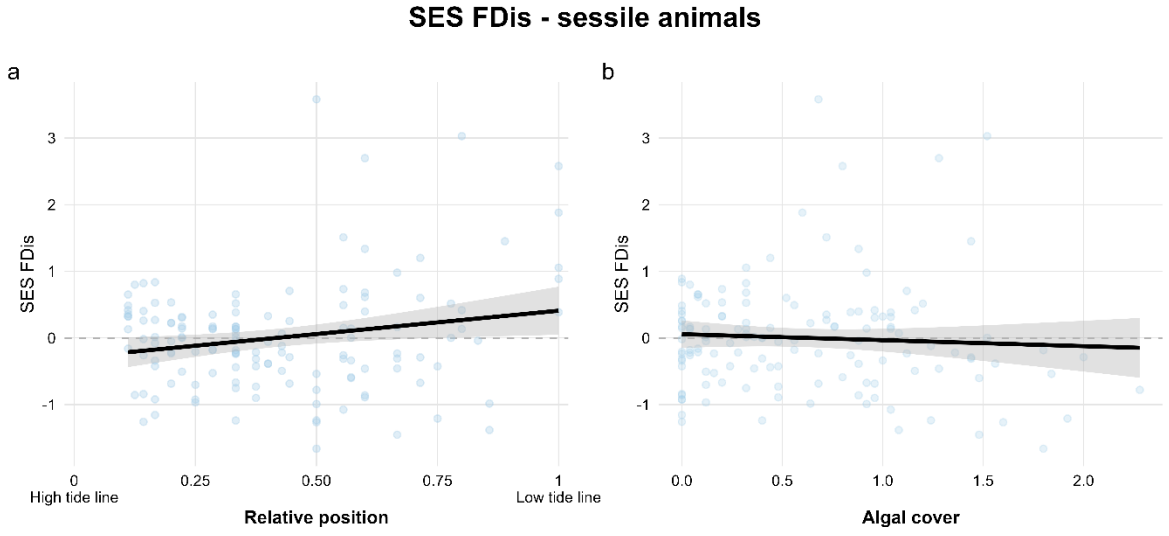


Figure 14 *Relationship between SES functional dispersion (SES-FDis) of sessile taxa and (a) relative position along the intertidal gradient and (b) algal cover. The fitted line represents fitted linear models, and shaded areas indicate 95% confidence intervals.*

In contrast, when plotted against relative position (GLMM: $p = 0.970$, Site SD = 0.897) and algal cover (GLMM: $p = 0.077$, Site SD = 0.921), no significant differences in functional dispersion were observed for sessile taxa. This pattern is consistent with random assembly in sessile communities along both gradients (Figure 14).

Building on this, RLQ analysis was conducted. RLQ analysis identifies how environmental factors are linked to the functional trait composition of communities. It does this by simultaneously ordinating sites by their environment and taxa by their traits through the abundance matrix. In contrast to the SES-FDis analysis, which determines if trait space is wider or narrower than expected, RLQ determines which functional traits increase or decrease in response to environmental gradients (Appendix 6).

For motile animal assemblages, RLQ axis 1 (RLQ1, Figure 15 a) explained 68.7% of co-inertia, and RLQ axis 2 (RLQ2, Figure 15 b) explained another 18.08%. Environmental structuring of community composition was significant (Model 2: permutation test, $p = 0.001$). Both gradients, algal cover and relative position, loaded on RLQ1 (negative direction, Figure 15 a), implying that the primary axis describes a gradient from lower intertidal/high algal cover to upper intertidal/low algal cover. Along this gradient, detritivores, predators and non-calcareous animals are mostly found in the algae-dominated lower intertidal, whereas the algae-poor upper intertidal predominantly comprises grazers (Figure 15 c).

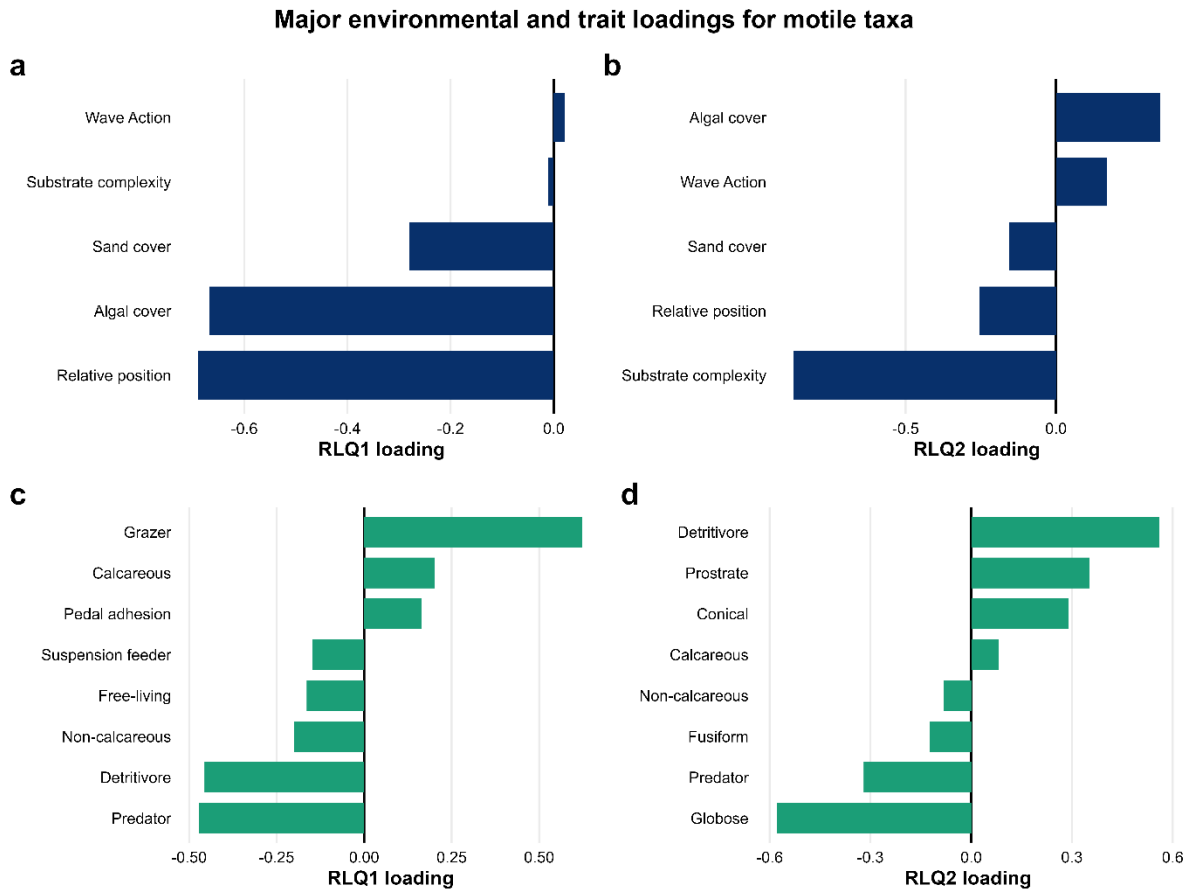


Figure 15 *Major environmental variables and functional trait modalities associated with the first two RLQ axes for motile taxa. Panels (a) and (b) show the loadings of environmental variables on RLQ1 and RLQ2. While panels (c) and (d) show the corresponding functional trait loadings. Positive and negative values indicate the strength and direction of association with each RLQ axis. Variables and traits in the same direction along an axis tend to be associated with one another.*

For sessile animal assemblages, RLQ1 represents 70.19% of co-inertia, while RLQ2 adds another 19.99%. Environmental structuring was significant once more (Model 2: p = 0.001). The dominant environmental factor loading on RLQ1 was relative position (Figure 16 a), with sand cover also contributing. Algal cover loaded strongly on RLQ2 (Figure 16 b). Along the RLQ1 gradient, tubular, non-calcareous, mat-forming animals were associated with the lower intertidal, while prostrate, calcareous forms characterised the upper intertidal (Figure 16 c). On the other hand, along RLQ2, byssate organisms represented areas with high algal cover, whereas low algal cover habitats were associated with prostrate, cemented taxa (Figure 16 d).

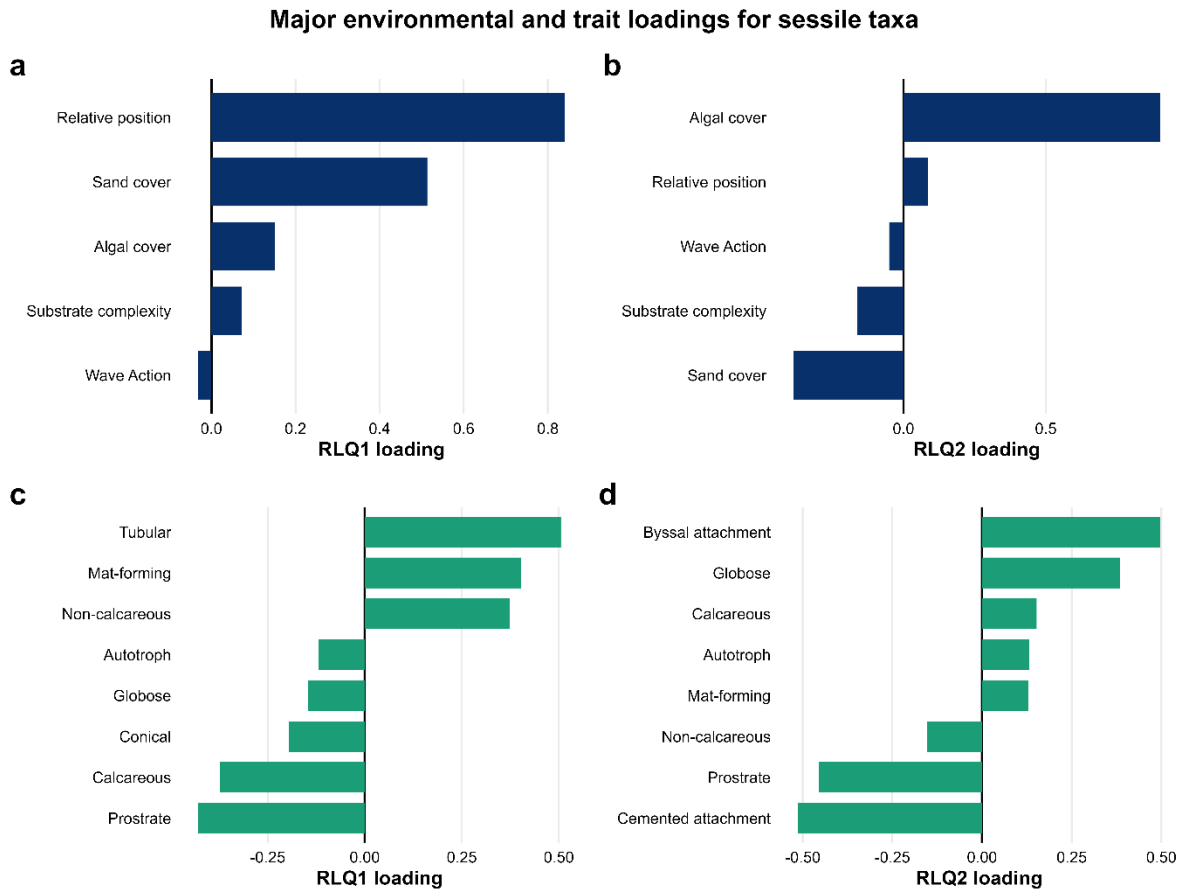


Figure 16 *Major environmental variables and functional trait modalities associated with the first two RLQ axes for sessile taxa. Panels (a) and (b) show the loadings of environmental variables on RLQ1 and RLQ2. While panels (c) and (d) show the corresponding functional trait loadings. Positive and negative values indicate the strength and direction of association with each RLQ axis. Variables and traits in the same direction along an axis tend to be associated with one another.*

Lastly, the fourth corner analysis was used to test whether particular trait modalities were associated with specific environmental variables along the RLQ ordination axes. For motile animals, algal position and relative position showed a strong association but were statistically non-significant. However, for sessile organisms, relative position was significantly associated with the RLQ1 trait gradient (BH-adjusted $p = 0.004$). This confirmed that the shift in trait combinations from calcareous/prostrate ones up-shore to tubular/non-calcareous ones down-shore is statistically robust.

The global fourth-corner (Model 4) permutation that tests the trait-environment association was non-significant ($p = 0.246$). However, this is a known property of the combined

RLQ/Fourth corner test, in which the global model is extremely conservative relative to the axis-specific tests, which show significance for sessile taxa RLQ 1. Underlying biological gradients can exist even when model 4 results show non-significance (Ter Braak et al., 2012).

5.4 DISCUSSION

In rocky intertidal ecosystems, abiotic and biotic gradients affect motile and sessile taxa differently. Motile taxa exhibit significant functional dispersion in high-algal zones, potentially indicating biotic facilitation. The RLQ showed that the increase in algal cover in lower zones was associated with predators, detritivores, and non-calcareous animals, while the upper intertidal zones with low algal cover were linked to biofilm grazers. Put together, this makes a case for stress release, further ameliorated by biotic facilitation in motile taxa. The association of the RLQ axis with trophic-level traits may point to a trophic shift consistent with increased food resources (primary producers) in the lower zones (Abrams, 1993). Overall, a decrease in stress is linked to increased primary productivity, which, in turn, may result in higher trophic richness (Oksanen et al., 1981). This inference serves as a secondary mechanism through which the environmental stress model can be perceived. Menge & Sutherland's (1987) model suggested an increase in trophic levels with the lowering of stress. However, this increase in trophic levels could also be attributed to biotic facilitation, through an indirect effect of the stress gradient. This idea aligns with Bruno et al.'s (2003) newer model that incorporates facilitation into the earlier stress model. Biotic facilitation, in this context, may occur through microhabitat creation: algal taxa may increase niche availability and provide respite from desiccation stress (Bertness & Leonard, 1997; Bertness et al., 1999; Watt & Scrosati, 2013). It should be noted that the fourth corner tests did not show significance for specific trait-environment associations. This is because RLQ tests for overall covariation structure among environment, site, and traits, while fourth-corner tests each trait-environment pair individually

under conservative correction, so the two can disagree without contradiction (ter Braak et al., 2012; Dray et al., 2014).

For sessile taxa, environmental filtering is the primary driver of functional assemblages (Fourth-corner: $p = 0.004$). The organisms shift from calcareous, prostrate forms to tubular, soft-bodied mats. Calcareous exteriors and prostrate body plans are associated with stress-tolerant organisms, such as oysters and barnacles, found in the upper intertidal (Jackson, 1977), while the tubular, soft-bodied mats are associated with taxa that experience comparatively little thermal stress (Vermeij, 1973). In contrast to prior expectations, the functional assemblages of sessile taxa are structured by stress (relative position), instead of algal cover. However, both variables loaded strongly on different RLQ axes, meaning both variables filter traits in different directions. That, alongside the non-significant functional dispersion responses to algal cover and relative position, may indicate a change in trait composition but no change in trait space. More speculatively, a potential cancellation of effects is also possible. The environmental stress gradient may lead to functional dispersion for sessile taxa if it weren't for intense competition with algae for space. The non-significant dispersion result may in itself be indicative of abiotic stress release and biotic algal competition having opposing effects of similar magnitude (Kraft et al., 2015). However, further studies would be required to tease apart these effects.

Together, these findings highlight that biotic and abiotic gradients do not have the same effects on all functional groups. They elicit different responses in taxa with different life-history traits. Future work should combine the trait-based surveys with manipulative experiments to test whether the hypothesised cancellation in sessile taxa is potentially true.

Chapter 3
Effects of Predation on Community Assemblages

6.1 INTRODUCTION

Odxel's middle intertidal hosts a sparsely distributed predator and its ubiquitous prey. The predators are *Muricid* sea snails, and the prey species are primarily *Brachidontes* mussels. The keystone predator concept discussed earlier was tested in this system.

Two similar muricid sea snails, *Indothais blanfordi* (Blanford's rock shell) and *Semiricinula tissoti* (Tissot's Rock Shell), were commonly encountered during the study. Both species were restricted to the middle and lower intertidal zones. Throughout the study, 215 individuals were recorded in the lower intertidal, while 42 were recorded in the middle intertidal. *Indothais blanfordi* was approximately 2.7 times more abundant than *Semiricinula tissoti,* making *Indothais* the focal predator. Muricid sea snails are known to feed primarily on mussels and barnacles (Xu et al., 2017), and repeated field observations revealed that *Brachidontes* mussels were their main prey. These predators employ a chemo-mechanical mechanism wherein shell-softening chemicals are secreted onto the prey's shell, after which the radula is used to rasp through the weakened shell and consume the mussel (Lau & Leung, 2004).

Brachidontes (scorched mussel) is a suspension-feeding bivalve, and approximately 80.4% of all recorded individuals occurred in the middle intertidal zone during the study period. It is the dominant space-holding taxa and therefore the most likely candidate for competitive monopolisation in the absence of predators. The community also included another suspension feeder, *Amphibalanus* barnacles, although these occurred at lower densities in the middle intertidal and are usually more common in the upper intertidal. Co-occurring with these are ten types of algae that compete with suspension feeders for space. The algal assemblage also

supported several molluscan grazers, including *Cerithium*, *Siphonaria*, *Clypeomorus*, *Turbo* and *Peronia.* In addition, a few subordinate groups, such as polychaetes, oysters and crabs, were present. Together, these characterise the immediate rocky-shore community associated with *Indothais* and *Brachidontes* (Figure 17).

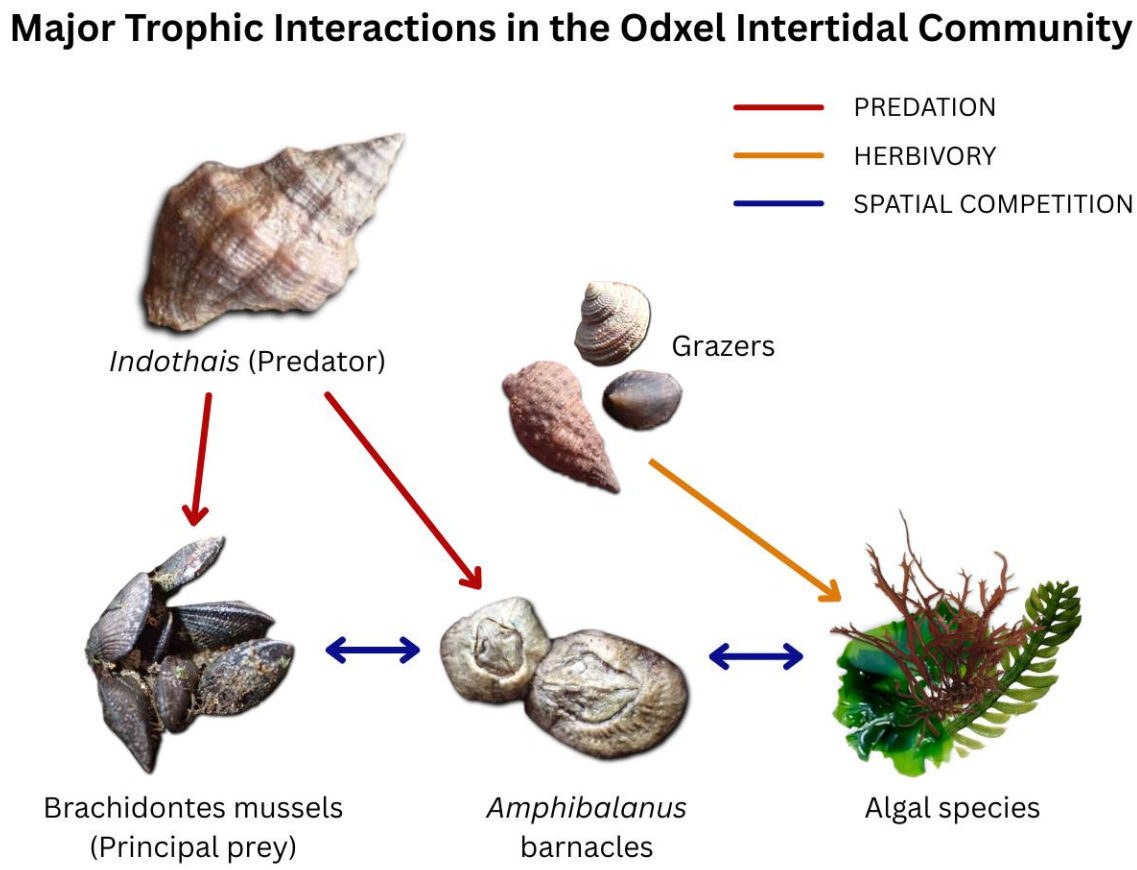


Figure 17 *Conceptual representations of the major trophic interactions within the Odxel rocky intertidal community.*

A collapse of the above-mentioned community is expected following predator exclusion. The mechanisms underlying this collapse are the monopolisation of space by mussels, which would reduce the availability of substrate for algal taxa. As algal abundance declines, the grazers that depend on these resources are also expected to decrease. Over longer timescales, this could result in a simplified community dominated by suspension-feeding mussels. However, given the time scale of this study, a complete collapse is not expected. This is because peak recruitment of *Brachidontes* occurs during and after the south-west monsoons,

and mussel growth then takes almost a year to grow to perceivable sizes (Rajagopal et al., 2006), limiting the extent to which mussel dominance can develop within the study period. Instead, an effect on the primary prey species is anticipated, potentially accompanied by declines in algal taxa.

The experiment tests whether predator exclusion initiates the trajectory towards competitive dominance predicted by Paine (1966, 1974) for temperate shores, within a tropical intertidal system where stronger biotic interactions and greater functional redundancy may alter the trajectory.

6.2 METHODS

6.2.1 Field methods

For this chapter, manipulative experiments were conducted at a single rocky intertidal site from 24th March 2026 to 4th June 2026. This was undertaken at a single site due to logistical constraints. Among several suitable locations, Odxel was chosen due to its proximity to a fishing village with a cooperative local community and relatively low levels of tourism pressure. A secondary survey identified the middle intertidal zone as the experimental area because it supported a good population of *Indothais* snails and extensive *Brachidontes* mussel beds with a diverse assemblage of algae and grazing gastropods. Six experimental units were placed in the middle intertidal zone, each consisting of a treatment plot, a procedural control, and an open control plot (Menge, 1976; Miller & Gaylord, 2007). Plot descriptions are as follows:

Treatment plot: This was a 25 × 25 × 10 cm stainless steel (grade 304) predator-exclusion cage with a 5 cm skirt anchored to the substrate using screws, aluminium bands, and washers. A 1 × 1 cm mesh size excluded adult and most juvenile predatory gastropods while allowing access

to grazing gastropods and most small fish. The cage included an opening flap for sampling, which was sealed with zip ties afterwards (Figure 18 a).

Control plot: This was an open, unmanipulated 25 × 25 cm area. It was marked with stainless steel nails at the corners and sampled using a quadrat of the same size. This served as the baseline for experimentation (Figure 18 b).

Procedural control plot: A partial cage was used that was identical in size and material but had two 15 × 4 cm openings at the base on opposite sides, allowing predator movement while retaining cage-related effects such as shading and altered water flow (Carroll et al., 2015). This allowed the effects of caging artefacts to be separated from predator exclusion (Figure 18 c).

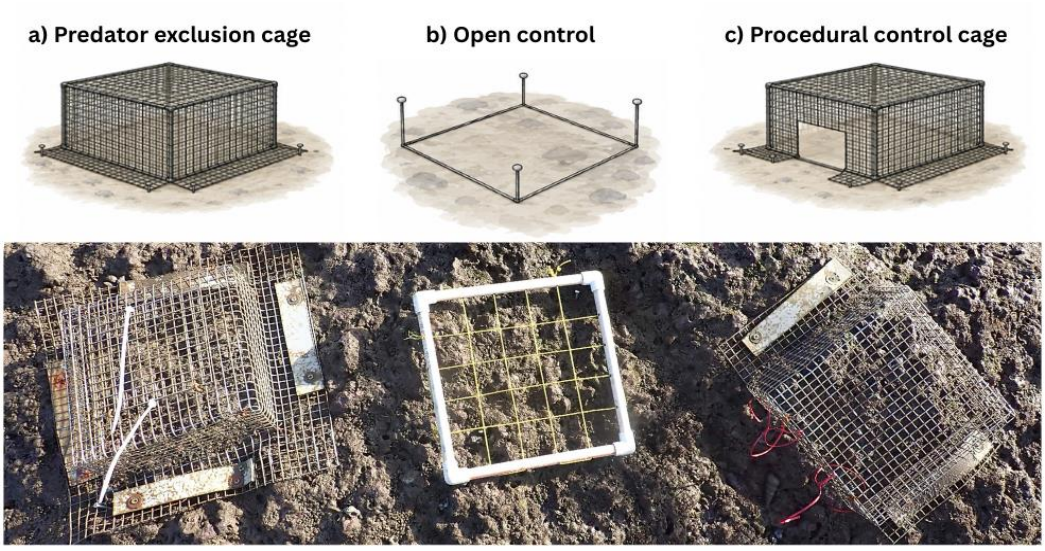


Figure 18 *Schematic representation of the treatments used in the predator exclusion experiment.*

Plots within each experimental unit were spaced sufficiently to minimise spillover effects while avoiding the introduction of confounding factors. All experimental units were located within the middle intertidal and served as spatial replicates. Cages were cleaned regularly to prevent biofouling, and any opportunistic predatory gastropod that entered treatment plots was removed. Sampling was conducted during low tide conditions (<0.4 m) using the same protocol described for Chapter 1.

6.2.2 Analytical methods

To test whether procedural control cages affected community structure, procedural controls and open controls were first compared before assessing predator exclusion effects. Presence-absence data were combined into a single matrix, aggregated by experimental unit, sampling replicate, treatment and genus, and analysed using Jaccard dissimilarity. Differences in composition were tested using PERMANOVA with 9999 permutations, with experimental unit identity set as a permutation stratum. Dispersion was checked using PERMDISP. The difference in key prey species, *Brachidontes,* was also assessed between control and procedural controls. A negative binomial GLMM was used with treatment, replicate, and their interactions as fixed effects, while experimental unit identity was a random effect. After confirming that the cage artefact was not altering community composition meaningfully, predator exclusion effects were assessed by comparing exclusion and open control plots using the same PERMANOVA framework. Subsequently, *Brachidontes'* response to predator exclusion was quantified using a log response ratio (LRR) calculated for each experimental unit and sampling replicate.

$$LRR = \ln\left(\frac{Brachidontes\ abundance\ in\ Predator\ Exclusion\ plot}{Brachidontes\ abundance\ in\ Control\ plot}\right)$$

Mean LRR values calculated across experimental units for each sampling unit were then plotted through time. Temporal trends in LRR were analysed using a linear mixed model. Finally, algal cover was analysed using a similarly computed LRR ratio and changes in overall richness were analysed using a linear mixed model with experimental unit ID as a random effect.

6.3 RESULTS

Differences in community composition of procedural control and control plots through time were assessed so as to test for cage artefacts. A PERMANOVA revealed a non-significant

interaction between these treatments and time ($F = 1.70$, $R^2 = 0.0238$, $p = 0.052$), indicating that communities in these plots did not differ through time. Additionally, a negative binomial mixed-model showed no difference in temporal trajectories of *Brachidontes* between the procedural control and control ($\chi^2 = 0.20$, $p = 0.655$). Although both treatments showed a decline in abundance through time ($\chi^2 = 63.05$, $p < 0.001$), the rate of decline was similar (Figure 19). Overall, these analyses attested that the cage did not produce any meaningful procedural artefacts, as a consequence of which open controls were taken as baselines for evaluating the effects of predator exclusion.

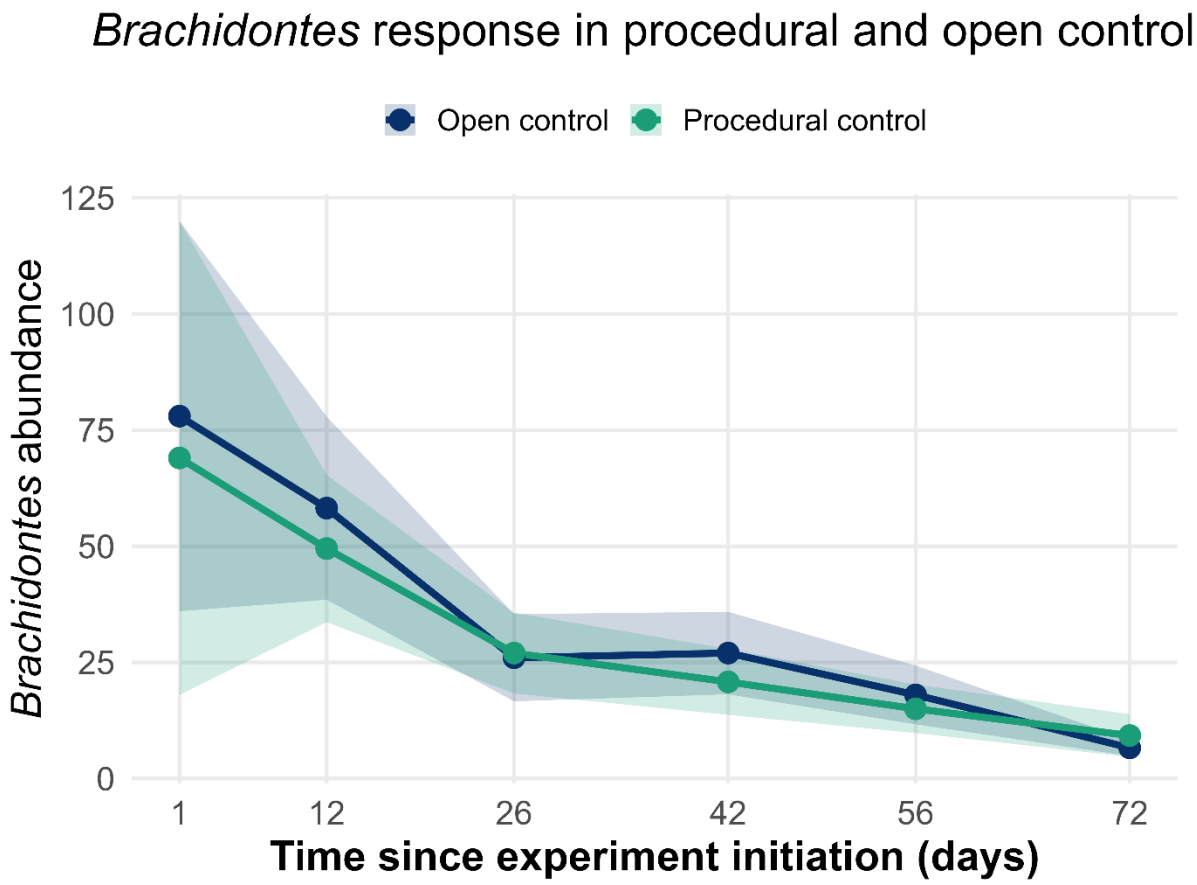


Figure 19 *Brachidontes abundances for procedural and open control plotted against time since experiment initiation. Shaded areas represent ±1 SE.*

Subsequently, log response ratios were analysed using a linear mixed model with sampling replicate number as a fixed effect and experimental unit ID as a random effect. A significant positive effect of sampling replicate on LRR was observed ($\beta = 0.298 \pm 0.070$ SE,

F = 18.34, p < 0.001). This analysis revealed that *Brachidontes* mussel abundance in exclusion plots increased relative to open controls over the course of the experiment (Figure 20).

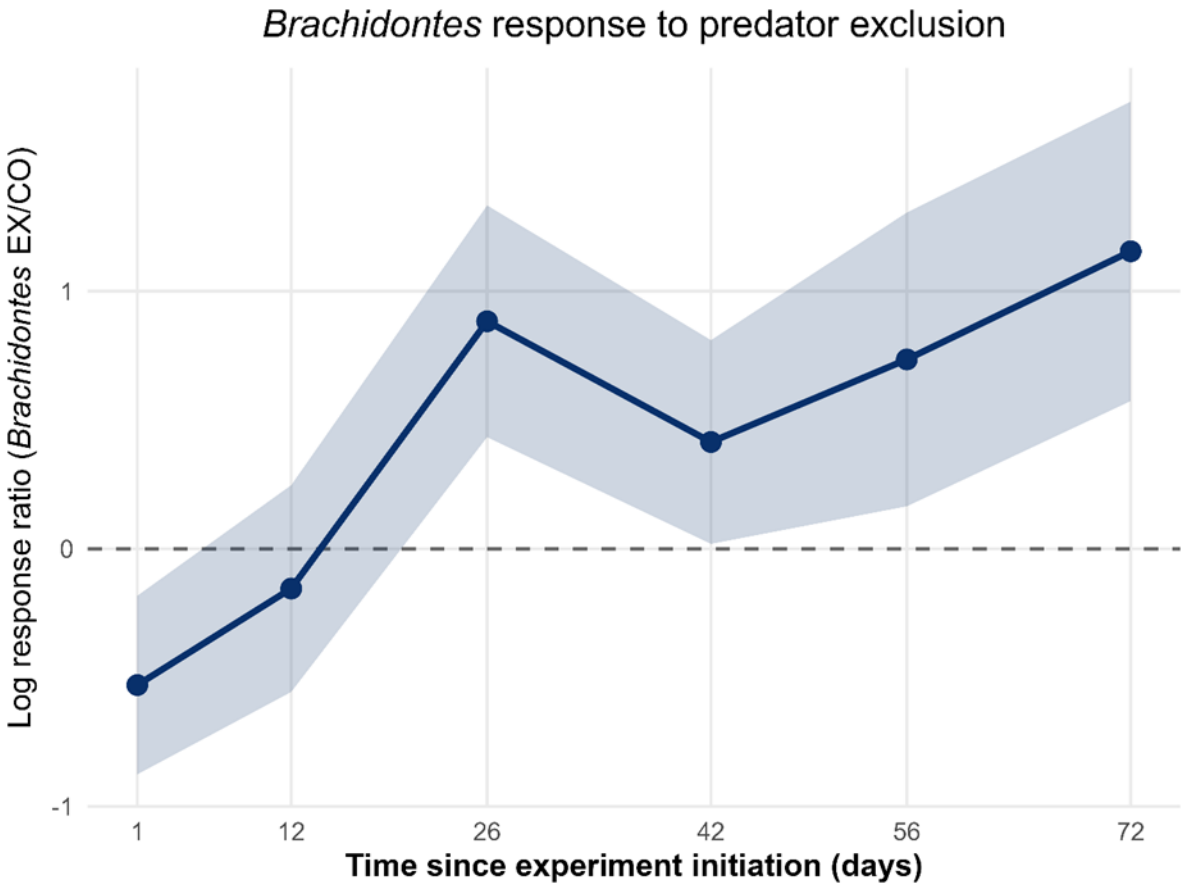


Figure 20 *Brachidontes LRR calculated using exclusion/control values plotted against time since experiment initiation. Shaded areas represent ±1 SE.*

Building on this, predator exclusion produced a significant change in overall community composition relative to open control plots (PERMANOVA: F = 4.749, R^2 = 0.1919, p < 0.001). As *Brachidontes'* LRR values showed an increase, a linear mixed model was used to examine whether co-occurring algal taxa showed a decrease in their LRR values through time. No significant association was found in the case of algae (p = 0.174). Additionally, the response of taxonomic richness to predator exclusion was tested. Richness showed no significant difference between treatments through time (p = 0.113).

To investigate the mechanisms underlying the observed effects of predator exclusion, further analysis was conducted. *Brachidontes* abundance declines across both treatments, though the decline was steeper in control plots (Figure 21).

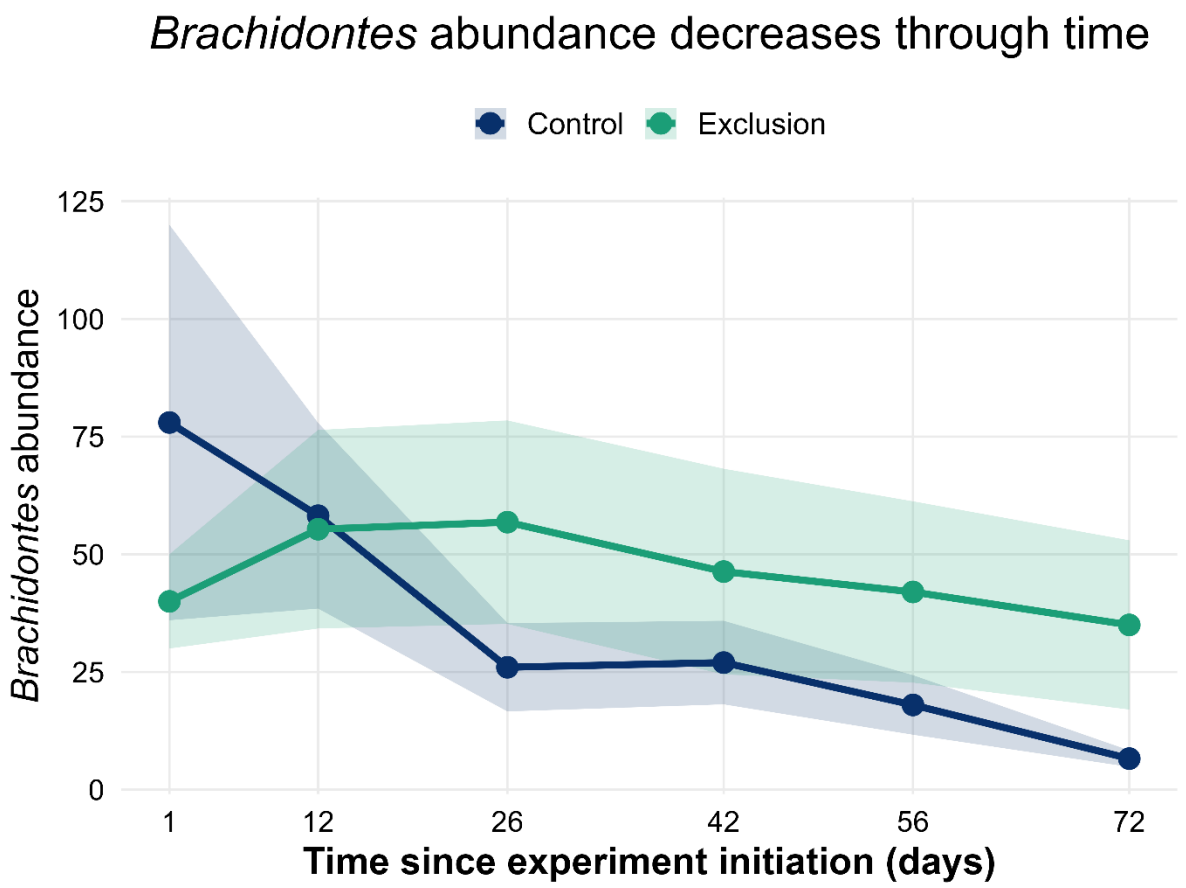


Figure 21 *Brachidontes raw abundances plotted against time from experiment initiation for exclusion and control plots. Shaded areas represent ±1 SE.*

To test whether this pattern was seasonal or mediated by higher *Indothais* abundances over time, a negative binomial mixed model was used. The model used the community dataset from chapters 1 and 2, with sampling replicate as a fixed effect and site/transect as a random effect, with *Indothais*/*Brachidontes* abundances as the response variable. Both showed weak non-significant decrease over time.

Overall, these results show that cage artefacts did not confound the experiment and that open controls served as appropriate baselines. Predator exclusion produced a clear shift in

community composition and a strong effect on the principal prey species' abundance. In contrast, algal taxa and overall richness showed no treatment-driven changes.

6.4 DISCUSSION

Predation was a dominant ecological force shaping the communities of the rocky intertidal ecosystem studied. In the absence of predators, the focal prey species showed decreased mortality; however, a clear increase in abundance wasn't seen. In addition, as the monsoon approached, *Brachidontes* abundances declined steadily in control plots, while only a slight decline was observed in predator-exclusion plots.

This pattern may reflect a combination of seasonal changes in the prey abundance and predator feeding ecology. *Brachidontes* mussels are known to exhibit narrow tolerance limits to fluctuations in temperature and salinity (Astudillo et al., 2017). Other species in the same genus have also shown a decline in abundance during summer temperature spikes (Alhassan, 2025). Similar responses have been reported for other mussel taxa, including blue mussels, which are highly sensitive to seasonal variation (Carrington, 2002) and may even experience mass mortalities. Comparable patterns have also been observed in the Mediterranean mussels (Bracchetti et al., 2024). Some studies have further shown that mussels can shift their reproductive efforts in anticipation of seasonal stress or mortality (Zając & Zając, 2025).

These seasonal effects were likely compounded by predator activity. *Indothais* and other muricid species are known to target physiologically stressed prey. Environmental stressors can force mussels to reallocate energy away from defence, reducing their ability to maintain anti-predator responses (Manríquez et al., 2021). This can cause altered shell composition and weaken byssal attachment (Shen et al., 2026). Consequently, predatory gastropods tend to prefer physiologically stressed prey individuals because they require less handling time and lower effort to drill through the shell (Gestoso et al., 2015).

Together, these factors corroborate the patterns observed in the experiment. The decline in *Brachidontes* abundance likely reflects both rising temperatures and the approaching southwest monsoon. In addition, the stronger decline in control plots suggests an added effect of predation on already stressed individuals. Both treatment and control plots showed declining mussel abundances, but the effect was more pronounced in the control plots.

Although the community as a whole changed in the absence of predators, algal taxa did not exhibit the predicted decline. This outcome could be ascribed to two causes. Firstly, the 72-day study period was too short for *Brachidontes* mussels to monopolise space and produce a substantial indirect effect on algal cover. Even though mussels show constant recruitment throughout the year, their settlement peaks towards the end of the south-west monsoon. After which *Brachidontes* mussels take 30 to 49 days to grow to an observable size (Rajagopal et al., 2006). A longer study would therefore be needed to detect any delayed effects on the mussel expansion on algal taxa. Secondly, the algal taxa were measured as per cent cover within 5 × 5 cm subsections of the quadrat, whereas *Brachidontes* abundances were recorded as counts. Hence, the algal covers were quantified at too coarse a resolution for meaningful comparison between the two groups.

Indothais had a strong effect on its immediate prey species, but did not produce community-level changes consistent with those expected of a keystone species. Given the study period, the role of functional redundancy in Goa's tropical intertidal communities could not be assessed. Even so, predation appears to be an important biotic interaction in this system and may be stronger than in temperate intertidal communities. Similar studies in temperate areas showed little or no community change even after more than seven months (Menge, 1976, 1978), whereas this study recorded a change in community composition within three months of predator removal. This could indicate genuinely strong predation intensity, but it may also

reflect the seasonal decline of mussels on tropical shores, which could have amplified the apparent effect of predator removal.

In conclusion, although predatory interactions strongly shaped the intertidal communities, monopolisation was not observed, and the keystone predation hypothesis could not be tested. Longer predator exclusion experiments are required to assess whether functional redundancy and stronger biotic interactions play a role in tropical intertidal ecosystems, and whether muricid gastropods in Goa function as a keystone predator. Ideally, a multi-year dataset would answer these questions conclusively, as suggested by Menge (1976). This study provides a methodological framework for exclusion experiments under tropical shore conditions and may serve as a baseline for future research into predator-prey interactions in Indian intertidal ecosystems.

CONCLUSION

The study set out to determine the drivers of community assemblages in Goa's rocky intertidal ecosystem. A system that remains mechanistically underexplored despite India's extensive coastline. The influence of environmental stress, functional trait assemblages, and top-down predation on the community structure of this ecosystem was examined. Collectively, the three chapters demonstrate that the environmental stress gradient is the key determinant of community assemblages. This was broadly consistent with the predictions of Menge & Sutherland's (1987) environmental stress model.

Chapter 1 demonstrated that community composition and structure shift along the environmental stress gradient, with the upper intertidal representing a nested subset of the taxa found in the lower zones and taxon replacement driving the middle-lower zonal dissimilarities. Within these zones, each with its stress regimes, finer-scale habitat characteristics further mediate community structure. These include sand cover and wave action. The complexity of the substrate increased taxa richness throughout the intertidal, irrespective of zonation. Thus, the drivers of community assemblages were found to be a hierarchical structure, wherein broad-scale abiotic stressors dictate which species can persist, while local habitat characteristics determine how taxa are distributed within each stress regime. Chapter 2 examines the same gradient through a functional trait-based approach. The stress gradient mediates functional responses in animals depending on fundamental differences in their life histories. Motile taxa showed significant functional dispersion in algae-rich zones, possibly due to increased food resources and spatial niches. This was consistent with Bruno et al.'s (2003) newer facilitation-based stress model, as well as the trophic increase predicted by Menge & Sutherland (1987) at lower stress levels. In contrast, sessile taxa showed a significant functional shift along the stress gradient. Contrary to expectations, the increase in algal cover did not elicit functional

convergence; instead, it had no effect. This may indicate a simultaneous opposing force between stress release and competitive pressures from algae, effectively cancelling out their effects. Chapter 3 tested the influence of top-down interactions on the community assemblages. A strong effect of the muricid predators on their principal prey, *Brachidontes* mussels, was found. The prey species showed a slight decline in the absence of predators, while a steeper decline was observed in the unmanipulated plots due to the combined effects of seasonal change and predation pressure. Predator removal also significantly altered community composition at a shorter timescale than similar experiments conducted along temperate shores. This is tentatively consistent with the idea that biotic interactions are stronger in tropical regions.

Several limitations affect how these findings can be interpreted. The dataset for chapters 1 and 2 spanned three environmentally similar sites and two seasons (winter and summer), while that for Chapter 3 covered one site and 72 days. Additionally, all sites were sheltered and lateritic, without any representation of exposed basaltic sites. This design, while intensive, compromises on generalisability. Additionally, taxa could only be identified to the genus level, and a morphospecies approach was resorted to when identification was not possible. This may have resulted in a slight overestimation of community structure by separating congeneric individuals into multiple morphospecies. Functional traits were also assessed using categorical classifications rather than continuous quantitative measures due to data unavailability. The abiotic variables were ocular estimates rather than quantitative measurements, which limited the resolution needed to tease apart finer-scale variations. The use of Wisconsin double-standardised data did not preserve evenness data very well, making it unsuitable for analysing evenness patterns. Moreover, the functional analysis did not control for the confounding effect of phylogenies, making it difficult to distinguish between the effects of ecological processes and those of shared evolutionary history. Lastly, within the experimental setup, the algal taxa

were quantified at too coarse a resolution. Quantification at higher resolutions would have allowed the detection of the monopolisation signal if it existed. Collectively, these constraints mean that the findings are best interpreted as an ecological baseline rather than a definitive characterisation of Indian intertidal community dynamics.

Nevertheless, the study makes several contributions. It provides ecological information for a predator exclusion experiment conducted along a tropical Indian shoreline. The differential functioning responses for motile and sessile taxa to the biotic gradient, which test facilitation and filtering, represent a distinction that, to the best of my knowledge, has not been explicitly examined in a tropical intertidal ecosystem. The coherence of the studies' results with temperate intertidal ecosystems shows that the basic mechanistic framework that structures communities is generalisable to a tropical system. Furthermore, much like temperate shores, Indian intertidal ecosystems can serve as natural laboratories for testing ecological theory. Future work should prioritise a larger spatial and temporal scale to improve the generalizability of results. Based on this study, the effects of the environmental stress gradient across shores with variable exposure levels and substrate composition should be tested. Furthermore, manipulative experiments should be undertaken to tease apart the effects of environmental and biotic gradients on the functional responses of sessile animals. Additionally, the keystone predation concept should be tested in light of stronger biotic interactions and higher functional redundancy. The present study provides an ecological foundation and methodological framework from which these questions can now be pursued.

REFERENCES

Abrams, P. A. (1993). Effect of increased productivity on the abundances of trophic levels. *The American Naturalist*, *141*(3), 351-371.

Agadi, V. V., & Untawale, A. G. (1978). Marine algal flora of Goa coast. *Seaweed Res Util*.

Airoldi, L. (2003). The effects of sedimentation on rocky coast assemblages. In *Oceanography and Marine Biology* (pp. 169-171). CRC Press.

Al Usmani, S. M. P., & Ansari, Z. A. (2020). Status of coastal marine biodiversity of Goa and challenges for sustainable Management-An overview. Journal of Ecophysiology and Occupational Health, 20(3&4), 222-231.

Alhassan, M. (2025). *Resilience and Responses of the Invasive Mussel Brachidontes pharaonis to Combined Temperature and Pollution Stress: Implications for Physiology, Microbiome, and Contaminant Bioaccumulation in the Mediterranean Sea* (Master's thesis, University of Haifa (Israel)).

Apte, D. (2012). *Field guide to the marine life of India*. Deepak Apte & Animesh Apte.

Astudillo, J. C., Bonebrake, T. C., & Leung, K. M. (2017). The recently introduced bivalve Xenostrobus securis has higher thermal and salinity tolerance than the native Brachidontes variabilis and established Mytilopsis sallei. *Marine Pollution Bulletin*, *118*(1-2), 229-236.

Bauer, B., Kleyer, M., Albach, D. C., Blasius, B., Brose, U., Ferreira-Arruda, T., ... & Hillebrand, H. (2021). Functional trait dimensions of trophic metacommunities. *Ecography*, *44*(10), 1486-1500.

Beauchard, O., Mestdagh, S., Koop, L., Ysebaert, T., & Herman, P. M. (2022). Benthic synecology in a soft sediment shelf: habitat contrasts and assembly rules of life strategies. *Marine Ecology Progress Series*, *682*, 31-50.

Bernard-Verdier, M., Navas, M. L., Vellend, M., Violle, C., Fayolle, A., & Garnier, E. (2012). Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a M editerranean rangeland. *Journal of ecology*, *100*(6), 1422-1433.

Bertness, M. D. (1981). Predation, physical stress, and the organization of a tropical rocky intertidal hermit crab community. *Ecology*, *62*(2), 411-425.

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in ecology & evolution*, *9*(5), 191-193

Bertness, M. D., & Ellison, A. M. (1987). Determinants of pattern in a New England salt marsh plant community. *Ecological monographs*, *57*(2), 129-147.

Bertness, M. D., & Leonard, G. H. (1997). The role of positive interactions in communities: lessons from intertidal habitats. *Ecology*, *78*(7), 1976-1989.

Bertness, M. D., Leonard, G. H., Levine, J. M., Schmidt, P. R., & Ingraham, A. O. (1999). Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology*, *80*(8), 2711-2726.

Bertness, M.D., Gaines, S.D. & Hay, M.E. (1999). Marine Community Ecology

Boaden, A. E., & Kingsford, M. J. (2015). Predators drive community structure in coral reef fish assemblages. *Ecosphere*, *6*(4), 1-33.

Boet, O., Arnan, X., & Retana, J. (2020). The role of environmental vs. biotic filtering in the structure of European ant communities: A matter of trait type and spatial scale. *PloS one*, *15*(2), e0228625.

Bracchetti, L., Capriotti, M., Fazzini, M., Cocci, P., & Palermo, F. A. (2024). Mass mortality event of Mediterranean mussels (Mytilus galloprovincialis) in the middle Adriatic: potential implications of the climate crisis for marine ecosystems. *Diversity*, *16*(3), 130.0

Brind'Amour, A., Laffargue, P., Morin, J., Vaz, S., Foveau, A., & Le Bris, H. (2014). Morphospecies and taxonomic sufficiency of benthic megafauna in scientific bottom trawl surveys. *Continental Shelf Research*, *72*, 1-9.

Brown, J. H. (2014). Why are there so many species in the tropics?. Journal of biogeography, 41(1), 8-22.

Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in ecology & evolution*, *18*(3), 119-125.

Carrington, E. (2002). Seasonal variation in the attachment strength of blue mussels: causes and consequences. *Limnology and Oceanography*, *47*(6), 1723-1733.

Carroll, J. M., Marion, J. P., & Finelli, C. M. (2015). A field test of the effects of mesopredators and landscape setting on juvenile oyster, Crassostrea virginica, consumption on intertidal reefs. *Marine Biology*, *162*(5), 993-1003.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*, *31*(1), 343-366.

Chevene, F., Doleadec, S., & Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater biology*, *31*(3), 295-309.

Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. *Ecology*, 710-723.

Connell, J. H. (1972). Community interactions on marine rocky intertidal shores. *Annual review of ecology and systematics*, 169-192.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state. *Science*, *199*(4335), 1302-1310.

Cornwell, W. K., Schwilk, D. W., & Ackerly, D. D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology*, *87*(6), 1465-1471.

Daniel, A. 1955a. Gregarious attraction as a factor influencing the settlement of barnacle cyprids. Ibid., 25 B : 97-107.

D'Antonio, C. M. (1986). Role of sand in the domination of hard substrata by the intertidal alga Rhodomela larix. *Marine Ecology Progress Series*, 263-275.

Dayton, P. K. (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological monographs*, *41*(4), 351-389.

Denny, M. (1988). *Biology and the mechanics of the wave-swept environment*. Princeton University Press.

Dolédec, S., Chessel, D., Ter Braak, C. J., & Champely, S. (1996). Matching species traits to environmental variables: a new three-table ordination method. *Environmental and ecological statistics*, *3*(2), 143-166.

Dray, S., & Dufour, A. B. (2007). The ade4 package: implementing the duality diagram for ecologists. *Journal of statistical software*, *22*, 1-20.

Dray, S., & Legendre, P. (2008). Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology*, *89*(12), 3400-3412.

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., & ter Braak, C. J. (2014). Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology*, *95*(1), 14-21

Eckersley, L. K., & Scrosati, R. A. (2012). Temperature, desiccation, and species performance trends along an intertidal elevation gradient. *Current Development in Oceanography*, *5*, 59-73.

Emery, N. C., Ewanchuk, P. J., & Bertness, M. D. (2001). Competition and salt-marsh plant zonation: stress tolerators may be dominant competitors. *Ecology*, *82*(9), 2471-2485.

Fattorini, M., & Halle, S. (2004). The dynamic environmental filter model: how do filtering effects change in assembling communities after disturbance. *Assembly rules and restoration ecology: Bridging the gap between theory and practice*, 96-114.

Flores, A. A., Christofoletti, R. A., Peres, A. L. F., Ciotti, A. M., & Navarrete, S. A. (2015). Interactive effects of grazing and environmental stress on macroalgal biomass in subtropical rocky shores: Modulation of bottom-up inputs by wave action. *Journal of Experimental Marine Biology and Ecology*, *463*, 39-48.

Freestone, A. L., Ruiz, G. M., & Torchin, M. E. (2013). Stronger biotic resistance in tropics relative to temperate zone: effects of predation on marine invasion dynamics. *Ecology*, *94*(6), 1370-1377.

Ganapati, P. N., & Rao, G. C. (1962). Ecology of the interstitial fauna inhabiting the sandy beaches of Waltair coast. J. mar. biol. Ass. India, 4, 44-57.

Gestoso, I., Arenas, F., & Olabarria, C. (2015). Feeding behaviour of an intertidal snail: Does past environmental stress affect predator choices and prey vulnerability?. *Journal of Sea Research*, *97*, 66-74.

Gibson, R. N. (1982). Recent studies on the biology of intertidal fishes. *Oceanography and marine biology: an annual review*, *20*, 902.

Gonor, J. J., & Kemp, P. F. (1978). *Procedures for quantitative ecological assessments in intertidal environments*. Environmental Protection Agency, Office of Research and Development, Corvallis Environmental Research Laboratory.

Gotelli, N. J. (2000). Null model analysis of species co-occurrence patterns. *Ecology*, *81*(9), 2606-2621.

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, 857-871.

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The american naturalist*, *111*(982), 1169-1194.

Grime, J. P. (1979, November). Primary strategies in plants. In *Transactions of the Botanical Society of Edinburgh* (Vol. 43, No. 2, pp. 151-160). Taylor & Francis Group.

Guiry, M. D., & Guiry, G. M. (2026). *AlgaeBase*. World-wide electronic publication, University of Galway. https://www.algaebase.org

Gusha, N. M., & Mcquaid, C. D. (2025). Traits without boundaries: The environmental influence on biological traits across an intertidal region. *Journal of Sea Research*, *203*, 102559.

Han, G. D., Cartwright, S. R., Ganmanee, M., Chan, B. K., Adzis, K. A., Hutchinson, N., ... & Dong, Y. W. (2019). High thermal stress responses of Echinolittorina snails at their range edge predict population vulnerability to future warming. *Science of the Total Environment*, *647*, 763-771.

Heaven, C. S., & Scrosati, R. A. (2008). Benthic community composition across gradients of intertidal elevation, wave action, and ice scour in Atlantic Canada. *Marine Ecology Progress Series*, *369*, 13-23.

Helmuth, B. S., & Hofmann, G. E. (2001). Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. *The Biological Bulletin*, *201*(3), 374-384.

Hill, M. O., & Smith, A. J. E. (1976). Principal component analysis of taxonomic data with multi-state discrete characters. *Taxon*, 249-255.

Huey, R. B., Carlson, M., Crozier, L., Frazier, M., Hamilton, H., Harley, C., ... & Kingsolver, J. G. (2002). Plants versus animals: do they deal with stress in different ways?. *Integrative and Comparative Biology*, *42*(3), 415-423.

iNaturalist. (n.d.). *Home*. Retrieved January–May 2026, from inaturalist.org

Jackson, J. B. (1977). Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *The American Naturalist*, *111*(980), 743-767.

Jenkins, S. R., Marshall, D., & Fraschetti, S. (2009). Settlement and recruitment. In *Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change* (pp. 177-190). Berlin, Heidelberg: Springer Berlin Heidelberg.

Jha, B., Reddy, C. R. K., Thakur, M. C., & Rao, M. U. (2009). *Seaweeds of India: The diversity and distribution of seaweeds of the Gujarat coast*. Dordrecht: Springer Netherlands.

Jonsson, P. R., Granhag, L., Moschella, P. S., Åberg, P., Hawkins, S. J., & Thompson, R. C. (2006). Interactions between wave action and grazing control the distribution of intertidal macroalgae. *Ecology*, *87*(5), 1169-1178.

Kohn, A. J., & Leviten, P. J. (1976). Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. *Oecologia*, *25*(3), 199-210.

Kraft, N. J., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional ecology*, *29*(5), 592-599.

Kraufvelin, P. (2007). Responses to nutrient enrichment, wave action and disturbance in rocky shore communities. *Aquatic Botany*, *87*(4), 262-274.

Krebs CJ (1999) Ecological methodology. Benjamin Cummings, Menlo Park, CA

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*(1), 299-305.

Lau, D. C., & Leung, K. M. (2004). Feeding physiology of the carnivorous gastropod Thais clavigera (Kuster): do they eat “soup”?. *Journal of Experimental Marine Biology and Ecology*, *312*(1), 43-66.

Legendre, P., Galzin, R., & Harmelin-Vivien, M. L. (1997). Relating behavior to habitat: solutions to thefourth-corner problem. *Ecology*, *78*(2), 547-562.

Littler, M. M., Martz, D. R., & Littler, D. S. (1983). Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. *Marine ecology progress series*, *11*, 129-139.taylor

Loke, L. H., & Todd, P. A. (2016). Structural complexity and component type increase intertidal biodiversity independently of area. *Ecology*, *97*(2), 383-393.

Luckens, P. A. (1970). Breeding, settlement and survival of barnacles at artificially modified shore levels at Leigh, New Zealand. *New Zealand journal of marine and freshwater research*, *4*(4), 497-514.

MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The american naturalist*, *101*(921), 377-385.

Manríquez, P. H., Jara, M. E., González, C. P., Seguel, M. E., Domenici, P., Watson, S. A., ... & Brokordt, K. (2021). The combined effects of climate change stressors and predatory cues on a mussel species. *Science of the Total Environment*, *776*, 145916.

Marshall, D. J., Rezende, E. L., Baharuddin, N., Choi, F., & Helmuth, B. (2015). Thermal tolerance and climate warming sensitivity in tropical snails. *Ecology and evolution*, *5*(24), 5905-5919.

McAfee, D., Bishop, M. J., Yu, T. N., & Williams, G. A. (2018). Structural traits dictate abiotic stress amelioration by intertidal oysters. *Functional ecology*, *32*(12), 2666-2677.

McCune, B., & Grace, J. B. (2002). *Analysis of ecological communities*

McGuinness, K. A., & Underwood, A. J. (1986). Habitat structure and the nature of communities on intertidal boulders. *Journal of Experimental Marine Biology and Ecology*, *104*(1-3), 97-123.

McIntire, L. C., & Miller, L. P. (2025). The role of mobility in intertidal invertebrates' responses to thermal stress. *Integrative and Comparative Biology*, *65*(4), 812-821.

Meager, J. J., Schlacher, T. A., & Green, M. (2011). Topographic complexity and landscape temperature patterns create a dynamic habitat structure on a rocky intertidal shore. *Marine Ecology Progress Series*, *428*, 1-12.

Menge, B. A. (1978). Predation intensity in a rocky intertidal community: relation between predator foraging activity and environmental harshness. *Oecologia*, *34*(1), 1-16.

Menge, B. A. (1992). Community regulation: under what conditions are bottom-up factors important on rocky shores?. *Ecology*, *73*(3), 755-765.

Menge, B. A., & Lubchenco, J. (1981). Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecological Monographs*, *51*(4), 429-450.

Menge, B. A., & Olson, A. M. (1990). Role of scale and environmental factors in regulation of community structure. *Trends in Ecology & Evolution*, *5*(2), 52-57.

Menge, B. A., & Sutherland, J. P. (1987). Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist*, *130*(5), 730-757.

Menge, B. A., Daley, B. A., Lubchenco, J., Sanford, E., Dahlhoff, E., Halpin, P. M., ... & Burnaford, J. L. (1999). Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecological monographs*, *69*(3), 297-330.

Menge, B. A., Lubchenco, J., & Ashkenas, L. R. (1985). Diversity, heterogeneity and consumer pressure in a tropical rocky intertidal community. *Oecologia*, *65*(3), 394-405.

Menge, B. A., Lubchenco, J., Ashkenas, L. R., & Ramsey, F. (1986). Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. *Journal of Experimental Marine Biology and Ecology*, *100*(1-3), 225-269.

Menge, B. A., Olson, A. M., & Dahlhoff, E. P. (2002). Environmental stress, bottom-up effects, and community dynamics: integrating molecular-physiological and ecological approaches. *Integrative and Comparative Biology*, *42*(4), 892-908.

Miller, A. W., & Ambrose, R. F. (2000). Sampling patchy distributions: comparison of sampling designs in rocky intertidal habitats. *Marine Ecology Progress Series*, *196*, 1-14.

Miller, L. P., & Gaylord, B. (2007). Barriers to flow: the effects of experimental cage structures on water velocities in high-energy subtidal and intertidal environments. *Journal of Experimental Marine Biology and Ecology*, *344*(2), 215-228.

Mohan Joseph, M. (2007). *Field guide to the common marine molluscs of India*. ICAR-Central Marine Fisheries Research Institute (CMFRI).

Mondy, C. P., & Usseglio-Polatera, P. (2014). Using fuzzy-coded traits to elucidate the non-random role of anthropogenic stress in the functional homogenisation of invertebrate assemblages. *Freshwater Biology*, *59*(3), 584-600.

Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J. E., Bender, M., ... & Bellwood, D. R. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences*, *111*(38), 13757-13762.

Murley, M., Hovey, R. K., & Prince, J. (2024). Temperate intertidal ecosystems are functionally richer but more vulnerable to loss than tropical ecosystems. *Ecology and Evolution*, *14*(12), e70657.

Oksanen, J. (2015). Vegan: community ecology package. *R package version*, *2*, 3.

Oksanen, L., Fretwell, S. D., Arruda, J., & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, *118*(2), 240-261.

Oliver, I., & Beattie, A. J. (1996). Invertebrate morphospecies as surrogates for species: a case study. *Conservation biology*, *10*(1), 99-109.

Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist*, *100*(910), 65-75.

Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, *103*(929), 91-93.pow

Paine, R. T. (1974). Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, *15*(2), 93-120.

Paine, R. T. (1980). Food webs: linkage, interaction strength and community infrastructure. *Journal of animal ecology*, *49*(3), 667-685.

Palanisamy, M., & Yadav, S. K. (2022). *Seaweed flora of Goa coast*. Botanical Survey of India.

Palmer, J. D. (1973). Tidal rhythms: the clock control of the rhythmic physiology of marine organisms. *Biological Reviews*, *48*(3), 377-418.

Patrohay, E., Gradinger, R., Marquardt, M., & Bluhm, B. A. (2022). First trait-based characterization of Arctic ice meiofauna taxa. *Polar Biology*, *45*(12), 1673-1688.

Pavoine, S., Vallet, J., Dufour, A. B., Gachet, S., & Daniel, H. (2009). On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos*, *118*(3), 391-402.

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., ... & Paine, R. T. (1996). Challenges in the quest for keystones: identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *BioScience*, *46*(8), 609-620.

Raffaelli, D. G., & Hawkins, S. J. (1996). *Intertidal ecology*. Springer Science & Business Media.

Raijman-Nagar, L., Goren, L., Shefer, S., & Ilan, M. (2024). Sponge abundance and diversity patterns in the shallow and mesophotic reefs of the northern Red Sea. *Frontiers in Marine Science*, *11*, 1370089.

Raja, B. A. (1959). Studies on the distribution and succession of sedentary organisms of the Madras Harbour. J. Mar. Biol. Assoc. India, 1, 180-197.

Rajagopal, S., Venugopalan, V. P., Van der Velde, G., & Jenner, H. A. (2006). Mussel colonization of a high flow artificial benthic habitat: byssogenesis holds the key. *Marine Environmental Research*, *62*(2), 98-115.

Rajendra, S., Mondal, T., Ghosh, S., & Raghunathan, C. (2026). Evaluating intertidal molluscan assemblages along the Goa coast: Spatial trends in species richness and community structure. *Journal of Asia-Pacific Biodiversity*

Risk MJ. Fish diversity on a coral reef in the Virgin Islands. Atoll Res Bull. 1972; 153: 1-6.

Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M., & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions?. *Annu. Rev. Ecol. Evol. Syst.*, *40*(1), 245-269.

Scrosati, R. A., Knox, A. S., Valdivia, N., & Molis, M. (2011). Species richness and diversity across rocky intertidal elevation gradients in Helgoland: testing predictions from an environmental stress model. *Helgoland Marine Research*, *65*(2), 91-102.

Scrosati, R. A., van Genne, B., Heaven, C. S., & Watt, C. A. (2011). Species richness and diversity in different functional groups across environmental stress gradients: a model for marine rocky shores. *Ecography*, *34*(1), 151-161.

Scrosati, R., & Heaven, C. (2007). Spatial trends in community richness, diversity, and evenness across rocky intertidal environmental stress gradients in eastern Canada. *Marine Ecology Progress Series*, *342*, 1-14.

Shen, H. L., Lu, H., Chen, Z. Y., Wang, Y. Q., Ni, J. Y., & Li, Y. F. (2026). Impact of climate change-induced temperature and salinity fluctuations on mussel byssus production and attachment strength. *Marine Environmental Research*, 107936.

Sonak, S. M. (2017). Marine shells of Goa. *Goa: Springer International Publishing*.

Sousa, W. P. (1979). Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, *60*(6), 1225-1239.

Sousa, W. P. (1984). The role of disturbance in natural communities. *Annual review of ecology and systematics*, *15*, 353-391.

Sousa, W. P., Schroeter, S. C., & Gaines, S. D. (1981). Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. *Oecologia*, *48*(3), 297-307.

Sridharan, B., & Namboothri, N. (2015). Factors affecting distribution of fish within a tidally drained mangrove forest in the Andaman and Nicobar Islands, India. *Wetlands ecology and management*, *23*(5), 909-920.

Stephenson, T. A., & Stephenson, A. (1949). The universal features of zonation between tide-marks on rocky coasts. *The Journal of Ecology*, 289-305.

Swenson, N. G. (2014). *Functional and phylogenetic ecology in R* (Vol. 639). New York: Springer.

Taylor, P. R., & Littler, M. M. (1982). The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced, rocky-intertidal community. *Ecology*, *63*(1), 135-146.

Ter Braak, C. J., Cormont, A., & Dray, S. (2012). Improved testing of species traits–environment relationships in the fourth-corner problem. *Ecology*, *93*(7), 1525-1526.

Tomanek, L., & Helmuth, B. (2002). Physiological ecology of rocky intertidal organisms: a synergy of concepts. *Integrative and Comparative Biology*, *42*(4), 771-775.

Underwood, A. J. (2000). Experimental ecology of rocky intertidal habitats: what are we learning?. *Journal of Experimental Marine Biology and Ecology*, *250*(1-2), 51-76.

Uno, H., Utsumi, S., Morita, K., Kishida, O., Alam, M. K., & Negishi, J. (2025). Hydrological Connectivity and Local Environment Alternately Drive Spatial Structure of Floodplain Aquatic Community Across Seasons. *Ecology and Evolution*, *15*(2), e70880.

Valdivia, N., Scrosati, R. A., Molis, M., & Knox, A. S. (2011). Variation in community structure across vertical intertidal stress gradients: how does it compare with horizontal variation at different scales?. *PLoS One*, *6*(8), e24062.

Valdivia, N., Segovia-Rivera, V., Fica, E., Bonta, C. C., Aguilera, M. A., & Broitman, B. R. (2017). Context-dependent functional dispersion across similar ranges of trait space covered by intertidal rocky shore communities. *Ecology and Evolution*, *7*(6), 1882-1891.

Vermeij, G. J. (1973). Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. *Marine biology*, *20*(4), 319-346.

Viejo, R. M. (2009). Resilience in intertidal rocky shore assemblages across the stress gradient created by emersion times. *Marine Ecology Progress Series*, *390*, 55-65.

Watt, C. A., & Scrosati, R. A. (2013). Regional consistency of intertidal elevation as a mediator of seaweed canopy effects on benthic species richness, diversity, and composition. *Marine Ecology Progress Series*, *491*, 91-99.

WoRMS Editorial Board. (2026). *World Register of Marine Species*. VLIZ. Retrieved [Insert Date of Access], from https://www.marinespecies.org

Xu, X. Y., Yip, K. R., Shin, P. K. S., & Cheung, S. G. (2017). Predator–prey interaction between muricid gastropods and mussels under ocean acidification. *Marine Pollution Bulletin*, *124*(2), 911-916.

Zając, T. A., & Zając, K. (2025). Spawning in a threatened freshwater mussel shifts to earlier dates as a result of increasing summer mortality. *Scientific Reports*, *15*(1), 7733.

Zamprogno, G. C., Fernandes, F. C., & Fernandes, L. L. (2012). Temporal and spatial variation of rocky shores intertidal benthic communities in Southeast Brazil. *Iheringia. Série Zoologia*, *102*, 375-383.

APPENDICES

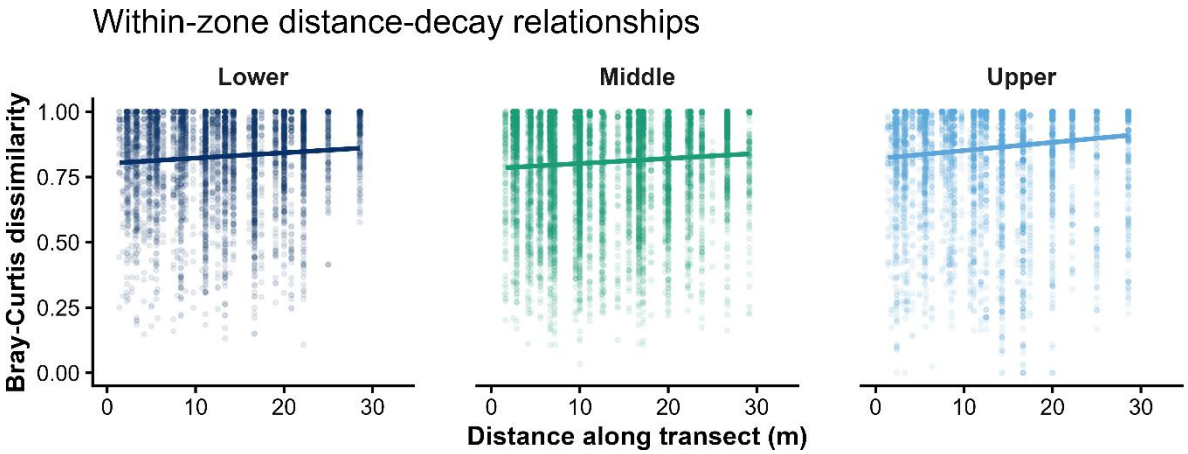
Appendix 1 *Genera/Morphospecies recorded in the rocky intertidal ecosystems of Cacra, Hollant and Siridao, with the study site(s) at which each taxon was observed.*

Sr. No.	Genus	Sites(s) where recorded
1	*Acanthochitona*	Cacra, Siridao
2	*Amphibalanus*	Cacra, Siridao
3	*Anachis*	Cacra, Hollant
4	*Anthopleura*	Cacra, Hollant
5	*Arakawania*	Hollant
6	*Ascidia*	Cacra
7	*Brachidontes*	Cacra, Hollant, Siridao
8	*Bunodosoma*	Cacra
9	*Caloglossa*	Cacra, Hollant, Siridao
10	*Catenella*	Hollant, Siridao
11	*Caulerpa*	Hollant
12	*Cellana*	Cacra, Hollant, Siridao
13	*Celleporina*	Siridao
14	*Centroceras*	Cacra, Hollant
15	*Cerithium*	Cacra, Hollant
16	*Chaetomorpha*	Cacra, Hollant
17	*Champia*	Cacra, Hollant, Siridao
18	*Chondracanthus*	Cacra, Hollant, Siridao
19	*Chthamalus*	Cacra, Hollant, Siridao
20	*Cladophora*	Cacra
21	*Clanculus*	Hollant
22	*Clypeomorus*	Cacra, Hollant, Siridao
23	*Colpomenia*	Cacra, Siridao
24	*Conopeum*	Siridao
25	*Costacallista*	Siridao
26	*Dictyota*	Cacra, Hollant, Siridao
27	*Dysidea*	Hollant
28	*Echinolittorina*	Cacra, Hollant, Siridao
29	*Ectocarpus*	Cacra, Siridao
30	*Engina*	Hollant
31	*Ergalatax*	Hollant
32	*Euchelus*	Cacra, Siridao
33	*Gelidium*	Cacra, Hollant, Siridao
34	*Gyrineum*	Hollant
35	*Haliclona*	Cacra, Hollant
36	*Haloa*	Siridao
37	*Hymeniacidon*	Hollant
38	*Hypnea*	Cacra, Hollant, Siridao
39	*Indothais*	Cacra, Hollant, Siridao
40	*Iyengaria*	Cacra, Siridao

41	*Kappaphycus*	Cacra
42	*Lithophyllum*	Cacra, Hollant
43	*Littoraria*	Cacra, Hollant, Siridao
44	*Lobophora*	Hollant
45	*Mactra*	Siridao
46	*Megabalanus*	Hollant
47	*Nerita*	Cacra, Hollant
48	*Padina*	Cacra, Hollant, Siridao
49	*Palythoa*	Hollant
50	*Perna*	Cacra, Siridao
51	*Peronia*	Cacra, Siridao
52	*Phyllodictyon*	Hollant
53	*Planaxis*	Cacra, Hollant
54	*Pseudoralfsia*	Hollant
55	*Sabellaria*	Hollant
56	*Saccostrea*	Cacra, Hollant, Siridao
57	*Sargassum*	Cacra
58	*Semiricinula*	Cacra, Hollant, Siridao
59	*Siphonaria*	Cacra, Hollant, Siridao
60	*Suberites*	Hollant
61	*Tethya*	Hollant
62	*Timoclea*	Hollant
63	*Trochus*	Hollant
64	*Turbo*	Hollant, Siridao
65	*Ulva*	Cacra, Hollant, Siridao
66	*Zoanthus*	Hollant

Sr. No.	*Morphospecies*	
1	*Green algae 1*	Cacra, Hollant, Siridao
2	*Green algae 2*	Cacra, Hollant, Siridao
3	*Muricid gastropod 1*	Cacra, Hollant
4	*Polychaete 1*	Cacra, Hollant
5	*Polychaete 2*	Cacra, Siridao
6	*Red algae 1*	Cacra, Hollant, Siridao
7	*Red algae 2*	Cacra, Hollant, Siridao
8	*Red algae 3*	Hollant
9	*Red algae 4*	Siridao
10	*Suspension feeder 1*	Cacra, Siridao
11	*Tubeworm 1*	Hollant, Siridao
12	*Tubeworm 2*	Hollant
13	*Vermetid snail 1*	Hollant, Siridao

Appendix 2 *Distance decay plots for each intertidal zone.*



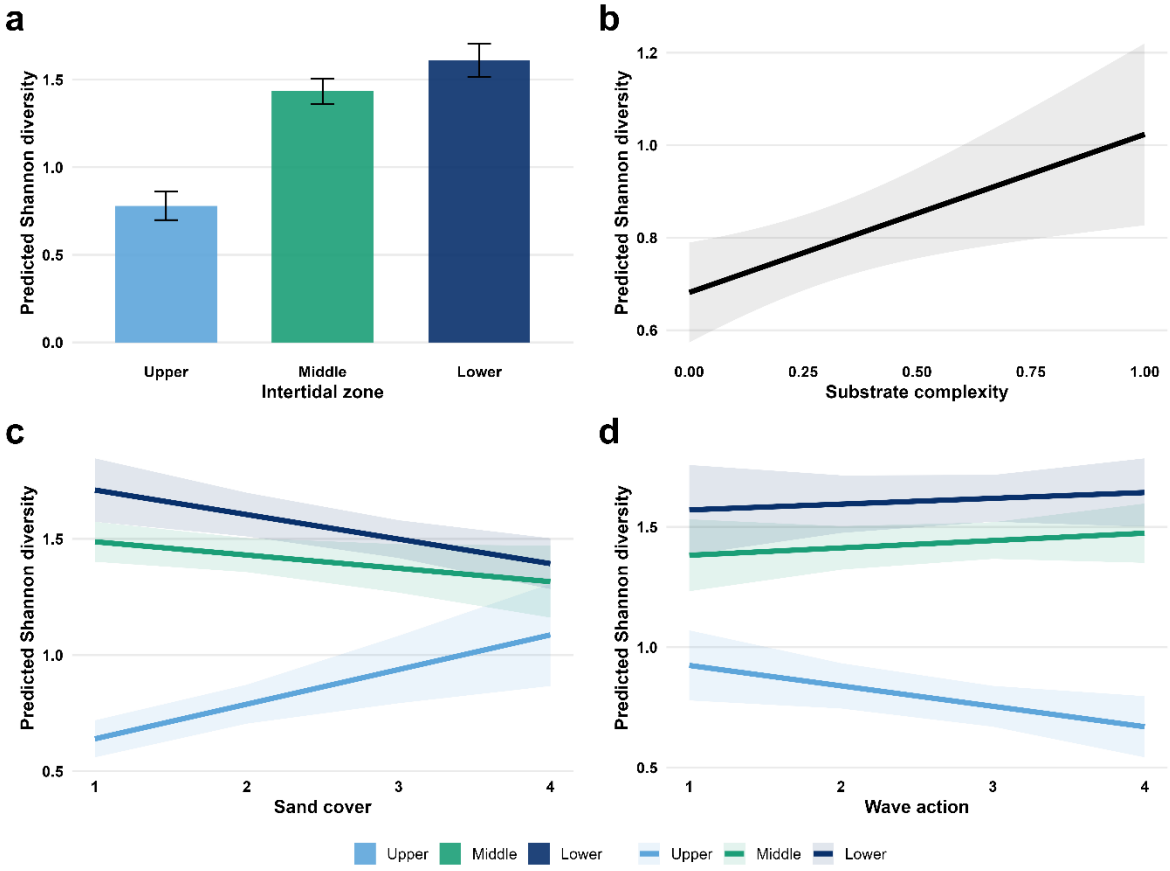
Appendix 3 *Model selection results for candidate GLMs explaining Wisconsin-standardised diversity across the intertidal gradient. Models were ranked using corrected Akaike's Information Criterion (AICc).*

Model	*Predictors*	*df*	*AICc*	*ΔAICc*	*Weight*
SAND–WAVE	Zone × Sand cover + Zone × Wave Action + Substrate complexity	11	501.1	0.00	0.521
SAND	Zone × Sand cover + Wave Action + Substrate complexity	9	502.7	1.54	0.242
GLOBAL	Zone × Sand cover + Zone × Wave Action + Zone × Substrate complexity	13	503.5	2.37	0.159
SAND–COMPLEXITY	Zone × Sand cover + Zone × Substrate complexity + Wave Action	11	504.9	3.80	0.078
WAVE	Zone × Wave Action + Sand cover + Substrate complexity	9	522.2	21.10	<0.001
WAVE–COMPLEXITY	Zone × Wave Action + Zone × Substrate complexity + Sand cover	11	522.4	21.26	<0.001
COMPLEXITY	Zone × Substrate complexity + Sand cover + Wave Action	9	525.9	24.82	<0.001
ADDITIVE	Zone + Sand cover + Wave Action + Substrate complexity	7	526.2	25.04	<0.001
ZONE-ONLY	Zone	4	529.4	28.30	<0.001

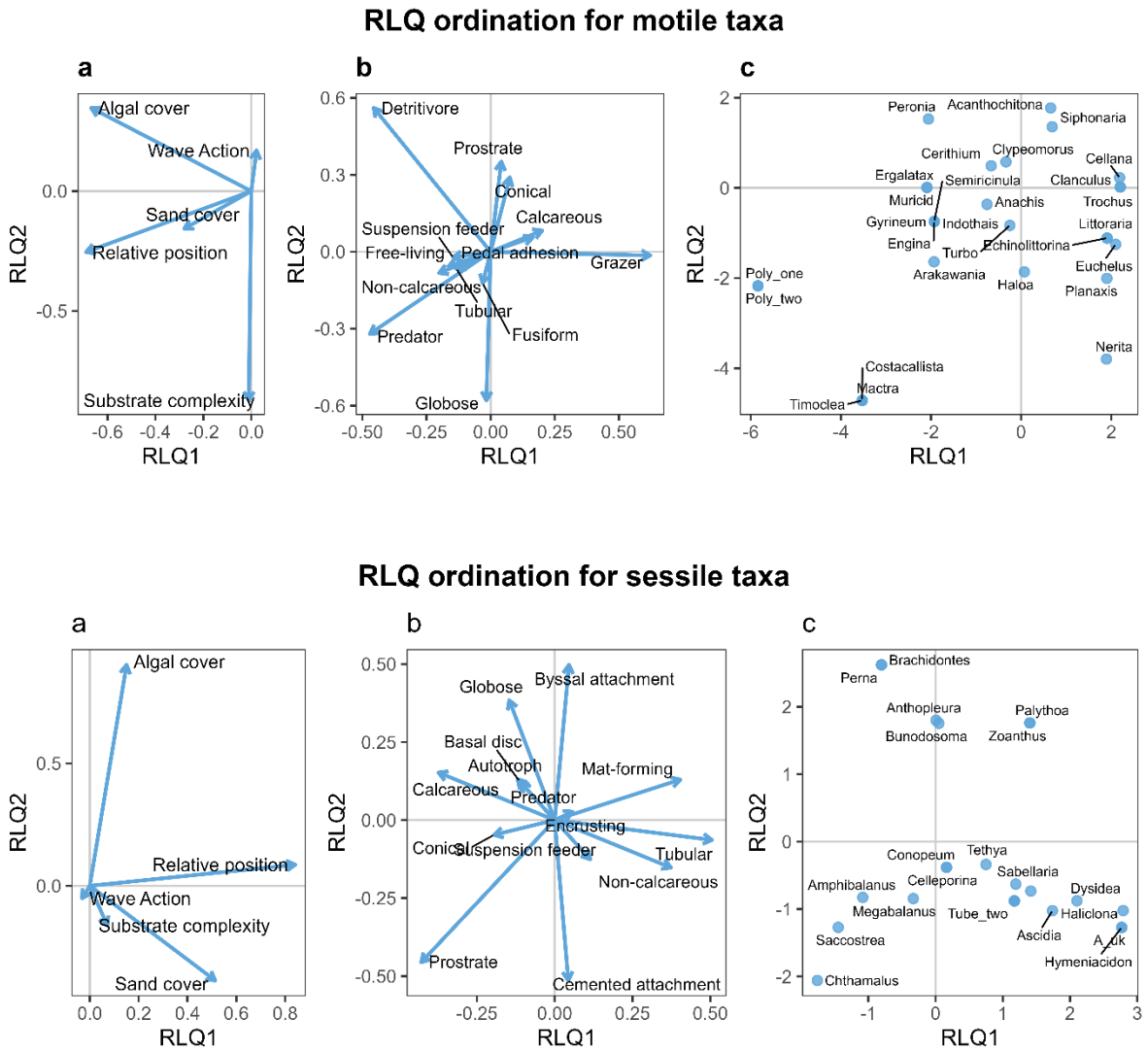
Appendix 4 *Estimates from the selected GLM explaining variation in taxa diversity. Estimates are presented, together with standard errors (SE) and t-statistics.*

Predictor	*Estimate*	*SE*	*t*
Intercept	0.623	0.132	4.731
Zone (Middle)	0.741	0.181	4.105
Zone (Lower)	1.030	0.210	4.910
Sand cover	0.149	0.042	3.592
Wave action	-0.085	0.037	-2.289
Substrate complexity	0.342	0.128	2.681
Zone (Middle) × Sand cover	-0.206	0.052	-3.966
Zone (Lower) × Sand cover	-0.255	0.052	-4.930
Zone (Middle) × Wave action	0.115	0.054	2.143
Zone (Lower) × Wave action	0.109	0.058	1.867

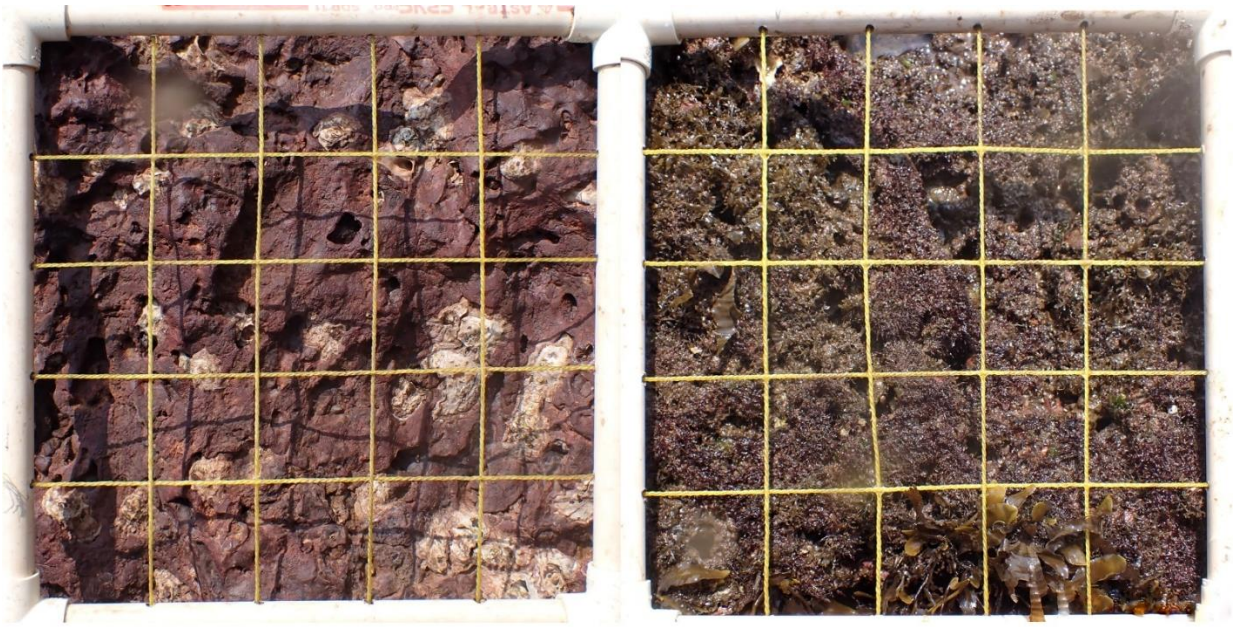
Appendix 5 *Effects of intertidal zone, substrate complexity, sand cover and wave action on Wisconsin-standardised Shannon diversity. (a) Variation in Wisconsin-standardised Shannon diversity with zonation presented as boxplots with overlaid quadrat-level observations. (b) Predicted relationship between substrate complexity and Wisconsin-standardised Shannon diversity, with shaded area representing 95% confidence intervals. (C) Predicted effects of sand cover on Wisconsin-standardised Shannon diversity across intertidal zones, displaying a significant interaction between sand cover and zone. (d) Predicted effects of wave action on Wisconsin-standardised Shannon diversity across intertidal zones, displaying a significant interaction between action level and zone. Predictions are shown with 95% confidence intervals and were derived from the best supported model identified using AICc-based model selection.*



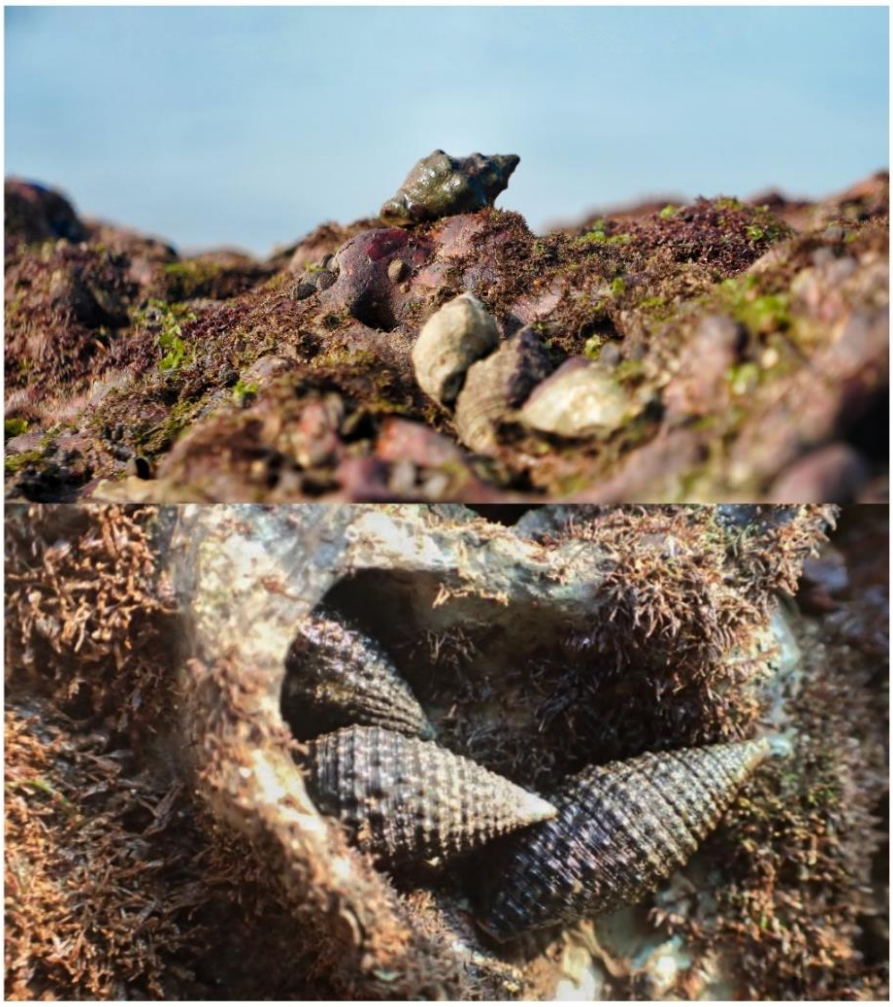
Appendix 6 *RLQ ordination for motile & sessile taxa. (a) Environmental variables, (b) functional trait modalities, and (c) taxa. The direction of arrows indicates increasing values of environmental variables or trait modalities, and arrow length represents the strength of their association with the ordination. Taxa positioned closer to an arrow are more strongly associated with that environmental variable or trait modality. Because all of these are projected onto the same RLQ axes, their directions and positions can be interpreted together to infer associations between environmental gradients, functional traits, and taxa.*



Appendix 7 *Left: Quadrat in the upper intertidal, Right: Quadrat in the lower intertidal.*



Appendix 8 *Top: Indothais blanfordi in its habitat; Bottom: Clypeomorus grazing on algae.*



Appendix 9 *Left: Experimental setup Right: Indothais gastropods feeding on Brachidontes mussels around the experimental plots.*

Appendix 10 *Experimental cages at Odxel.*

Appendix 11 *Setting up experimental plots.*